Mockingbird Tales: Readings in Animal Behavior

By:

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CONNEXIONS

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Introduction to "Mockingbird Tales: Readings in Animal Behavior"[1]

A female sinks her fangs into her mate, killing him as she slowly dissolves and drinks his bodily fluids. Why does this happen? Surely, it is apparent that he has been trapped against his will? Or has he collaborated in his own death?

Elsewhere in the forest a monkey responds to a call of a bird with its own alarm call. Why? Are they cooperating? Or is one using the signal of the other?

Animal behavior is a vivid field where the actions of natural selection are particularly apparent. In this collection of 24 chapters organized into 10 sections, we introduce the stories of animal behavior in their evolutionary context. These stories often involve conflicts of interest a context where the action of natural selection can be particularly clear. The students were asked to choose a specific animal or group of animals and a specific conceptual question, and explain both and their relationship in an assignment that lasted all semester. A copy of the assignment is at the end of the volume.

Undergraduate students who took Biosciences 321, Animal Behavior, at Rice University in 2009 or 2010, originally wrote all of these chapters. The chapters were read and edited by a team that included Aparna Bhaduri, Chandra Jack, Brian Maitner, and Joan Strassmann. In every case we checked them for accuracy and respect of copyright, and we edited them for clarity.

In keeping with the Connexions philosophy, we encourage you to take these chapters into your own space, reorder or modify them as suits your needs, and add new chapters to the collection. We feel that cost-free readings will help bring the wonder of animal behavior to a wider audience. We also think that student-written pieces educate both the writers and the readers. We hope these pieces are clear and useful and that the collection will grow.

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[1] This content is available online at <http://cnx.org/content/m36683/1.1/>.

Chapter 1

Why form groups?

1.1 Schooling in Fish[1]

Author: Aparna Bhaduri

Figure 1.1: The Trinidadian guppy is one of the most studied schooling fish. Its prevalence and ease in breeding both accommodate its study.

1.1.1 Introduction

Humans have been interested in schooling behavior in fish for centuries, often for very practical reasons. Before scientists marveled at schools as perfect examples of **aggregation** and products of fine tuned evolutionary action, schooling was important to fisherman. Understanding how and when these schools would arise, how they would travel, and where they could be found were important in many coastal cities and

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[1] This content is available online at <http://cnx.org/content/m34746/1.3/>.

civilizations. Aristotle himself once commented that the fish school ought to be what a society strives to be: as such, the human interest in schooling fish is one of the oldest forms of animal behavior study, one that has taken on an increasingly scientific perspective.

As evolutionary theory predicts, each individual within the school competes for resources, survival, and reproductive potential (Hamilton 1970). A school is a group of fish ranging from just a few fish to thousands of fish that acts like a single entity, where the behaviors that it engages in such as swimming, avoiding **predation**, and foraging benefits each member of the group distinctly (Edelstein-Keshet 1999). Therefore, questions about schooling behavior center on the evolutionary reasons for schools, potential **costs** and how they are overcome, as well as specific examinations of the school **dynamic**.

The methods of studying fish are quite diverse: **observation**, **experimentation**, **comparison**, and computer modeling are some of the most common ways fish schools are studied. The schooling fish that are studied range from the easily manipulated Trinidadian guppy, to the common herring, to parrotfish that are found near corals (Table 1.1: Species Used to Study of Schooling). Hundreds of species of fish school, and many of them have been studied.

Species Used to Study of Schooling

Species	Habitat	Notes	Researcher(s) Cited In Paper
Spottail Shiner (*Notropis hudsonius*)	Freshwater Rivers	A migratory and strongly schooling fish	Dr. Benoni Seghers,1981
Norwegian Herring (*Clupea harengus L.*)	Northeast Atlantic	One of few very inflexible fish in terms of schooling behavior	Dr. TJ Pitcher, 1991
Trinidadian Guppy (*Poecilia reticulata*)	Freshwater streams	Small fish that is easily manipulated and therefore good for experimental use	Dr. Anne Magurran, 1991, 1994.
Three spined stickleback (*Gasterosreus aculeaius*)	Freshwater lakes	Small fish that is common to North America and Europe	Dr. V Kaitala, Dr. E Ranta, 2006
Goldfish (*Carassius auratus*)	Freshwater	Have the ability to school, but rarely do so	Dr. Anne Magurran, 1982
Minnows (*Phoxinus phoxinus*)	Freshwater	Have the ability to school, but rarely do so	Dr. Anne Magurran, 1982
Juvenile roach (*Rutilus Rutilus*)	Freshwater	Does not always school, prefers shallow water	Dr. Dirk Bumann, 2004
Northern bluefin tuna (*Thunnus thynnus*)	Atlantic Ocean	Fast swimmers who often school	Dr. TJ Pitcher, 1999

continued on next page

North esk salmon (*Salmo salar*)	North Esk Freshwater River	Migrating fish that are a prime target of fishermen	Dr. ADF Johnstone,1995
Eastern mosquitofish (*Gambusia holbrooki*)	Freshwater	Famous for sexual schooling preferences	Dr. Angelo Bizazza, 2007
Banded killifish (*Fundulus Diaphanus*)	Freshwater	Adjust schooling behavior to resource availability often	Dr. DJ Hoare, 2004
Juvenile chum salmon(*Oncorhynchus keta*)	Freshwater rivers	Usually always school	Dr. Bori Olla and Dr. Clifford Ryer, 1991
French grunts (*Haemulon flavolineatum*)	Coral Reefs	Famous for involvement in mixed schooling	Dr. E Ranta, 1994
Golden shiners (*Notemigonus crysoleucas*)	Freshwater lakes	Used in communication studies often	Dr. E Ranta, 1994

Table 1.1

Schooling was initially thought to be a behavior with little structure or adaptive significance (Keenleyside 1955), however further study has revealed an intricate and developed structure behind the school. Individuals are capable of **plastic behavior** in terms of when and where they school. The banded killifish (*Fundulus Diaphanus*), which live in isolated populations, stay in close proximity of one another and when there is a shortage of food or a predation threat, they quickly band together and school. Staying close together affords them this flexibility and is seen as a function of external stimuli (Hoare et al 2004). Scientists have discovered that schools are much more complex in their structure than originally thought, lacking almost any randomness. Instead, individuals compete for positions within the school, with edge positions typically falling to those with the least **fitness** (Hamilton 1970). These schools are often are controlled by signals within the group from neighbor to neighbor. The signals are used to direct traffic, indicate the presence of food, aid recognition of school members, and send out alarm calls in the face of predators (Magurran 1994). Consequently, the reactions to finding food or encountering a predator are well orchestrated and coordinated. Fish may or may not school, and these choices depend on food availability, predator density, and sometimes for females, even the level of sexual **harassment** present. Here we examine the evolutionary reasons for schools, how these schools are able to adapt to environmental changes, and the known aspects of school **mechanics**.

1.1.2 Evolutionary Basis of Schools

Although schools themselves operate as a single, cohesive unit that collectively makes decisions, the evolutionary study of schools focuses on the benefit reaped for each individual, as aggregation theory explains that individuals must school for selfish reasons (Hamilton 1970). Individuals school only because it is better for themselves and their genes. As an example of the advantages of schooling, studies of the spottail shiner (*Notropis hudsonius*) show that individuals within a school spend less time engaging in antipredator behavior (which is energetically costly) and allow them to locate more food because more individuals are searching for it (Seghers 1981).

1.1.2.1 Predation Avoidance

Schools help fish avoid the risk of predation by getting away more easily in a group, evaluating predators more effectively, and sharing learned behaviors. The use of schools to avoid predation is one of the most studied evolutionary explanations for schooling in fish and may very well be one of the main reasons schooling evolved.

At the most basic level, schools protect the individual members from predation by confusing a predator (Parrish 1991). When many fish swim together, it becomes harder to focus on one fish and make a catch, especially since the school tends to continuously move. Without a visual target, most predators are unsuccessful in catching their prey. As an individual, unless one is on the edge of the school, one is safer from predators simply because there is a barrier between one fish and another. This is definitely a source of conflict, as if a predator catches a fish from the school, it will be a fish on the edge (Hamilton 1970), however these fish still get some level of protection because the school still can confuse the predator.

When approached by a predator, solitary herring (*Clupea harengus L.*) react much more quickly than those in a school (Figure 1.2). While it is possible that herring in schools move slower so as to avoid collisions with other members, the slower speed likely indicates decreased urgency (Batty and Domenici 1997), indicative of the benefit to individuals in the schools. Evolutionarily, fitness is optimized when the energy invested in any behavior is just good enough: in this case, it takes less energy for fish that are schooling to avoid the predator than it does for solitary fish, because the school confuses the predator. This allows more energy to be invested in other behaviors, such as finding food or a mate.

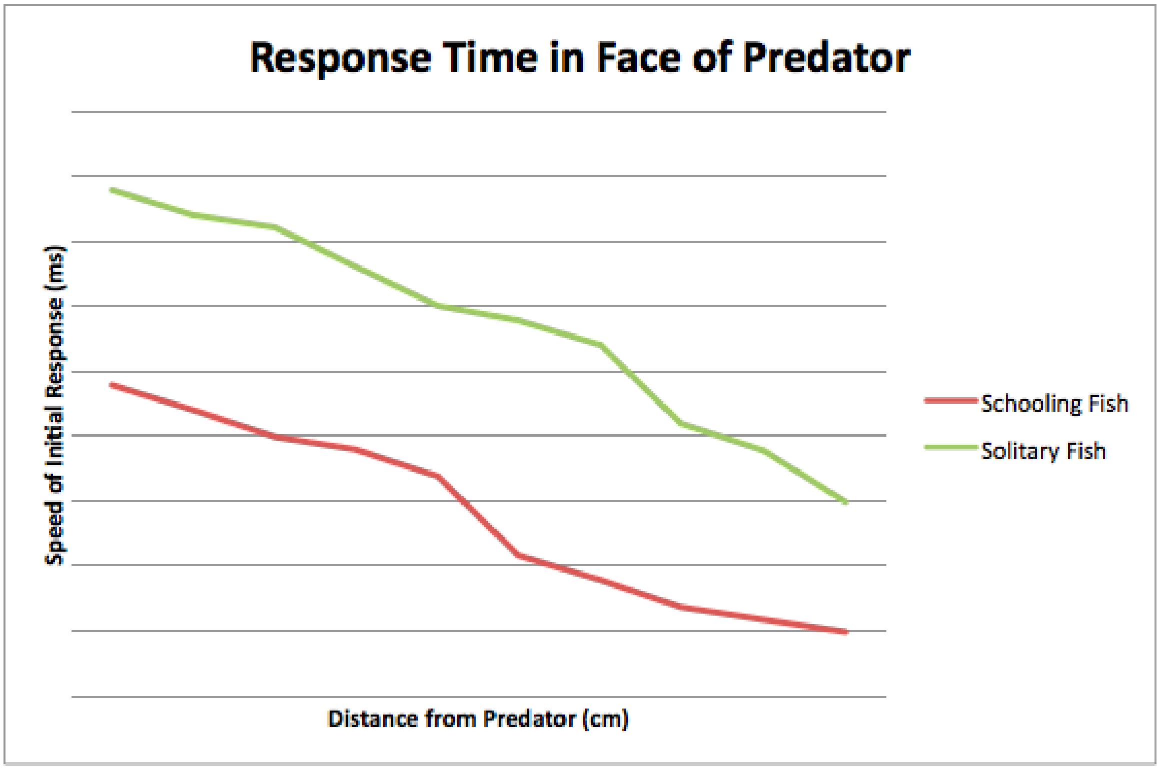


Figure 1.2: Individuals within a school react less quickly than solitary fish. This can be attributed to the additional protection afforded to schooling individuals by the group. This difference is very noticeable. (Batty and Domenici 1997).

Schools dilute the effect of predators: by taking individuals from an environment and concentrating them into one unit, this decreases the probability of ever meeting a predator (Parrish 1991). Additionally, fish commonly approach a threat the first time they encounter it in order to decide how much energy needs to be exerted to avoid the threat in the future. Evaluation behavior, though useful, can be risky as it requires a fish to get close enough to the potential predator to evaluate size, shape, or other factors. The hypothesis that schools increase survivorship during predator evaluations was tested in the Trinidadian guppy (*Poecilia reticulata*) by observing the mortality of individuals within schools compared to solitary individuals who attempted evaluations of predators. Individuals in a school had virtually no mortality (Magurran 1994), because no one individual was likely to be attacked due to confusion effects, allowing a collective examination without the threat to any individual.

Interestingly enough, many individual fish from a school try to examine a predator alone, or be the first from the school to do so. At first, this may appear altruistic, but experiments with the Trinidadian guppy show that individuals who have information about a predator are more likely to be protected within a school and given extra resources in attempts by others to coax this valuable information from the informed individual. Therefore, competition often exists to be the informed fish so that one may garner the later benefits of protection by the group (Pitcher 1991) - predator evaluation is actually not an altuistric behavior! This one behavior highlights an important aspect of schooling: competition does exist within the school to have the safest positions and best resources as this increases chances of more reproduction, and therefore individual fitness. The Geometry of the Selfish Herd very accurately analyzes that fish will compete for the best spots within the school (Hamilton 1970), and this type of evaluation behavior is just another way to compete for those spots.

The ability of fish to evaluate predators and adapt to new predator densities indicate that fish do have learning capabilities. The ability to identify predators is learned, rather than innate, from other individuals in a high density predator area (Kelley et al 2002). Trinidadian guppies from streams without predators were placed individually into high predator environments with schools. These individuals quickly followed the lead of others in the school and engaged in **anti-predatory** behavior they never engaged in before, particularly schooling itself, indicating that schooling can improve individual fitness by allowing the opportunity to learn from examples () (Kelley et al 2002). Once again, individuals with limited knowledge of a new area are more likely to school for the selfish advantages it could provide them. It was also seen that those who did not catch on quickly were the first to be eaten, demonstrating that anti-predator behavior is selected for in high predator environments (Magurran et al 1992).

Aggregations of fish are more likely to attract predators that might not have otherwise seen them. To test the hypothesis that fish do have a mechanism to adapt to predator density to compensate for this potential cost, a study of Norwegian herring observed that percentage of time schooling is proportional to the density of predators. Fish do not school as often in low predator density areas because they have a higher chance of attracting predators that would not have otherwise noticed them as solitary individuals (Pitcher 1996).

Box 1.1: The shaping of a school

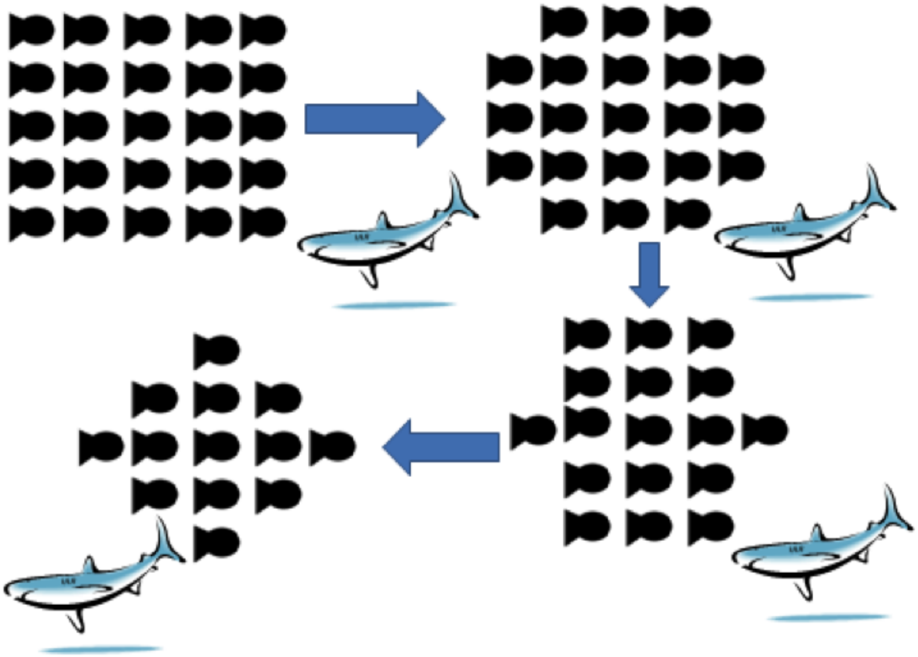


Figure 1.3

The shape of fish schools evolves in response to various **stressors**. The most obvious of these stressors is a predator. A fish that decides to school in the corners of a square shaped school are most likely to be eaten first by a predator (Parrish 1991). Over the course of time, the school adapts to the manner in which the predator attacks the school, and develops an ideal density, shape, and movement direction. Stressors can be either positive or negative. Fish in a more ideal position for food will be healthier and therefore more likely to mate, and fish who school in locations where they will continually run into objects in the environment will be more likely to lose the school (Zheng et al 2005). As such, forces like predation, foraging efficiency, and prime location influence the evolution of school shape, each of which is unique for a specific environment. The ability to obtain the best location within a school is driven by fitness, with the most fit getting the center positions (Hamilton 1970). The predator also adapts to the schooling, as seen in piscivorous fish who feed on rock cod. The predators are forced to eat less nourishing prey for periods of time until the number of fish skilled in catching the schooling cod increases and the pressure to school decreases. Then once again, schooling behavior increases as predatorial success also increases, demonstrating the coevolution between predator and prey (Beukers-Stewart and Jones 2003).

Another interesting cost is seen in only a few species. The herring (Clupea harengus) does not change its schooling patterns once it gets into adulthood, despite environmental change. Therefore, in certain environments it can become extremely costly to school if there are conditions that favor solitary individuals (Corten 2001), such as low predator densities.

1.1.3 Foraging

The positive effect of schooling on foraging efficiency has been well documented in both observational and experimental trials. Experiments with the three spined stickleback (*Gasterosreus aculeaius*) show individuals within a school find food quicker and consume more of it than they would if they foraged alone (Kaitala and Ranta 2006). This has also been seen in goldfish (*Carassius auratus*) and minnows (*Phoxinus phoxinus*), two species who do not always school, but when they do, are able to find food sooner (Magurran et al 1982). It is easier to feed in a school because individuals do not need to exert as much energy on anti-predatory activities and are more likely to spot food based upon overlapping sight lines. This increases the chances of eating, and therefore surviving to mate, which is ultimately fitness. The increased success of foraging often helps solitary individuals and other species, who search for schools, follow them to sites with food, and copy their feeding and anti-predatory behavior. The ability of others to eavesdrop on these behaviors indicates that these behaviors do greatly benefit the individuals in the school (Olla and Ryer 1990). An interesting aspect of foraging within schools was discovered in the juvenile roach (*Rutilus Rutilus*): the most nutritionally deprived fish in an experimental setup regularly led the school, and when nutritional deprivation was equal within a school, those at the front ate the most. These findings strongly indicate that schools are functionally preferred (Bumann et al 2004) and are evidence of selfish behavior: the most fit individual will be able to get to the front of the school when nutritional deprivation is equal, and will benefit the most (Hamilton 1970). It is important to understand that one reason more fit individuals will allow more nutritionally deprived individuals to eat first, or fish in the back will still school if they get food last, is often because of schooling within kin groups. Fish do have the ability to recognize others, as discovered through experiments across various species (Griffiths 2003). This recognition suggests a mechanism may exist for kin recognition and knowledge of one's spatial position with a school. For female guppies (*Poecilia reticulate*), it takes 12 days to get to know one another. This ability to recognize, once established, determines schooling preferences, which are then maintained. (Griffiths and Magurran 1997). This previous knowledge is valuable in reciprocal relationships, such as joint foraging, where it is useful to remember who cooperated withother individuals in previous interactions. In terms of kin recognition, schooling with kin is always better for your own fitness than schooling with strangers, and the ability to remember individuals can assist in this type of behavior (Griffiths 2003). Schools often do exist between strangers or even different species, but these schools appear less stable than familial schools because of increased competition for safe positions and resources (Wolf 1985).

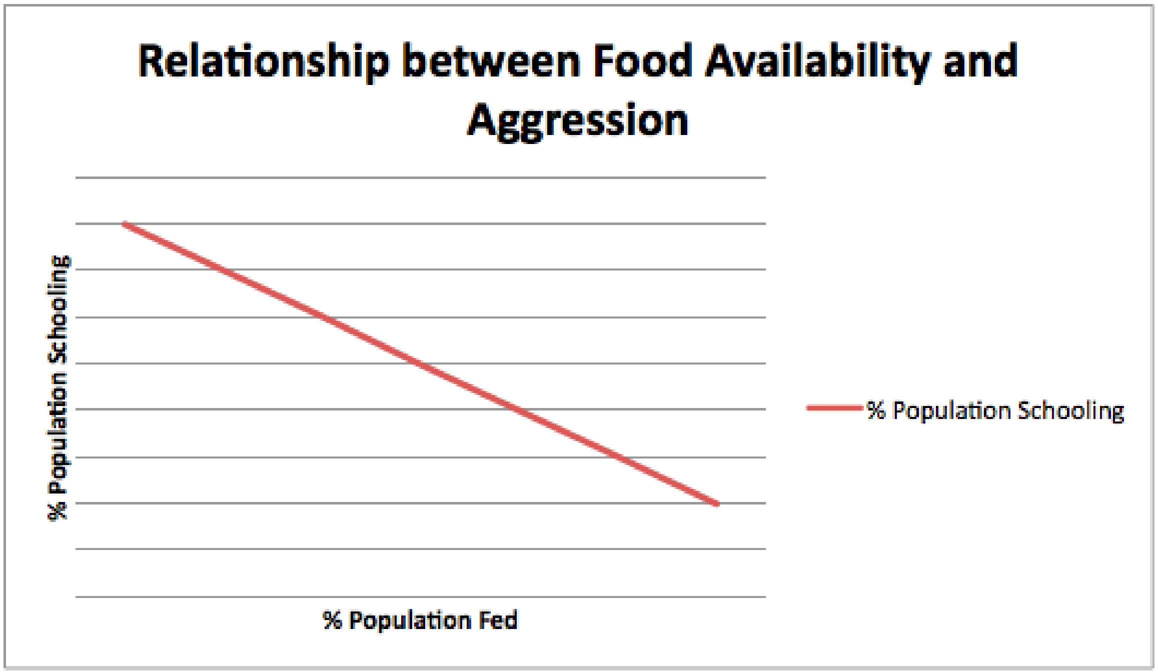


Figure 1.4: The number of individuals in a population who school is proportional to the availability of food in the banded killifish (Hoare et al 2004). Schooling improves the chances of finding food if there is a scarcity, while schooling increases competition unnecessarily if there is plenty available.

Because not all species school consistently, however, individuals of these species are more inclined to become aggressive to other in their school. Schooling increases competition for food and resources, especially when these are scarce (Magurran 1991), and cross species comparative studies show that there is less aggression among various species of commonly schooling fish as compared to guppies who do not necessarily school regularly (Magurran 1991). Selfish herd theory predicts this behavior in terms as each individual is selfishly joining the school when it is in trouble, and is therefore more inclined to fight for limited resources (Hamilton 1970).

Alternatively, juvenile chum salmon, (*Oncorhynchus keta*) are a schooling fish until presented with a large food source (Olla and Ryer 1991). In the presence of this very extensive source of food, they abandon the school, become aggressive and hoard food. This behavior is usually one responsive to scarcity or increased competition, but in this case it is responsive to a resource-rich environment. Individuals are be expected not to school so as to not attract predators, and because individuals with lower fitness may actually get less food in a school than individually, but the aggression and hoarding is a seemingly unnecessary energy expenditure. However, because this species is rarely presented with a resource rich environment, it rarely roams solitarily. It is hypothesized that this behavior is simply a reaction to an altered environment that has not been refined by selection (Olla and Ryer 1991).

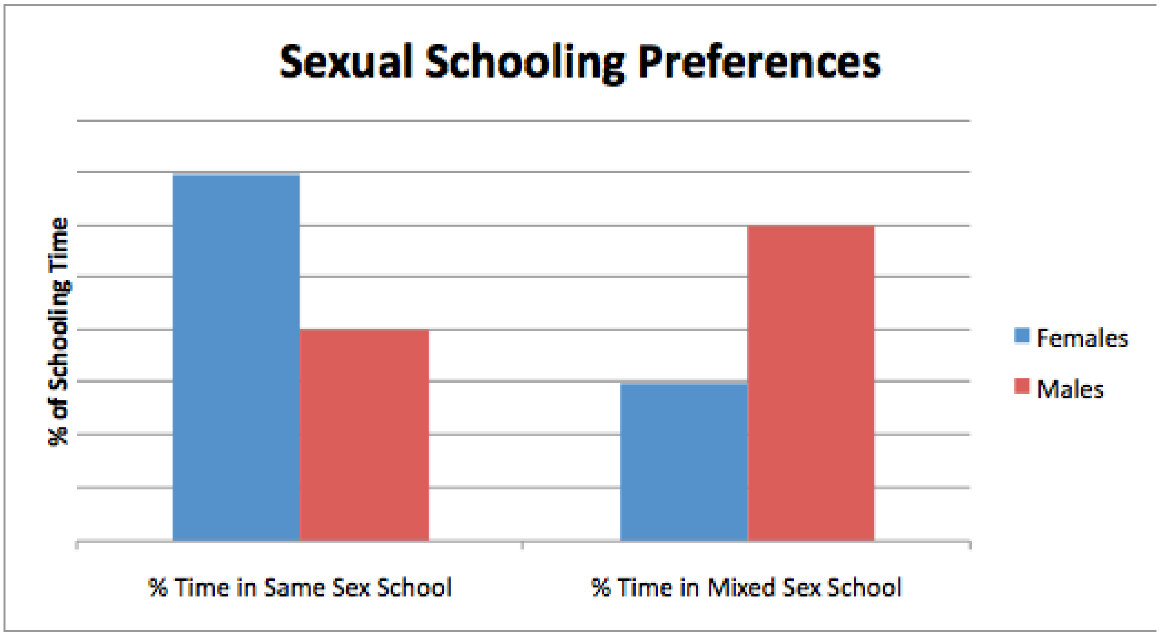


Figure 1.5: This shows the preference based on sex to school within either same sex or mixed sex school. These data show that females tend to prefer same sex schools compared to males, often to protect themselves from costly male harassment. Schools can provide males with opportunities to encounter females when engaging in mixed sex schooling. (Magurran 1994).

Box 1.2: Unexplained aspects of schooling

In addition to the behaviors of a school that are easily explained in terms of individual fitness, many other aspects of schooling are harder to explain. Northern bluefin tuna (*Thunnus thynnus*), in particular are often seen milling around unidentified core, first attracted to the area by a particulate or other object, but the school soon grows to a point that this could not be the motive for aggregation (Edestein-Keshet and Parrish 1999).

Fig. 1. Fish schools provide an example of emergent pattern such as milling in which individual members circle about an unoccupied core. [Photo: ©1999 Norbert Wu]

Figure 1.6

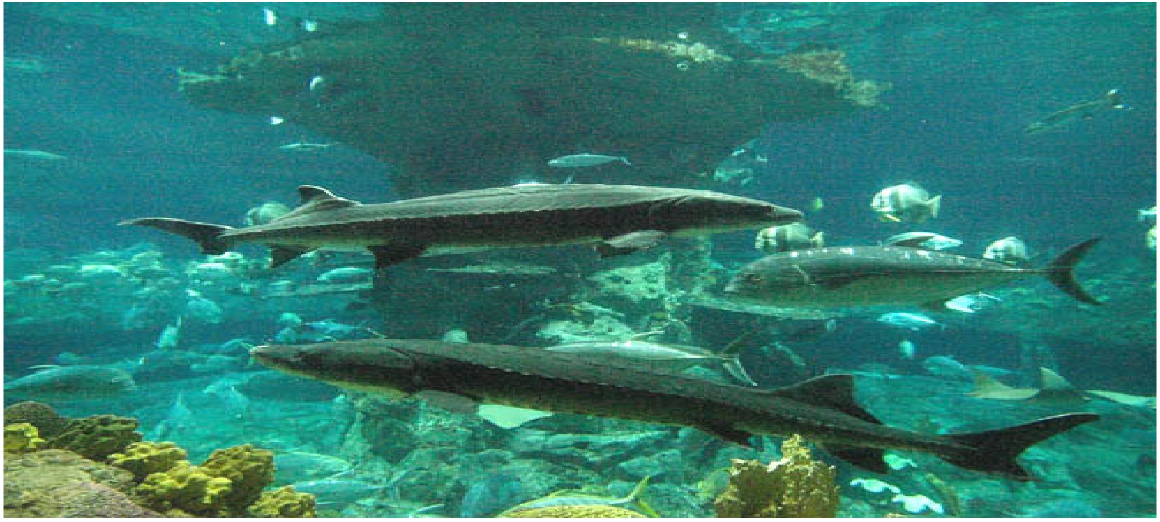
North esk salmon (*Salmo salar*) smolts introduced to a new environment school for the first 24 hours, and then disperse. New introductions to these tanks immediately try to seek out existing schools, or form their own, suggesting that fish may school as a way of alleviating stress (Johnstone et al 1995), however no evidence exists to support this hypothesis.

It has also been observed across species that schools tend to contain individuals with uniform phenotypes such as size or color, and studies indicate that fish within a school also have comparable foraging abilities, leading to the idea that fish self-segregate based upon phenotypes (Ranta et al 1994). Although this may indicate fitness advantages for the more skilled fish, it does not explain how the less skilled schools are selected for or why phenotypes such as color also aid aggregation. This does make sense from the perspective of the selfish herd because you would only school with groups in which you have an opportunity to get to the center, and this is most likely to occur with individuals similar to you. Cross species studies show that small schools can also be selected for in instances where large resources are monopolized by larger or more skilled schools, allowing for the added protection of the school without the necessity for increased competition (Guimaraes 2007).

1.1.4 Sexual Schooling

Sexual segregation can be seen in many fish schools. In eastern mosquitofish (*Gambusia holbrooki*) it is costly for females who are foraging to be sexually harassed by males (Bisazza et al 2007), which often happens to solitary females. Therefore, they school with other females when males are in sight, or school with schools of males (who do not sexually harass), staying closest to the largest males (Bisazza et al 2007). In guppies, females form the base of a school, while males tradeoff schooling with the intention of finding mating opportunities. Males cannot search for mates while schooling, as schools either engage in anti-predatory or foraging behavior. Therefore, they must tradeoff between increased motility for mating opportunities and the increased defenses and resources that accompany schooling (Griffiths and Magurran 1998). In high predator areas, females school more, but are harassed more too because males spend less time schooling, foraging, and avoiding predators than females, and more time looking for mates, who are easier to find in groups (Magurran and Seghers 1994). These situations form the crux of the sexual conflict between the sexes: females try to avoid harassment by males through schooling, though this is not the only reason for schooling behavior (Figure 1.5), while males pursue these schools as opportunities for increased mating potential. The "winner" of the conflict is determined by the strength of the school as well as the threat posed to solitary males, especially in high predator areas. Males increase their fitness by mating more, while females increase their fitness by acquiring resources to support current and future offspring. As such, the threat to males is only significant if it outweighs the benefit of increased mating opportunities. The conflict between males and females can be found in many species, but the use of schools as a defense is an interesting physical manifestation of this evolutionary tug of war to harass and defend.

Box 1.3: Mixed Schooling



Mixed schooling is an interesting phenomenon that is observed in a few species. Stoplight parrotfish, striped parrotfish, and ocean surgeonfish will school together, but only the largest constituent uses the school for protection: in the event of a threat the lesser represented species will leave and hide behind coral. A possible explanation for this behavior is that underrepresented fish may stick out and would not be protected within a mixed school (Wolf 1985). Other than the potential for better foraging, no explanation has arisen as to why mixed schooling of this nature occurs. Especially since the school is composed of different species, there is reason to believe that competition would be significantly increased, though this has not been observed. However, the reason for mixed schooling between postlarval French grunts, (*Haemulon flavolineatum*)and mysids is much more obvious. Postlarval French grunts form schools based on visual recognition, and mysides look like grunts up until 5 days. After 5 days, the grunts abandon the mysids as they look different. This is an example of young fish being unable to distinguish between species and mysids going along for the ride so long as they can get food out of the association (Kotchian and MacFarland 1982).

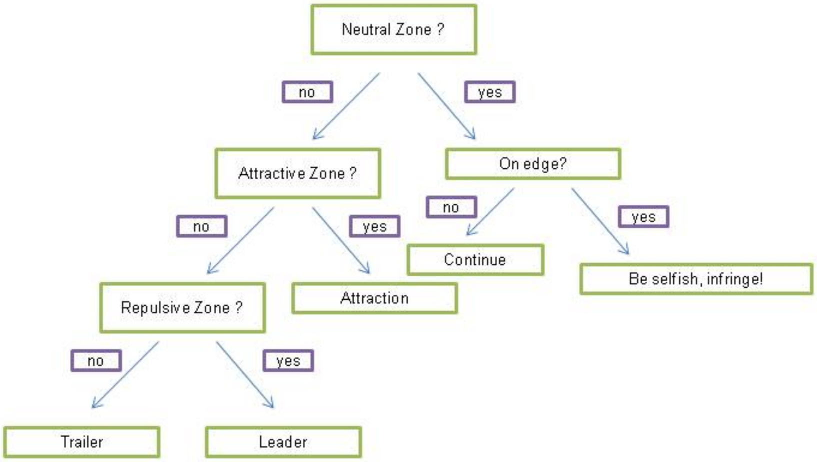
1.1.5 Mechanisms

The way in which schools operate is something that has undergone much research recently, especially since the advent of modeling technologies that can accurately represent fish populations. The basics of the mechanisms of schooling are known, but much is yet to be understood. It has been determined that across most species, the mechanisms of schooling are more or less conserved and rely on individual physiology and environment (Gobert et al 2001). Mechanisms are evolutionarily relevant to the study of aggregation because they demonstrate the results of generations of selective pressure, and the mechanism behind how the school physically operates is the basis for why predator avoidance, foraging, and sexual schooling can occur.

1.1.5.1 Sensory Perception

Sensory perception, or some form of identifying how one relates to others spatially within a school, is imperative to avoid collisions and synchronize movement. Models show that for the school to move and change direction, strong boundaries of repulsion, neutrality, and attraction must exist in order to shape the school. This suggests a sensory mechanism works to establish these regions and provide for the uniformity within schools. (Grunbam et al 2007) . This is supported by response mechanisms at the individual level that create these accommodations (Gueron 1996). It is unknown when these mechanisms evolved, however it is surmised that they evolved in conjunction with the aggregate behavior of schools. Either way, these mechanisms subtly allow competition for safe positions to continue while mostly maintaining a constant dynamic that allows the school to benefit the individuals that comprise it.

Box 1.4: Knowing your place in the school



This flow chart shows the mechanism of identifying how one should alter direction in order to stay with the school (Gueron 1996). There are several zones in which evaluation needs to occur. The neutral zone means that you are neither too close nor too far from any one, and if one is on the edge and in the neutral zone, you may try to squeeze into the repulsive zone as it is more advantageous for you to be closer to the school. Even in the mechanics of schooling, the individual selfishness that is at the heart of schooling is very evident. If one is not on the edge, then one will try to maintain your position far enough from each fish so that you are out of your neighbors' repulsive zones, but not so far so that you are in the attractive zones. The repulsive zone means one is too close, and the attractive zone means one is too far. These zones are models of how position evaluation likely occurs in order to maintain the equal spacing and uniformity of the school (Grunbam et al 2007).

1.1.5.2 Density and Volume

The **density** and **volume** of a school often dictate the schools shape and mechanics. It is observed that under specific positions and velocities, aggregations are more likely to form. However, it is not known whether these positions and velocities occur by chance or if they are contrived by individuals seeking to school (Cucker and Mordecki 2007). Once schools are made, the size of the school is regulated by normal distributions, and fission or fusion events occur when the school is either too large or too small in relation to normal distribution (Niwa 1998). In order for these events to occur, an optimal degree of synchronization must occur, though it cannot be determined if this synchronization is a function of school size or if individuals adjust synchronization in anticipation of changes (Skaret and Vabo 2008). Additional observations indicate that speed regulates the density of a school, with faster swimming resulting in denser schools (Pitcher 1979). These observations, however, often cannot separate individual intent from coincidental happenings. Studies show that just as predators tailor their hunting styles to suit the school, fishing gear can be evaluated and updated to reflect the hydromechanics within a school (Weihs 1973). The application of this information is a creative way that brings schooling theory and research back to where it initially began - practical ways for humans to acquire food, a noticeable parallel to the coevolution of predator and prey.

An energetic cost may be incurred, as models of fish behavior show "burst and coast" swimming, where they perform a quick burst of energy followed by gliding, which appears to be the most energetically efficient form of swimming for fish. However, within a school this becomes virtually impossible as constant changes of velocity, direction, and synchrony must occur. Therefore, only if the energy saved by decreased anti-predatory behavior or increased foraging outweighs this energetic cost is schooling a valuable strategy (Fegelya et al).

Figure 1.7: These expansive schools still follow positional evaluation and are regulated by the same density and volume characteristics as smaller schools.

1.1.6 Communication

Because of the ability of schools to operate in unison and come together at important times, it seems obvious that there ought to be communication between fish. However, the ability of researchers to discern exactly how this communication occurs has been challenging and controversial. In 1887 studies proposed that fish use pheromones as alarm signals within the school, encouraging movement of the school away from a threat. Although this explanation was accepted for nearly a century, newer studies in minnows show no evidence of pheromones. Instead communication seems circumstantial and may be based upon learned behavioral cues, although it is still unclear how this may work (Magurran et al 1996). Modeling experiments show that individual movements within a school can change the direction and trajectory of the entire group, indicating that any individual can decide where the group should go (Romey 1996). In support of these models, guppies often school without an obvious leader, instead following movement cues of the neighbors to decide how to swim (Gungi 1998), which is also consistent with the ideal that neutral, attractive, and repulsive zones exist to direct spacing and movement inside the school. Additionally, it has been proposed that territorial cues such as boundaries, foraging sites, and danger zones also serve as signals for fish within the schools (Gungi1998). This behavioral signaling is extremely relevant because it indicates that schooling is much more complex than originally thought, and that many decisions are made as a group.

1.1.7 Impact of humans

A new emerging area of study of schools has examined how human interactions with the environment and fish affect these schooling species. For example, it has been determined that the energetic costs of barriers, such as bridges, are larger than hypothesized because these barriers force the school to be manipulated in shape, changing the overall streamlined effect and demanding excessive energy input by each individual (Lemasson 2008). In terms of fishing, it has been seen that synthetic marine reserves increase the overall biomass of the fish, but decrease the number of catches due to increased schooling (Moustakas 2006). Additionally, another study warns that although fish populations do self regulate, and can increase reproduction in shrinking populations, excessive fishing can exploit this ability and actually irreparably damage a population (Bakun and Weeks 2006). Each of these studies reminds us that our knowledge of schools can be used for a variety of purposes, and this knowledge could help humans engage in more responsible development and fishing behavior in an effort to preserve the natural balance of fish in the wild.

1.1.8 Glossary

- **Anti-predatory behavior** – Behavior that either looks out for predator or seeks to avoid high predator density areas. Anti-predatory encompasses all behaviors in evaluating, avoiding, and fleeing predators.
- **Aggregation**- A group of like individuals that acts a whole. Schools are aggregations because they are groups that, although made of individuals, act as a single unit while schooling.
- **Costs**- Disadvantages of a behavior. Costs are reasons not to school, including increased visibility to predators or more competition. Especially if the benefits are not greater than the costs.
- **Competition**- The interactions between individual for a specific resource. This is most common for spots within the school that are safest, but can also be for mates or food.
- **Density**- The number of occupants per unit space. Used to describe closeness between fish in a school, a descriptive term of the school. Density can change within a school, and is often related to the speed the fish are swimming.
- **Experimentation**- The best way to draw specific cause/effect relationships about behavior. Experiments often manipulate the environment or transplant individuals from one environment to another in order to isolate behavioral observations from the surroundings.
- **Fitness**- The ability to propagate genes to the next generation. Fitness can be described by ability to get mates, avoid predators, and collect resources because all these behaviors increase either survival (to allow more reproduction) or reproduction opportunities themselves.
- **Foraging**- The behavior of searching for and collecting resources, often used in terms of food. Fish forage by looking for areas with enough food for either themselves or an entire school.
- **Harrassment**- The behavior of colliding, interfering, or otherwise disturbing another individual. Commonly seen by males against females in hopes of mating, however harassment disturbs the harassed individual and decreases their fitness by interfering with their anti-predatory or foraging efficiency.
- **Mechanics**- Similar to dynamics, but focuses more on the physical scope of knowing where to swim and how to move. Mechanics are most often modeled by computer technology and conclusions drawn from these studies.
- **Membership**- Being part of a school as an individual. This is not constant within a school and change depending on sex, age, or phenotype; membership of specific school can turnover completely while the school is still constant.
- **Mixed Schooling**- Schooling between species, either on purpose or by accident. Mixed schooling is an aspect of schooling not well understood.
- **Observation**- One of the most common ways of studying schools, primarily by watching schools in either their natural habitat or in tanks. Observation allows for patterns of behavior to be established

but not for cause/effect conclusions to be determined definitively.

- **Plastic Behavior**- Behavior that can change based upon environmental or other external cues. Schooling is a plastic behavior in most species as it only occurs when there is a need for it: when its benefits outweigh its costs.
- **Predation**- Hunting for the purposes of eating; a form of foraging. Many schools are shaped evolutionarily by their interaction with predators, as they formed to avoid predation.
- **School**- A group of fish that act as an aggregate, swimming together in unison and engaging in anti-predatory, foraging, or other behaviors.
- **Shoal**- A group of fish that are found in close proximity but do not have the mechanics or dynamics that make a school. Shoals are collections of fish that do not act as one entity or aggregate.
- **Solitary**- An individual who might school, but at a certain point of time is not part of a school. Solitary individuals offer a good comparison for how behaviors change in schools and what costs and benefits are obtained through schooling.
- **Stressor**- An aspect of the environment that shapes evolution, ranging from predation to physical barriers. Stressors alter behavior, either at the individual level or of the species by selecting for advantageous behaviors.
- **School volume**- The amount of space taken up by a school, either because of the number of individuals is larger or smaller or because the shape of the school changes in response to an environmental cue. Predation often changes the volume of school so that foraging can continue without being eaten by a predator.

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1.1.10 About the Author

Aparna Bhaduri grew up in Wisconsin where she was an avid Green Bay Packers fan and loved biking. Upon coming to Rice University, she became interested in a variety of subjects, being involvemed with on campus research as well as the speech and debate team. Because of her diverse interests, she obtained a degree in both Biochemistry and Cell Biology as well as Political Science. She has chosen to pursue the scientist route and will be going to graduate school in cancer biology.

1.2 Sharks: Solitary or Group Animals?[2]

Author: Rui Zheng

1.2.1 Introduction

One of the most widely found forms of group behavior is social grouping (Conradt, 1998); animals of social species often divide themselves into groups of specific size or sex. Thus it’s not surprising when sharks and other elasmobranches were observed to practice **size segregation** and **social segregation**. A common misconception is that sharks are **solitary animals** (Conradt, 1998); after evolving for the past 350-400 million years, alongside the 24,000 different species of bony fish and 900 different species of cartilaginous fish,

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[2] This content is available online at <http://cnx.org/content/m34737/1.3/>.

sharks have not only evolved heightened predatory instincts towards scavenging fish and other invertebrates, they have also developed relatively large brains with complex structures (Compagno, 1984 and Long & Jones, 1996 as cited in Sims, 2003) as well more efficient social groupings.

This chapter will cover the different reasons why size and social segregation occur in different shark species. It will examine the limitations of the two suggested reasons for why size-specific groups are naturally selected for (increased hunting efficiency and increased protection) and the five hypotheses for social segregation: predation-risk (reproductive strategy) hypothesis, forage selection (sexual dimorphism-body-size) hypothesis, activity budget (body-size dimorphism) hypothesis, thermal niche-fecundity hypothesis, and social factors (social preference and social avoidance) hypothesis (Guttridge et al. 2009)(Wearmouth & Sims, 2008).

Box 1.5: Grouping Behavior

Grouping is a common behavior observed in many species of animals (Alexander, 1974). Groups can consist of unrelated individuals, uniformly related individuals that aren't siblings, close relatives, siblings, and genetically identical individuals. Depending on the relationship between the individuals that form the groups, the nature and significance of the groups differ; however all groups share one main goal: increasing the fitness of the participating members despite intrinsic interest conflicts. Overall, the benefits of grouping behaviors increase the fitness of the participating organism in spite of universal detriments. While increased competition for shared resources, increased transmission of diseases and parasites, and more conspicuous to predators may lower overall fitness, lowered chances of being predated due to either group defense or larger numbers and increased efficiency at securing resources, such as food and territory, increase participants' overall fitness (Alexander, 1974).

There are two main subcategories of grouping behavior: **aggregations** and **social groups** (Alexander, 1974). The main difference lies in the reason for gathering. Aggregations of animals form when organisms gather due to a specific resource within a specific area. The members of these groups gain no fitness from cooperating from each other. Meanwhile, social groups form because the individuals gain from the actions and general presence of other members (Alexander, 1974).

(a) (b)

Figure 1.8: Right An example of aggregation where the animals gathered due to the water. Left An example of a social group; the lions form a pride in order to increase direct fitness.
Image on the left from http://www.flickr.com/photos/98334721@N00/25901056.
Image on the right from http://www.flickr.com/photos/aggleton/2117753340/.

1.2.2 Size Segregation or Coincidence?

Sharks do segregate according to size, but whether or not it's a conscious effort is debatable. At first, the results of Guttridge et al.'s experiment (2009) on juvenile lemon sharks, Negaprion brevirostris, seemed to suggest that these sharks consciously choose to remain in groups of similar size: when juvenile N. brevirostris were introduced to a two-compartment tank containing only other N. brevirostris (except for juvenile sharks between 0-1 years) the lemon sharks spent more time with those similar to themselves in age and size (Guttridge et al., 2009). In this controlled experiment where there are no external stimuli that might cause the lemon sharks to gather, the fact that these juveniles did indicates that there must be a benefit to this behavior.

Not only was size segregation observed in *N. brevirostris* under experimental conditions, bullsharks, *Carcharhinus leucas*, also gathered naturally in size-specific groups throughout the Southwest Florida Estuary within region-specific areas: the neonates and juveniles were concentrated mostly in rivers and lakes inland and the larger while full grown adults spread out in deeper, offshore bays (Simpfendorfer et al. 2005). Overall, the best model of size sorting behavior is exhibited by the widespread population of ragged-tooth shark, Carcharias taurus; unlike the bullsharks, whose grouping behavior is confined to a small region in the Southwest Florida Estuary, the C. taurus population is spread out along the coasts of Europe and Africa. With size groups located in distinct off shore areas of both two continents, segregation in these sharks are more apparent: the sub-adult and adult *C. taurus* were found mostly along the west coast along the tip of southern Africa while the juveniles were found near the east coast of the British Isles. The younger the shark, the further north along the British Isle coastline it was found. Similarly, the older and larger the shark, the further south along the African coast it was found (Dicken, Smale, and Booth 2006). Upon first glance, sharks appear to choose to separate into groups of varying size.

Figure 1.9: Two lemon sharks, Negaprion brevirostris, interacting without aggression

According to a study Lowry and Molta did in 2008, a direct relationship was identified between the age and diet of a shark. When they observed feeding efficiency in maturing leopard sharks (Triakis semifasciata) and whitespotted bamboo sharks (Chiloscyllium plagiosum), they found a positive correlation between suction power and their ontogeny (age). This increase in suction power resulted in dietary shifts as their feeding abilities increased (Lowry & Molta, 2008). Another study on the sevengill shark, Notorynchus cepedianus, also found similar results that correlated ontogeny to prey size: as the shark got older, they moved away from smaller prey they used to feed on in favor or larger, more nutritious game (Edbert, 2002). Thus not only is diet directly related to the age of a shark, so is the shark's size (Sims et al., 2006b): the older a shark gets, the larger it becomes. This indicates that the diet is also dependent on the size of the shark. Thus what initially appeared to be social interactions between sharks of similar physiques may simply be sharks gathering in an area because they hunt the same prey; size segregation is a direct result of overlapping diets (Wetherbee & Cortes, 2004).

Box 1.6: Did you Know...

Negaprion brevirostris, lemon shark, is unusually social for a shark. When juvenile N. brevirostris were introduced to an empty two-compartment tank, they showed no preference for either side; however, when they were introduced to a tank in which one compartment was empty and the other had another lemon shark, the juvenile N. brevirostris spent more time in the company of the other shark than in the empty compartment (Guttridge et al., 2009).

Compared to the aggregation behavior observed in ragged-tooth sharks and bull sharks, there is no factor aside from the presence of the other sharks in the laboratory setting that might cause N. brevirostris to aggregate. Unlike other sharks, such as the basking shark, who are observed to be alone most of the time, N.brevirostris have been seen swimming in groups of two or more individuals most of the time (Gruber, Nelson, & Morrissey 1988)(Sims et al. 2000).

Also, interestingly enough, unlike the display interactions Le Beouf (2004)observed between eavesdropping salmon sharks, Lamna ditropis, no reports of aggressive encounters were noted in interactions between the lemon sharks in laboratory setting (Guttridge et al., 2009).

Not only are lemons sharks more socially responsive to other lemon sharks, they also interact with many other species of marine teleosts by swimming behind an organism and mimicking its movements (Papastamatious et al., 2006). In Guttridge's experiment in 2009, N. brevirostris was observed interacting with a pair of nurse sharks in this way. Besides nurse sharks (Ginglymostoma cirratum), other common organisms N. brevirostris have been observed to interact with are schools of jacks (Caranx) and barracudas (Sphyraena barracuda), southern stingrays (Dasyatis americana), and under special conditions, slender suckerfish (Echeneis naucrates) (Papastamatious et al., 2006).

1.2.2.1 Hunting Efficiency

The size-specific grouping due to overlapping diets may not be the only reason why size segregation is practiced. Assuming that sharks do practice size segregation, this grouping behavior should increase the overall fitness of every participant (Conradt, 1998). Thus one plausible reason why sharks may benefit from forming size-specific groups may be that hunting efficiency and overall foraging success increase due to cooperative behavior between each of the members because of their similar levels of hunting experience (Guttridge et al, 2009). However, are the sharks really cooperating?

According to Klimley et al.'s observations in 2001, white sharks (*Carcharodon carcharias*) that gathered around a seal colony on Anõ Nuevo Island off the coast of California never interacted; sharks only approached one another after eavesdropping on a kill made by another shark (Le Beouf, 2004). Any attempts to steal food resulted in threatening displays of tail slaps and breaching – jumping out of the water – by the one who made the kill (Klimley *et al.*, 2001). These white sharks appear to have gathered in groups of similar size solely because of their shared prey: the seals (Le Beouf, 2004).

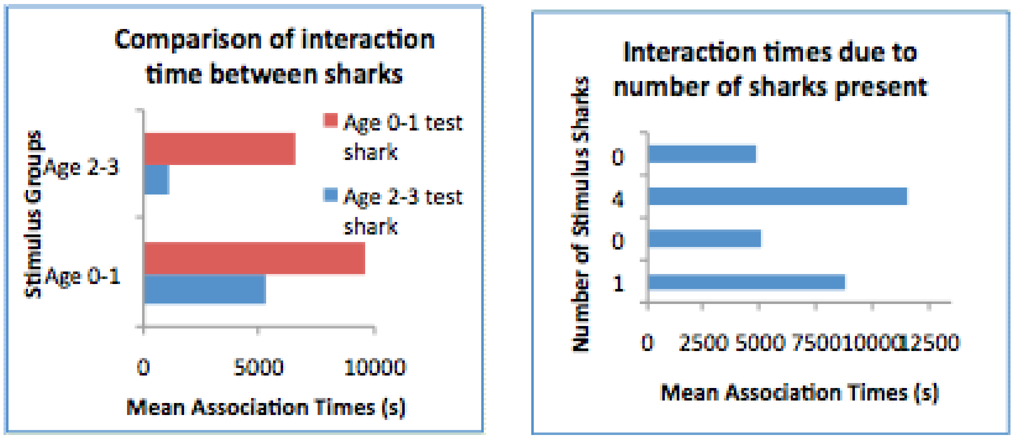
A similar form of aggregating was also observed in salmon sharks (Lamna ditropis) gathered off the coast of Alaska, waiting for the salmon migration (Hulbert et al., 2005). The salmon sharks switched between **focal foraging** and **foraging dispersal** strategies as they hunted, but they never cooperatively hunted for salmon as a group. Thus it appears there is no affiliation between hunting strategies and size segregation in sharks; the only social factor observed were warning displays (Klimley et al., 2001).

1.2.2.2 Protection

Although sharks do not segregate into groups of cooperative hunters, it's plausible that they might segregate themselves into groups of homogeneously sized individuals in order to protect themselves (Guttridge et al. 2009).

Since sharks aggregate due to overlapping dietary resources (Wetherbee & Cortes, 2004), it's no surprise that pregnant leopard sharks (*Triakis semifasciata*) aggregate in Humboldt Bay, California in order to give birth in clumps of eelgrass (Ebert & Ebert, 2005). The eelgrass is abundant with fish eggs, an important food source for newborn juveniles (Ebert & Ebert, 2005). In a similar manner, bluntnose sevengill sharks (*N. cepediamus*) enter the bay to birth their young after other elasmobranches have left. Just like how the juvenile *T. semifasciata* feed on fish eggs in the eelgrass, newborn bluntnose sevengill sharks feed on other newborn elasmobranches, especially juvenile leopard sharks.

However, Heupel and Heuter were astonished to find, in 2002, that juvenile blacktip sharks (*Carcharhinus limbatus*), despite living in the nutrient rich nursery, aggregate in the northern end of the bay rather than in the center where the prey is densest. According to the behavioral patterns observed in other elasmobranches, the juveniles should have aggregated where the food was most abundant. Instead, for the first 6 months after birth, the juveniles concentrated themselves in the kernel, the area in the northern end of the nursery (Heupel et al, 2004). A more indepth study of juvenile blacktip sharks by Heupel and Simpfendorfer in 2005 revealed that the young *C. limbatus* were observed to make daily foraging trips into the midst of where prey was densest; however, instead of remaining there, they return to the northern end of the nursery. The repeated behavior indicates that there must be a direct fitness benefit involved with such behavior. The occasional larger elasmobranch in the prey-rich area of the nursery may be the source of such a behavior (Heupel & Simpfendorfer, 2005). In gathering together away from areas of high prey density and areas containing possible predators in large, they use increase their survival rate. Thus despite the fact that protective segregation only applies to juvenile elasmobranches, the behavior observed indicate that sharks do in fact gather in order to protect themselves.



(a) (b)

Figure 1.10: Right As can seen from the amount of time spent with the different groups of sharks, the different ages have differential preference for those their own age and size. Left As seen with the bar graphs, the sharks preferred to spend more time with other sharks than to be solitary: the more sharks there are in one area, the more time spent with the sharks.
Both graphs are reproduced from Guttridge et al.'s (2009) data

1.2.3 Why Socially Segregate?

Unlike size segregation, social segregation is much more complex. Sharks tend to practice both **habitat segregation** and **spatial segregation**, both of which are types of social (sexual) segregation. Both **biotic** and **abiotic** factors influence how each sex approaches **habitat selection** (Conradt, 1998). Five different hypotheses exist, attempting to explain the variations in social segregation different species of elasmobranches were observed to practice (Wearmouth & Sims, 2008).

The predation-risk (reproductive strategy) hypothesis suggests that due to differences in rates of predation, both females and males act to maximize their reproductive potential by augmenting their behavior in order to lower their chances of being predated upon. On the other hand, forage selection (sexual dimorphism - body-size) hypothesis suggests that **sexual dimorphism** between the females and males create different nutritional needs, thus they feed in different areas according to prey densities. Alternately, the activity budget (body-size dimorphism) hypothesis suggests that sexual dimorphism creates conflict between the sexes due to different energy requirements, thus they separate to become more efficient. Thermal niche-fecundity hypothesis is similar to predation-risk hypothesis in that it suggests both sexes strive to maximize their lifetime reproductive success, but this hypothesis suggests that reproductive potential is maximized in the right temperature conditions rather than in lowered predation rates. Finally social factors (social preference and social avoidance) hypothesis focuses on how the sex-segregation is driven by social factors (sexual preferences) (Wearmouth & Sims, 2008).

Box 1.7: Did you Know. . .

Even though there is abundant evidence indicating that there is hardly a distinct social system within even socially segregated sharks, such as the Sychliorhinus canicula, the catshark, dominance hierarchy has been found to exist within Sphyrna tiburo, the bonnethead shark (Myrberg & Gruber, 1974).

Myrberg and Gruber found that within a group of 10 individuals, there is a distinct, size-dependent linear dominance hierarchy determined by size more than anything else. Similar to how a dog rolls over to show its belly to a higher ranked individual, the sharks act submissively before a higher ranked individual. When the courses of two sharks intersect, the lesser-ranked individual will abruptly change course to avoid the more dominant shark. Also, the order of a follow formation is believed to be in order of dominance, but this has yet to be proven.

However, one interesting fact was noted by the duo: more so than expected, the smaller sharks shied away more from the males of the group. Although reasons are unclear as to why male dominance is less size-correlated, Myrberg and Gruber attribute this behavior to fear. They reason that the violence exhibited by male bonnetheads during mating assert their dominance, along with fear, in the group.

Thus, even though most evidence indicate that segregation isn't a voluntary action exhibited by sharks, such sexual segregation found in the sexually dimorphic scalloped hammerhead sharks, Sphyrna lewini, the fact that an established social hierarchy exists indicates that sharks are more rational than their stereotypically counterparts, or that they are still continuing their evolution into intellectual organisms from over 350 million years ago (Klimely, 1987)(Myrberg & Gruber, 1974)(Sims, 2003).

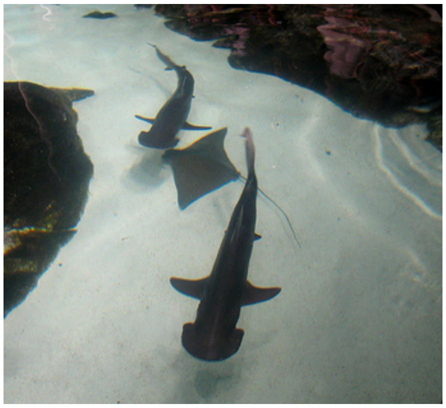


Figure 1.11: An example of rare following behavior of the Bonnethead shark http://www.flickr.com/photos/danarah/159354894/

1.2.3.1 Predation-risk, forage selection, or activity budget hypothesis?

The main difference that distinguishes these three hypotheses is their different emphases on the role food plays in maximizing sharks' reproductive success. The predation-risk hypothesis considers food to be less important than predation avoidance while both forage selection and activity budget hypotheses emphasis that it's because of differences in diet that sexual segregation occurs (Wearmouth & Sims, 2008). However, the forage selection hypothesis and activity budget hypothesis differ in that the latter states that energy cost differences causes group conflict that lowers fitness while the former emphasizes that there was no prior obligation to remain as a collective group, thus division of the sexes occurred independent of a mixed social group (Wearmouth & Sims, 2008).

Sphyrna lewini, the scalloped hammerhead shark, is a great example of a socially segregated elasmobranch species. Both males and females remain in the nursery after birth and successfully coexist as a size-segregated group until they reach adolescence (Klimely, 1987). As juveniles, the female hammerheads depart for the shallows to feed on larger pelagic prey while the males remain behind to continue feeding in the nursery.

According to the predation-risk hypothesis, this behavior is a result of increased predation on females (Wearmouth & Sims, 2008). However, at this time, no sexual dimorphism is observed in the juveniles: both the males and females are physically the same. Thus nothing distinguishes one sex from the other as preferable prey (Klimely, 1987) – the females aren't smaller or weaker than males, making them easier to feed upon. In fact, no biotic or abiotic condition differed for the two sexes during separation (Klimely, 1987). The absence of sexual dimorphism in juveniles of elasmobranches isn't confined to only scalloped hammerhead sharks; many juveniles of sexually-segregated elasmobranch species are commonly observed to form groups containing both sexes, such as the oceanic whitetip sharks, *Carcharhinus longimanus* (Coelho et al, 2009). Although they are often found in segregated groups as adults, juvenile whitetips caught in the Gulf of Mexico are found in groups composed of both females and males of similar sizes (Coelho et al, 2009). Hence size differences fail to account for why the sexes separate upon maturity: the predation-risk hypothesis remains largely unsupported.

Similarly, the activity budget hypothesis appears just as implausible. Since this hypothesis centers on the differences in energy consumption between sexually dimorphic organisms, the lack of difference in the physique of the two sexes at the time of sexual segregation indicate that energy expenditure isn't the source of the behavior (Klimely, 1987). Also, juvenile sharks are smaller than mature specimens of the same species, thus they would gain fitness by practicing protective segregation in the nursery (Heupel & Heuter, 2002)(Heupel & Simpfendorfer, 2005). Rather, if they separate according to sex while physically immature, the loss of protective cooperation would result in mutual lose of fitness. By this reasoning, the proposal that energy usage by males and females are different enough to incur loss of fitness is unlikely (Wearmouth & Sims, 2008). Thus the suggestion that sexual segregation resulted due to energy cost conflict between sexually dimorphic sexes remains largely unsupported.

While the predation-risk and activity budget hypotheses both focused on external differences that may inhibit possible fitness benefits, the forage selection hypothesis takes into account both the physical and physiological changes experienced by the developing juvenile scalloped hammerhead sharks (Wearmouth & Sims, 2008). As recounted, there are no differences in the physique of the juvenile male and juvenile female *S. lewini*, and other juvenile sharks of sexually dimorphic species, thus their underdeveloped states would indicate that they suffer from equal amounts of predation and should have continued their practice of protection segregation (Klimely, 1987). However, the fact that females deviated from such a behavior indicate that they suffer to lose rather than gain fitness if this behavioral pattern persists.

Since female fitness relies heavily on maximizing reproductive success, physiological needs compel them to leave the safety of the nursery (Klimely, 1987). Since scalloped hammerhead sharks are **viviparous**, females require larger body sizes to accommodate the young (Sims, 2003). If the females were to grow at the same rate as males, they would be at a reproductive disadvantage because there's less strain on the males when reproducing; males invest fewer resources (the sperm) compared to the females who have to house and feed the developing offspring. Thus, in order to match the reproductive output of similarly-aged males, the females need to reach reproductive maturity earlier than the males, resulting in sexually dimorphic adults. To initiate their earlier development, the female S. lewini leave the nursery ahead of the developing males to feed on larger, more nutritious prey in deep waters. This difference in prey preference leads to the sexual segregation observed in this shark species, as well as many other elasmobranches (Klimely, 1987)(Sims, 2003).

Figure 1.12: A scalloped hammerhead shark, *Sphyrna lewini*, in a school of fish.

When comparing the predation-risk, forage selection, and activity budget hypotheses, the model, *S. lewini*, clearly indicates that sexual segregation isn't an aggregative behavior that occurs due to physical needs but rather an act of lowering reproductive losses. While all three hypotheses cite sexual dimorphism as a factor of sexual grouping behavior, only the forage selection hypothesis indicates that sexual dimorphism is a result of physiological needs to increase reproductive output rather than the cause of segregation (Sims, 2003). Thus it's not surprising that females of elasmobranch species that are viviparous and **ovoviviparous** practice sexual segregation. This accounts for the fact that sexual dimorphism is only observed after sharks have evolved, as seen with both S. lewini and Carcharhinus longimanus, the oceanic whitetip sharks. On the other hand, both the predation-risk hypothesis and the activity budget hypothesis focused on how size differences in the adult specimens force different needs on the sharks rather than the ultimate cause. They both fail to note that sexual segregation occurs before sexual dimorphism does.

1.2.3.2 Thermal niche-fecundity and Social Factors Hypotheses

However, despite the clear association between sexual dimorphism (due to viviparous and ovoviviparous reproduction) and sexual segregation, none of the hypotheses presented above are able to explain the presence of sexual segregation within the catshark, *Sychliorhinus canicula* (Wearmouth & Sims, 2008). Since catsharks **oviparous**, the females do need larger physique for bearing live young. As a consequence, S. canicula is one of the few **monomorphic** species of elasmobranches, making it an ideal model of study for environmentally and socially instigated sexual selection (Sims, 2003).

The thermal niche-fecundity and social factors hypotheses are very different theories: where the thermal niche-fecundity hypothesis suggests that sharks maximize reproductive success by responding to changes in environmental temperatures, the social factors hypothesis proposes that the sharks consciously segregate themselves by sexual preference and other social factors (Wearmouth & Sims, 2008).

Sychliorhinus canicual practices both spatial and habitat segregation despite being monomorphic: the female catsharks are found to spend most of their time in small tunnels in tidal loughs while the males are found to spend most of their time in deep waters offshore (Sims et al, 2001). However the cause of segregation in the catshark, *S. canicula*, is very different from the previous model: the two sexes are segregated for different reasons. While the female catsharks may gain benefits from the warm temperature of the shallows, these benefits are speculative at best; their behaviors are better explained as a social response to male violence during copulation. On the other hand, the males segregate themselves from the females solely because of an abiotic factor. Since all physical traits and prey preferences are the same, the differing reasons for segregation boil down to one thing: reproductive benefits.

Sims *et al* speculated in 2001 that female *S. canicula* lounge in the warm shallows, rather than the colder water found offshore, in order to better facilitate egg development, as observed in similar behaviorisms exhibited by many other elasmobranch species, such *Triakis semifasciata*, the leopard sharks**. Refuging system** behavior is often observed in adult female leopard sharks shortly after early summer mating (Hight & Lowe, 2007). The leopard sharks would migrate in groups to the warmest areas in the shallows, occasionally shifting position in order to remain in the warmest spot at all times, to better facilitate digestion, somatic growth, and embryonic development (Hight & Lowe, 2007). However, despite helping with growth and digestion, embryonic development is the most important proximate cause that facilitates this refuging behavior since reproduction is the only factor that directly increases the fitness of the organism. This is further supported by the fact that only mature female *T. semifasciata* exhibit this basking behavior during August, a time period associated with early embryonic development (Hight & Lowe, 2007). If this behavior was solely for facilitating growth, then juvenile females and males would also be spotted.

Box 1.8: Abiotic Factors: How they Affect Shark Populations

In nature, the environment is not composed of biotic factors alone; temperature, climate, pressure, and other non-living variables all play vital roles in making a certain region habitable for organisms. For the sharks and especially the model of the study, Rhizoprionodon terraenovae, there are two main abiotic factors that influence the population density within a certain body of water: temperature and oxygen concentration (Parsons & Hoffmayer, 2005).

The population of Atlantic sharpnose shark, Rhizoprionodon terraenovae, fluctuates regularly with the seasons. Parsons and Hoffmayer found in their study (2005) that the sharks would always enter the freshwater regions of North Central Gulf of Mexico within certain range of temperatures and depart in a similar fashion. When water temperature approached 20-22°C in spring, R. terraenovae was found migrating into the region. However, when temperatures shift down in the fall from 24-20°C, the Atlantic sharpnose sharks were found departing.

When studying the changing flux of sharks entering and exiting the bay, an interesting relationship was found: with increasing temperatures, fewer male sharks were found throughout the region, making summer the month where the fewest number of sharks are counted (Parsons & Hoffmayer, 2005). However, the previous temperature ranges indicated that increases in temperature was favorable. However, Parsons and Hoffmayer found that increasing temperatures resulted in decreased saturation of oxygen throughout the body of water. Thus despite favorable temperatures, the lack of essential oxygen made this habitat less inhabitable.

Thus, sharks can be generalized to thrive within limited temperature ranges – warm enough for the cold-blooded shark to survive yet not too warm such that oxygen saturation is too low.

However the thermal niche-fecundity hypothesis lacks direct evidence of benefits *S. canicula* gain by remaining in the shallows during the day; from what was observed, the behavior of female catsharks better support the social factors hypothesis. Sims et al noted, in 2001, that after copulation, male catsharks often have blood on the claspers they use to hold females. This indicates that reproduction is an energetically demanding activity (Parker, 2006); thus, for females, the lowered fitness and vulnerability associated with copulation forces them to take preventative measures against the frequent attempts male catsharks make to copulate (Parker, 2006). The loss of fitness is so great that despite the fact that female *S. canicula* have the same diet as males, they choose to reside in narrow tunnels found in the warm shallows away from abundant amounts of prey in order to restrict male access and limit their movement (Sims et al, 2001). Thus social factors hypothesis best explains why females rebuff male advances: in order to minimize their loss of fitness due to copulation, female *S. canicula* not only rebuff males by taking refuge in inaccessible habitats but also only emerge to feed in the deeper waters during periods of predominant male inactivity (Wearmouth & Sims, 2008).

However, why don't male *S. canicula* pursue the females into the shallows to copulate? Sims et al found (2006a) that male catsharks will actually refuse to approach warmer water. The persistence of this behavior indicates that cost of fitness lost is greater than the benefits gained through copulation with the female catsharks. Sims found that the costs incurred are greater than any benefit gained by approaching females when the temperature is too high: not only is energy usage greater in increasingly warm water (due to increased metabolic rates), but spermatogenesis is also compromised (Sims, 2003). By using diel vertical movement to remain in the optimal temperature range (11-16oC), the male *S. canicula* can save up to 4% of energy as well as also maximizes its growth rate (Sims et al, 2006a). Spermatogonia division and testosterone biosynthesis also peak in this temperature interval, maximizing fitness (Sims, 2003). Thus male S. canicula behaviors are best explained thermal niche-fecundity hypothesis: by strictly adhering to specific temperature ranges, male catsharks minimize fitness loss.

1.2.4 Concluding Thoughts

After journeying through the causes and benefits of size and sexual segregation, one main conclusion is reached: sharks are more instinctive creatures rather than rational thinkers. With the exception of protective segregation and sexual segregation practiced by female *Sychliorhinus canicula*, all the social behaviors mentioned were merely the sharks' response to shifts their own physiology as well as biotic and abiotic factors. Overall, size segregation occurs due to prey-based aggregation, and sexual segregation, the more social grouping behavior, revolved around minimizing reproductive loss in response to environmental factors.

1.2.5 Discussion Questions

1. Looking at the evidence provided, especially on the catsharks, Sychliorhinus canicula, and bonnethead sharks, Sphyrna tiburo, do you believe that sharks are in the process of evolving more social behaviors? What selective pressures might be involved in this evolution?
2. What other abiotic factors might influence shark populations? Biotic factors?

1.2.6 Glossary

- **Abiotic** - nonliving factors in the environment that affect animals living in a particular habitat
- **Aggregations** - a group of organisms formed through common interest in a particular resource
- **Biotic** - living factors in the environment, including variables within the organism itself, that affect animals living in a particular habitat
- **Elasmobranch**- members of the class Chondrichtyes, the class in which sharks are taxonomically classified
- **Focal foraging** – a foraging pattern that consists of continuous patrolling in areas near the initial place of prey aggregation
- **Foraging dispersal** – a foraging patter that consists of continuous patrolling in areas about 500-600 km away from the initial site of prey aggregation; the organism actively moves through depths of 0-2 m to 60 m
- **Habitat segregation** - a subcategory of social segregation dealing with the separation of the sexes where each sex uses a different habitat; can overlap with spatial segregation if the habitats are in two different areas (Conradt, 1998)
- **Habitat selection** - the conscious actions of an organism's usage of space affected by a variety of co-factors in both the environment and physiology of the organism
- **Monomorphism** – no difference in body size between the females and males of a certain species
- **Oviparous** - a form of reproduction where produced eggs mature outside of the mother's body after expulsion
- **Ovoviviparous** - a form of reproduction where produced eggs, which development independent of the mother, aren't expulsed but rather matures and hatches inside the female's body
- **Refuging system** – a group of organisms that gather during a certain time period for social or environmental reasons and disperse to forage individually, in pairs, or in groups the during the other time periods (Klimley & Nelson, 1984)

- **Segregation** – a type of grouping behavior practiced by many organisms where they sort themselves into groups by phenotypic trait, i.e. size or sex.
- **Sexual dimorphism** - difference in body size between the females and males of a certain species
- **Size segregation** - separation of the species into size-specific groups according to physical body size
- **Social groups** - a group of organisms formed to mutually increase the fitness of all the members
- **Social segregation** - separation of the sexes into two different groups within a species
- **Solitary animal** - organisms that don't practice intersexual segregation since they don't socially interact between the sexes let alone the opposite sex; habitat and spatial segregation could still be applied to solitary animals if they gather in aggregated populations whose ranges overlap
- **Spatial segregation** - a subcategory of social segregation dealing with separation of the sexes where each sex lives in a different area; can overlap with habitat segregation if the habitats are found in different areas (Conradt, 1998)
- **Viviparous** - a form of reproduction where the young depends on the mother for development and is birthed alive

1.2.7 References

Alexander, Richard D. (1974). The Evolution of Social Behavior. Annual Review of Ecology and Systematics. 5, 325-383. 20 Mar 2010. <http://www.jstor.org/stable/2096892 >.

Source provided information on group behavior: causes and effects, detriments and benefits. Also introduced the different types of groups as well as relationships within groups.

Coelho, R., Hazin, F.H.V., Rego, M., Tambourgi, M., Oliveira, P., Travassos, P., Carvalho, F., Burgess, G. (2009). Notes on the reproduction of the oceanic whitetip shark, Carcharhinus longimanus, in the southwestern equatorial Atlantic Ocean. Collect. Vol. Sci. Pap. ICCAT. 64, 1734-1740. Web. 20 Feb 2010. <http://www.iccat.int/Documents/CVSP/CV064_2009/no_5/CV0640501734.pdf>.

Carcharhinus longimanus is used as an example indicating the existence of spatial size-segregation within sharks by observing the shark population caught in the Gulf of Mexico. Indications of sexual segregation setting in after adulthood is seen due to the lack of sexual segregation observed in juvenile whitetip sharks.

Conradt, Larissa. (1998). Measuring the degree of sexual segregation in group-living animals. Journal of Animal Ecology. 67, 217-26. Web. 15 Mar 2010. <http://www.jstor.org/stable/2647490 >.

Social segregation is defined and broken down into subcategories. A factor that measures segregation is called the degree of segregation that identifies groups to be not segregated, partially segregated, or completely segregated. The concept of solitary animals is also introduced.

Dicken, M.L., Smale, M.J., Booth, A.J. (2006). Spatial and seasoning distribution patterns of the ragged-tooth shark Carcharias taurus along the coast of South Africa. African Journal of Marine Science. 28, 603-616. Web. 20 Feb 2010. <http://www.sasaa.co.za/sasaaftp/spatialseasonalraggies1.pdf>.

Size segregation is observed in ragged-tooth shark, Carcharias taurus, according to population distributions along the European/African shores. Sharks of different ages aren't evenly distributed throughout the coastline but segregated to certain positions along the coasts. Temperature is found to be a large factor that governs the prey of C. taurus so relationship between the abundance of the sharks are found to be directly influenced by how abundant their prey is.

Ebert, D.A. (2002). Ontogenetic changes in the diet of the sevengill shark (Notorynchus cepedianus). Mar. Freshwater Res.53, 517-523. Web. 20 Feb 2010. <http://ps4ps6lm2r.scholar.serialssolutions.com/?sid=google&auinit=DA&aulast=Ebert&atitle=Ontogenetic+change
1650>.

In Notorynchus cepedianus, ontogenetic changes causes the sharks to go after larger prey and due to the experienced hunters moving away from the younger sharks' prey and geographic area, their survivorship greatly increases. This is another example of size segregation and why it occurs.

Ebert, D.A., Ebert, T.B. (2005). Reproduction, diet and habitat use of leopard sharks, Triakis semifasciata (Girard), in Humboldt Bay, California, USA. Mar. Freshwater Res. 56, 1089-1098. Web. 19 Feb 2010.

<http://ps4ps6lm2r.scholar.serialssolutions.com/?sid=google&auinit=DA&aulast=Ebert&atitle=Reproduction,+diet-
1650>.

Triakis semifasciata also exhibits sexual segregation sinc e the shallows around California is predominantly inhabited by females and their young. The source of sexual segregation doesn't appear to be for protective purposes since T. semifasciata have been found to reproduce annually. Cooperation among individuals isn't observed; they appear to forage as a loosely aggregated group with members "eavesdropping" on other's kills. They have been observed to forage in conspecific groups as well as with other shark species such as M. henlei, N. cepedianus, and M. californica.

Gruber, S.H., Nelson, D.R., Morrissey, J.F. (1988). Patterns of activity and space utilization of lemon sharks, Negaprion brevirostris, in a shallow Bahamian lagoon. Bulletin of Marine Science. 43, 61-76. Web. 20 Feb 2010. <http://www.ingentaconnect.com/content/umrsmas/bullmar/1988/00000043/00000001/art00003>.

Lemon sharks (Negaprion brevirostris) have been seen to interact with other species such as schools of jacks (Caranx) and barracudas (Sphyraena barracuda), nurse sharks (Ginglymostoma cirratum), southern stingrays (Dasyatis americana), and under special conditions, Echeneis naucrates. In situations of interaction, the lemon shark would mimic the other by matching its swim gait and follow it to keep it visible - no alarmed reactions between species. Also, lemon sharks appear to communicate among themselves since intraspecific interactions were observed where two or more individuals have been seen traveling together. These sharks are not solitary individuals: mostly seen in aggregations.

Guttridge, T.L., Gruber, S.H., Gledhill, K.S., Croft, D.P. Sims, D.W., Krause, J. (2009). Social preferences of juvenile lemon sharks, Negaprion brevirostris. Animal behavior. 78, 543-548. Web. 4 Feb 2010.
<http://ps4ps6lm2r.scholar.serialssolutions.com/?sid=google&auinit=TL&aulast=Guttridge&atitle=Social+preferenc
3472>.

Found that juvenile sharks tend to congregate in groups with individuals of approximately the same size and age. Sexual and size segregation were hypothesized to be a product of either communication, courtship, predatory, or protective behavior. An experiment in a controlled environment was commited on the Negaprion brevirostris.

Heupel, M.R., Hueter, R.E. (2002). Importance of prey density in relation to the movement patterns of juvenile blacktip sharks (Carcharhinus limbatus) within a coastal nursery area. Mar. Freshwater Res. 53, 543-550. Web. 19 Feb 2010.
<http://ps4ps6lm2r.scholar.serialssolutions.com/?sid=google&auinit=MR&aulast=Heupel&atitle=Importance+of+pr
1650>.

Juvenile Carcharhinus limbatus was observed to aggregate in the nurseries a certain point that doesn't correlate with the highest prey abundance. Thus such behavior was attributed to a factor other than prey location and it was hypothesized that this aggregation was an act towards group protection.

Heupel, M.R., Simpfendorfer, C.A. (2005). Quantitave analysis of aggregation behavior in juvenile blacktip sharks. Marine Biology. 147, 1239-1249. Web. 4 Feb 2010. <http://www.springerlink.com.ezproxy.rice.edu/content/v7148857lg2135m2/>.

Juvenile Carcharhinus limbatus were observed to aggregate at certain times of the days in what are observed as diel rhythms. The conclusion that such behavior is for group protection and feeding efficiency was drawn.

Heupel, M.R., Simpfendorfer, C.A., Hueter, R.E. (2004). Estimation of shark home ranges using passive monitoring techniques. Environmental Biology of Fishes. 71, 135-142. Web. 20 Feb 2010. <http://www.science.fau.edu/sharklab/courses/elasmobiology/readings/heupel.pdf>.

It is noted that Carcharhinus limbatus spent a significant portion of their first year (6 months) within the nursery area and spent 95% of their time in the kernel, making occasional forays away from it for food. Changes in atmospheric pressure was noticed to change the home range of the juvenile sharks so it was concluded that behavior isn't only due to the influence of prey and protection but also environment factors.

Hight, B.V., Lowe, C.G. (2007). Elevated body temperatures of adult female leopard sharks, Triakis semifasciata, while aggregating in shallow nearshore embayments: Evidence for behavioral thermoreg-

ulation? Journal of Experimental Marine Biology and Ecology. 352, 114-128. Web. 20 Feb 2010.
<http://ps4ps6lm2r.scholar.serialssolutions.com/?sid=google&auinit=BV&aulast=Hight&atitle=Elevated+body+tem
0981>.

Female Triakis semifasciata are found to bask in the warmest patches of water during the day despite an obvious lack of prey. They are found to become more active during the night so sexual segregation was concluded to support the thermal niche-fecundity hypothesis in conserving the energy of the sharks during the day to improve reproduction and to expand energy in colder waters to forage.

Hulbert, L.B., Aires-da-Silva, A.M., Gallucci, V.F., Rice, J.S. (2005). Seasoning foraging movements and migratory patterns of female Lamna ditropis tagged in William Sound, Alaska. Journal of Fish Biology. 67, 490-509. Web. 6 Feb 2010.
<http://ps4ps6lm2r.scholar.serialssolutions.com/?sid=google&auinit=LB&aulast=Hulbert&atitle=Seasonal+foraging
1112.2005.00757.x&title=Journal+of+fish+biology&volume=67&issue=2&date=2005&spage=490&issn=0022-1112>.

In the Lamna ditropis caught and tagged, 95% were female so sexual segregation in this species was noted. Also, the hunting behavior was observed to not be cooperative but rather of three types: focal foraging, foraging dispersal, and direct migrations. The different types of behaviors in the feeding of the sharks is attributed to the conservation of energy best of the shark by finding the optimal balance between optimal temperature and optimal prey quantity/quality.

Klimley, A.P., Nelson, D.R. (1984). Diel movement patterns of the Scalloped hammerhead Shark (Sphyrna lewini) in relation to El Bajo Espiritu Santo: a refuging central-position social system. Behav Ecol Sociobio. 15, 45-54. Web. 20 Feb 2010.
<http://ps4ps6lm2r.scholar.serialssolutions.com/?sid=google&auinit=AP&aulast=Klimley&atitle=Diel+movement+
position+social+system&id=doi:10.1007/BF00310214&title=Behavioral+ecology+and+sociobiology&volume=15&issu
5443>.

Refuging system as cited as a type of social system found within sharks where the sharks participate in everyday activities in cooperative manners. This source will be used to show the growth of theory from the 1980s to the present day model of group aggregation rather than coordinated hunting.

Klimley, A.P., Le Boeuf, B.J., Cantara, K.M., Richert, J.E., Davis, S.F., Van Sommeran, S., Kelly, J.T. (2001). The hunting strategy of white sharks (Carcharodon carcharis) near a seal colony. Marine Biology. 138, 617-636. Web. 12 Feb 2010. <http://www.seaturtle.org/PDF/author/Klimley_2001_MarBiol.pdf>.

The hunting strategies of Carcharodon carcharis is seen to be completely uncoordinated and that sharks often approached each others' kills in the hope of getting a bite. They were seen to aggregate only due to the common food source rather than a group assault on the prey.

Klimley, A. P. (1987). The determinants of sexual segregation in the scalloped hammerhead, Sphyrna lewini. Environmental Biology of Fishes. 18, 27–40. 29 Mar 2010.
<http://ps4ps6lm2r.scholar.serialssolutions.com/?sid=google&auinit=AP&aulast=Klimley&atitle=The+determinants
1909 >.

Introduced the concept that sexual dimorphism exist as a means for females to match male reproductive output. Also, introduced the idea that sexual dimorphism causes the sexes to practice habitat and spatial segregation due to dietary differences.

Le Beouf, B.J. (2004). Hunting and migratory movements of white sharks in the eastern North Pacific. Mem. Natl Inst. Polar Res. 58, 89-100. Web. 13 Feb 2010. <http://polaris.nipr.ac.jp/∼penguin/oogataHP/pdfarticles/09p89-100.pdf>.

Showed that Carcharodon carcharis is a solitary hunter and they tend to eavesdrop on each other's kills and aggregate at a common prey habitat.

Lowry, D., Motta, P.J. (2008). Relative importance of growth and behaviour in elasmobranch suction-feeding performance over early ontogeny. J.R. Soc. Interface. 5, 641-652. Web. 10 Feb 2010. <http://rsif.royalsocietypublishing.org.ezproxy.rice.edu/content/5/23/641.full.pdf+html>.

The skill at which sharks are able to capture their prey is seen to be directly proportional to the age of the shark. Also, relationship in the prey consumed and the shark's age is made.

Myrberg, A.A., Gruber, S.H. (1974). The behavior of the bonnethead shark, Sphyrna tiburo. Copeia. 2, 358-374. Web. 20 Feb 2010. <http://ps4ps6lm2r.scholar.serialssolutions.com/?sid=google&auinit=AA&aulast=Myrberg+Jr&atitle=The+behavio 8511>.

Sphyrna tiburo are observed to be a sexually segregated species where pairing and group travel have been observed in behaviors such as aggression, flight, food deprivation, and maintenance/courtship.

Papastamatiou, Y.P., Wetherbee, B.M., Lowe, C.G., Crow, G.L. (2006). Distribution and diet of four species of carcharhinid shark in the Hawaiian Islands: evidence for resource partitioning and competitive exclusion. Marine Ecology Progress Series. 320, 239-251. Web. 20 Feb 2010. <http://www.hawaii.edu/HIMB/sharklab/Papastamatiou_MEPS06.pdf>.

The overlapping diets of certain sharks bring them into interspecific competitions that determine their geographical habitats. Actual social interactions are not observed between species but rather competition of food determines their niches.

Parker, G.A. (2006). Sexual conflict over Mating and Fertilization: An Overview. Philosophical Transactions: Biological Sciences. 361, 235-259. Web. 17 Feb 2010. <http://ps4ps6lm2r.scholar.serialssolutions.com/?sid=google&auinit=GA&aulast=Parker&atitle=Sexual+conflict+ov

Sexual conflict is conflict that arises between individuals of different sexes due to opposing evolutionary interests. The diel rhythms observed in the different species of sharks can be attributed to sexual segregation where the different sexes performs different behaviors at different times to optimize their lifetime reproductive fitness.

Parsons, G.R., Hoffmayer, E.R. (2005). Seasonal changes in the distribution and relative abundance of the Atlantic Sharpnose Shark Rhizoprionodon terraenovae in the North Central Gulf of Mexico. Copeia. 4, 914-920. Web. <http://www.jstor.org/stable/4098665?&Search=yes&term=segregation&term=sharks&term=size&list=hide&search

Environmental stress, along with the need to procreate, acts upon the Rhizoprionodon terraenovae to migrate away from the male's normal geographic region. An environmental factor is shown to have great influence on the behavior of the shark, not only its biological needs.

Simpfendorfer, C.A., Freitas, G.G., Wiley, T.R., Heupel, M.R. (2005). Distribution and habitat partitioning of immature bull sharks (Carcharhinus leucas) in a Southwest Florida estuary. Estuaries and Coasts. 28, 78-85. Web. 20 Feb 2010. <http://www.springerlink.com/content/g366332878168232/>.

Carcharhinus leucas have been found to shift geographical sites of habitation as well as shift their diets with age and as a direct result of their size segregation, the younger sharks are able to have more food and have a higher fitness.

Sims, D.W. (2003). Tractable models for testing theories about natural strategies: foraging behaviour and habitat selection of free-ranging sharks. Journal of Fish Biology. 63, 53-73.

Different forms of reproduction and the general history of sharks were provided. Also, it discusses behaviors catsharks exhibit that indicate their segregation tendencies and what it says about why sexual segregation may occur.

Sims, D.W., Nash, J.P., Morritt, D. (2001). Movements and activity of male and female dogfish in a tidal sea lough: alternative behavioural strategies and apparent sexual segregation. Marine Biology. 139, 1164-1175.

Sexual segregation is observed in Scyliorhinus canicula since the female and male daily activities and habitats do not match – it's hypothesized that it's due to hurtful mating for the females that they avoid the males.

Sims, D.W., Southall, E.J., Quayle, V.A., Fox, A.M. (2000). Annual social behaviour of basking sharks associated with coastal front areas. Proceedings: Biological Sciences. 267, 1897-1904. Web. 6 Feb 2010. <http://www.jstor.org/stable/2665771?cookieSet=1>.

Sexual segregation is observed to end with courtship rituals in Cetorhinus maximus. During certain seasons of the year, sharks migrate along the thermal front and food-rich patches to copulate; in normal situations, basking shark is observed to be solitary and sexually segregated.

Sims, D.W., Wearmouth, V.J., Southall, E.J., Hill, J.M., Moore, P., Rawlinson, K.,

Hutchinson, N., Budd, G.C., Righton, D., Metcalfe, J.D., Nash, J.P., Morritt, D. (2006a). Hunt warm, rest cool: bioenergetic strategy underlying diel vertical migration of benthic shark. Journal of Animal Ecology. 75, 176-190. Web. 14 Feb 2010.
<http://ps4ps6lm2r.scholar.serialssolutions.com/?sid=google&auinit=DW&aulast=Sims&atitle=Hunt+warm,+rest+
2656.2005.01033.x&title=Ecology+(Durham)&volume=75&date=2006&spage=176&issn=0012-
9658>.

Scyliorhinus canicula is used as a case study in order to determine why there's diel DMV within sharks and this organism is being compared to the pelagic and mesopelagic organisms' diel DMV. It's seen that the DMV behavior of the catshark occurs as explained by the thermal niche-fecundity hypothesis in which they try to match energy conservation.

Sims, D.W., Witt, M.J., Richardson, A.J., Southall, E.J., Metcalfe, J.D. (2006b). Encounter success of free-ranging marine predator movements across a dynamic prey landscape. Proc. R. Soc. B. 273, 1195-1201. Web.
<http://ps4ps6lm2r.scholar.serialssolutions.com/?sid=google&auinit=DW&aulast=Sims&atitle=Encounter+success+
ranging+marine+predator+movements+across+a+dynamic+prey+landscape&id=doi:10.1098/rspb.2005.3444&title=
8452>.

Using a "random walk" model, sub-adult and adult shark predation behavior is concluded to not be random but rather something that is learned through experience. Thus size segregation is a byproduct of the sharks acting upon their instincts in hunting in an area with abundant prey.

Wearmouth, V.J., Sims, D.W. (2008). Sexual Segregation in Marine Fish, Reptiles, Birds, and Mammals: Behavior Patterns Mechanisms and Conservation Implications. Advances in Marine Biology. 54, 107-170.

Sexual segregation is hypothesized to be due to forage selection, predation-risk, active budget, thermal niches-fecundity, and social factors. Each is dependent on the individual organism and their lifestyle and the best way to optimize their lifetime reproductive fitness.

Wetherbee, B. M. & Cortes, E. (2004). Food consumption and feeding habits. Biology of Sharks and their Relatives. 223–244. Web. 19 Feb 2010. <http://www.uri.edu/cels/bio/wetherbee/pubs_files/FeedingChap.pdf >.

Overlap in habitat and prey is considered the factors that cause size segregation to occur in sharks since sharks' diets change with their ontogeny and size. Thus size segregation wasn't a conscious effort of the sharks. Dietary breadth is observed to generally increase with age and size.

Wilga, C.D., Motta, P.J., Sanford, C.P. (2007). Evolution and Ecology of feeding in Elasmobranchs. Integrative and Comparative Biology. 47, 55-69. Web. 20 Feb 2010.
<http://ps4ps6lm2r.search.serialssolutions.com/?sid=jstor:jstor&genre=article&issn=15407063&volume=47&pages=
69&spage=55&epage=69&atitle=Evolution+and+Ecology+of+Feeding+in+Elasmobranchs&date=2007&issue=1>.

In elasmobranchs who hunt using suction, there is a positive relationship between body size and force of suction - indirectly, this infers that prey that are further away can be captured. Size segregation is again seen in that the prey hunted change with the size and age of the organism, so this affect the relative geographic locations of the sharks.

1.2.8 About the Author

Figure 1.13

Born in and raised in Shanghai, China in 1991, I immigrated to America at the age of 6, meeting my parents for the first time since I was born. Since then, I've lived in San Antonio, Texas, a culturally diverse community seeped in history.

This topic on sharks was inspired after watching the Animal Planet Special, "Maneaters," which covered the increased aggressiveness of sharks off the coasts of Australia and the United States. I was fascinated by what made these animals tick. Sharks, being one of the living artifacts of the prehistoric age, are an awesome model for the study of the evolution of social behavior.

Thus in writing this paper, I attempted to explore fact and fiction: are sharks are primitive and instinctual as Hollywood stereotype them to be or are they a developing intellectual? After writing this paper, it made me understand sharks better as an organism.

1.3 Alliance formation in bottlenose dolphins (Tursiops sp.)[3]

Author: Natasha Sotolongo

1.3.1 Introduction

The formation of alliances between organisms has been an area of active study for many years (Connor and Norris 1982). The motives behind alliance formation within groups are not fully understood because when animals cooperate in groups, not all of the group members reap the same benefit. In Shark Bay, Australia, scientists have been studying a society of more than 600 Indian Ocean bottlenose dolphins (Tursiops aduncus) in a territory that extends over 200 km2, peppered with overlapping ranges of populations without apparent boundaries (Connor 2007). These bottlenose dolphins demonstrate a **fission-fusion grouping pattern** in which alliances are frequently formed and disbanded (Connor 2007). The stability of fission-fusion relationships is usually based upon benefits attained while allied, such as defense against predators, increased food acquisition, and social support (Gero et al. 2005).

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[3] This content is available online at <http://cnx.org/content/m34723/1.3/>.

Male bottlenose dolphins form **primary alliances** that usually consist of two or three males and vary in stability and relatedness. Alliances compete against each other over females. Two primary alliances may combine to form a **secondary alliance** that works together to steal females from other primary alliances. A very large secondary alliance is called a "super-alliance," consisting of up to fourteen members that frequently change their primary alignment. Alliances among males occur to create a stronger group that will acquire more females (Connor 2000). In response to male aggression, female bottlenose dolphins form groups of their own, consisting of only females and their calves.

Several theories have been proposed to explain alliances in bottlenose dolphins. The first of the theories is **kin selection**, where members form alliances of related members, creating an **inclusive fitness** advantage by aiding relatives. Individuals act according to **Hamilton's rule**, where relatedness between actor and recipient, benefit to the recipient, and cost to the actor are taken into account. A second theory is **reciprocal altruism**, where a dolphin will perform a seemingly altruistic act toward an ally, but expect future remuneration and cease to act altruistically if the favors are not reciprocated (Connor & Norris 1982).

Figure 1.14: Bottlenose dolphin (Tursiops sp.)

1.3.1.1 About Bottlenose Dolphins

Bottlenose dolphins (Figure 1.14) are marine mammals named for their characteristic bottle-shaped, elongated snout (Gunter 1943). There are actually two species: the common bottlenose dolphin (Tursiops truncates) and the Indo-pacific bottlenose dolphin (Tursiops aduncus). Growing to an average adult length of 2.5 m and weight of 200-300 kilograms, bottlenose dolphins are adept, quick swimmers (Gunter 1943).

They navigate by using echolocation to perceive their surroundings and use varying vocalizations to communicate with each other (Connor & Smolker 1996). Using their strong tail and aquiline shape, bottlenose dolphins are famous for their aerial and swimming displays.

1.3.2 Structure of male dolphin alliances

A **first-order (primary) alliance** consists of two or three males that band together to consort a single female. A **second-order (secondary) alliance** consists of two or three primary alliances that work together to steal females from other alliances (Connor 1992).

1.3.2.1 First-order alliances are usually related

First-order alliances vary in stability, remaining together anywhere from several days to 20 years. Stable primary pairs and trios spend the majority of their time together, regardless of whether they are actually herding females (Gero et al. 2005). This long-term association is thought to maximize their reproductive success because males in alliances are more successful in consorting unwilling females, confronting female alliances, and defending themselves against harassment by other male alliances. In a study by Krutzen et al., it was found that primary alliances are more closely related than expected by chance, which presents **inclusive fitness** benefits as a possible driving force for the formation of primary alliances (2003).

1.3.2.2 Second-order alliances are not necessarily related

Second-order alliances experience frequent reshuffling of their primary alliance components (Connor et al. 1999). A study by Krutzen et al. revealed that secondary alliances are also closely related (2003). Second-order alliances are most likely to band together at the peak of mating season, when competition for females is most fierce. Figure 1.15 shows bottlenose dolphins in close proximity.

Box 1.9: Super-alliances are very large, labile secondary alliances

An unusually large secondary alliance, called a "superalliance", with 14 individuals (4-6 primary alliances) was observed in Shark Bay, Australia (Connor et al. 1999). The primary alliances in the super-alliance were quite **labile** (Connor 2007). Alliances were analyzed by calculating an association coefficient based on the cooperation observed in consorting a female (Connor et al. 1996). Males were considered to be members of the same party if there were within 10 meters of each other. The analysis gave a number between 0 and 100 (0 meaning a pair is never together and 100 meaning a pair that is always together). No stable alliances (association coefficient >25) were observed in the super-alliance. Connor et al. theorized that switching partners may serve to keep the stability of the super-alliance because dolphins are able to make a large number of affiliative bonds (1999) However, the lability of super-alliances could also be dictated by the **equivalence rule**, where animals group things into classes of equivalent value and all member of a certain class are interchangeable (Connor et al. 1999). In a super-alliance, first-order alliances may be fluid because individuals view each other as interchangeable members of the same equivalence class. However, Connor et al. found that bottlenose dolphins in Shark Bay show marked preferences and avoided certain members, suggesting that these dolphins do not follow the equivalence rule.

1.3.2.3 Marked paternity advantage for males in alliances

The prevalence of alliance formation for consortships can support the idea that individuals in alliances get to mate more, but a question remains: is it essential to be in an alliance for reproductive success? Once a primary alliance captures a female, the fertilization is not divisible (Krutzen et al. 2004). Connor et al. observed simultaneous mounting of the female by two males, but mating was difficult to attribute to a single individual because of difficulty in underwater observation (1992). In a study done in Shark Bay, Australia, Krutzen et al. found that the vast majority of offspring were sired by males in alliances (2004). Moreover, it was observed that 75% of paternities were achieved by 2 out of 15 males. Additionally, 2 of 6 observed alliances procured 62.5% of paternities, suggesting that some individuals (and alliances) are more successful than others (Krutzen et al. 2004).

1.3.2.4 Female dolphin alliances are usually related

Female dolphins in the same reproductive state find it advantageous to associate because they have similar requirements for food and defense against male alliances (Gero et al. 2005). In a study by Duffield and Wells, it was found that female alliances are usually composed of related individuals (1991).

Bottlenose dolphin females are often observed engagng in **contact swimming**, where one dolphin's pectoral fin rests near the other's dorsal fin and the pair swims in synchrony. Because of the aggressive nature of male harassment and the fact that contact swimming is increasingly found in **male-biased** populations, it is hypothesized that contact swimming may help females fend off males. In a survey taken of participants in contact swimming, estrous females were overrepresented and lactating females were underrepresented, supporting the idea that females support each other against males through contact swimming when they are most likely to be accosted.

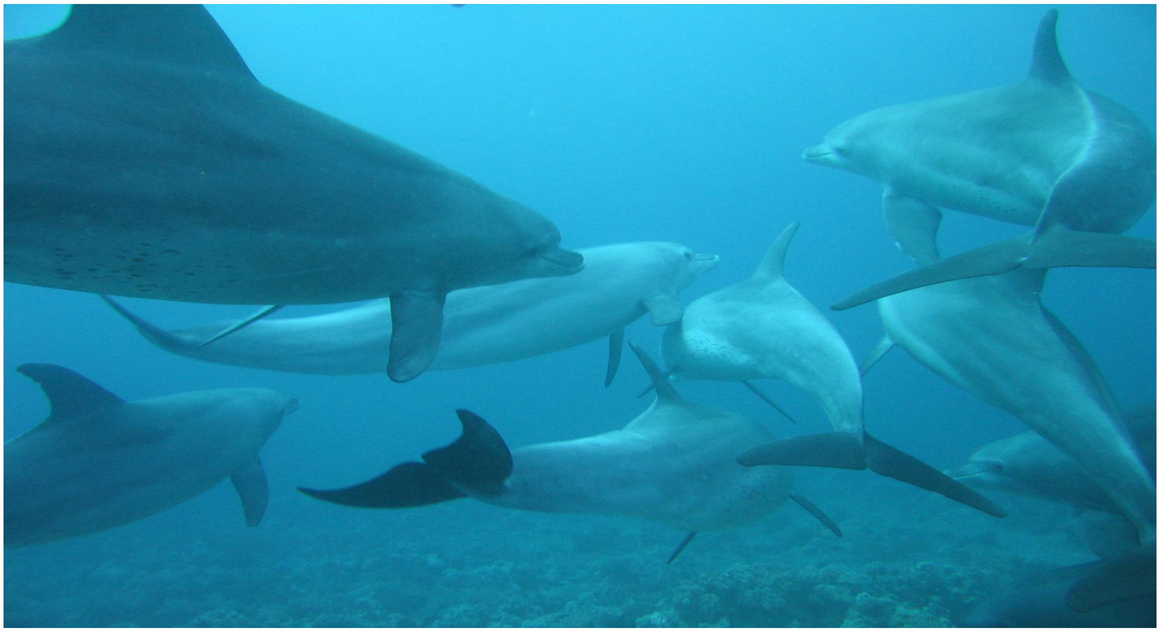

Figure 1.15: Nine bottlenose dolphins within close proximity

Female bottlenose dolphins maintain bonds with their mothers throughout their adult life while males do not. It has been observed that the majority of contact swimming occurs between females (Figure 1.16, $p<0.001$), especially in male-biased groups. Female-female swimming accounted for 83.3% of all observed events. Moreover, when juvenile contact swimming was excluded and only adult contact swimming was analyzed, 96.4% of the pairs were female-female (Connor et al. 2006).

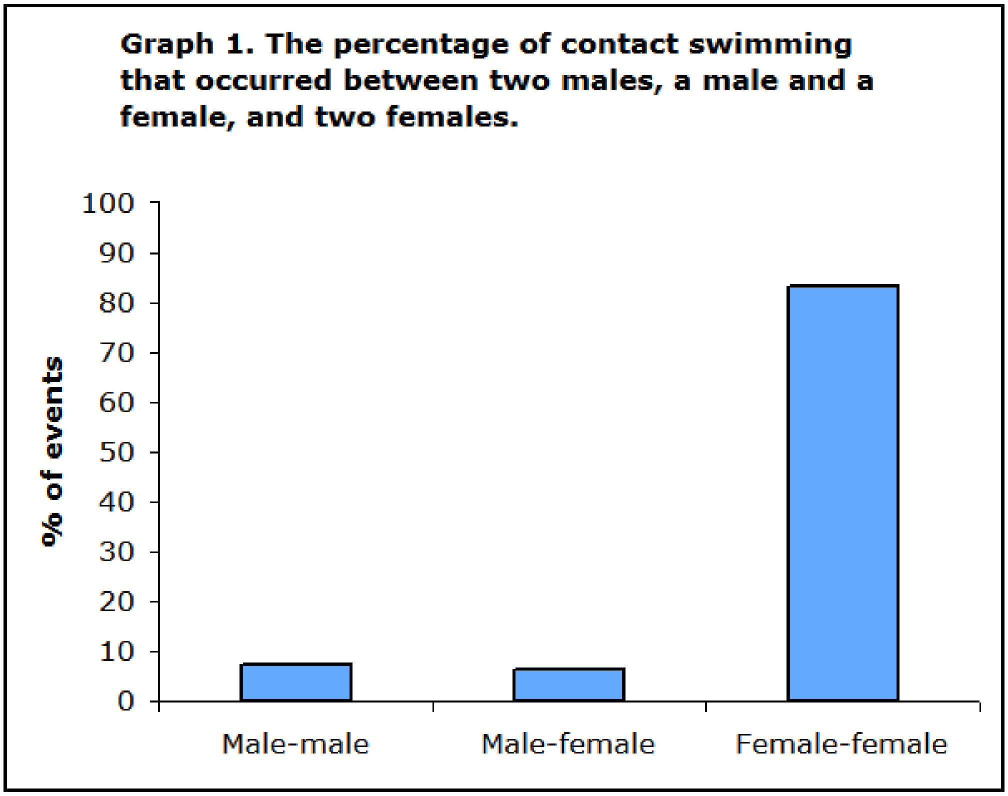

Figure 1.16: Reproduced from data in Connor et al. 2006.

1.3.2.5 Being in an alliance is costly

Dolphins, as well as other organisms, choose groups based on the efficient number of individuals for tasks such as hunting, foraging, consorting, and raising young. An individual will remain in a group only if group living provides a greater advantage than living alone (Brager 1994).

Alliance formation in dolphins is an effort to exploit resources more efficiently (e.g. food for females or estrous females for males) (Connor & Whitehead 2005). Connor & Whitehead observed that alliances are more readily formed in groups of higher density, perhaps because density increases the competition for scarce resources (2005). High densities of males with fewer females increase the competition for female, prompting males to form alliances to partition the limited amount of females. A high density of females increases competition for resources and alliances form for foraging (Connor & Whitehead 2005).

Members who live in groups must be in the same place at the same time, which calls for a degree of synchrony (Conradt & Roper 2000). It is costly for an organism to coordinate activities with a group because he may be forced to give up his optimal habits to synchronize with the group. This cost affects the decision of an individual to remain in a group, impacting group stability, composition, and organization. This is why often individuals are found in groups of similar individuals based on age, sex, or size (Conradt & Roper 2000). Individuals choose group living and alliance formation when benefits outweigh costs.

1.3.2.6 Herding

Males use herding to isolate a female, culminating in fertilization. However, herding is only successful if the male mates with the female when she is most likely to conceive (Connor et al. 1996). Males exhibit aggressive behavior when trying to accost a female. If a male is interested in a female, he will make a distinct popping sound to get the female's attention. It has been shown that popping induces females to turn toward males because females may associate popping with male aggression. Often, if the female does not respond to male popping, the male will attack her (Connor & Smolker 1996). In addition, males perform aggressive head jerks while popping. The popping noise is of a lower frequency than the usual high-pitched vocalizations because sounds of lower frequencies are less directionally oriented, so the female can hear the noise even if the male is not facing her (Connor & Smolker 1996). Once a male has the female's attention, he and his alliance cooperatively display to the female, engaging in synchronized underwater turns, aerial leaps, and flips (Connor 1992). If the female again does not respond or tries to swim away, the males aggressively chase her, slap with their tails, bite her, charge at her, and even body-slam her (Connor 1992). During a chase, males swim in formation, flanking her from each side to effectively cut her off. In 1992, Connor et al. observed that out of 179 courtships observed, only 45 females tried to escape (25%) and males chased 25 out of the 45 attempted escapes (45%). Female choice may be playing a part with the displays of males. If the female tries to escape from the male, she increases the probability that she will mate with the fittest male because the quickest male will be the one who catches up with her (Connor et al. 1996).

Box 1.10: Alliances in Primates and Triadic Interactions

Interactions between male primates are similar to alliance interactions in male bottlenose dolphins in that both primates and bottlenose dolphins associate nonagonistically and agonistically, may become allies with past agonists, and use alliances to aggressively consort females (Connor et al. 1992). In chimpanzees, females mate with multiple males, so males may use alliance formation as a strategy to monopolize females. In a study by Nishida, a society of wild chimpanzees was observed to study the formation of alliances and distribution of paternity (1983). In this society, alliances were formed between three males, alpha, beta, and gamma. The alpha male fathered the most offspring, followed by beta, then gamma. However, the gamma male, although the male with least paternities, played a pivotal role in the alliance dynamics. It was observed that sometimes the gamma male would side with the alpha male and sometimes with the beta male. When the beta and gamma male joined against the alpha male, he lost his paternity advantage. This ability to tip the scales gives the gamma male the ability to manipulate alliance interactions (**triadic interactions**) (Nishida 1983).

1.3.2.7 Female attractiveness

Males form alliances to consort with females, so female attractiveness can be measured by how many propositions she receives from males (Connor et al. 1996). Female bottlenose dolphins begin their menstrual cycle at 5-7 years of age and begin mating at 10-12 years of age (Schroeder 1990). Females may have 2-7 cycles per year, ovulate spontaneously, and are seasonally polyestrous. The varying cycle of the female may be responsible for the seasonal nature of consortships. Before ovulation, females have a period of 5-7 days of rising estrogen levels. Males have been seen to inspect the genitals of females by placing the snout within a few centimeters of the female's genital area and making echolocation noises (Connor et al. 1996). With allied males, often one male approaches the female's genital area from each side. This behavior is suspected to have the purpose of assessing the female's state of fertility, whether in estrus, ovulating, or pregnant. Often, ovulating females are swollen in the genital region and male dolphins may use echolocation to detect this swelling. Another hypothesis is that males may taste the urine of the female to detect certain chemicals that indicate fertility (Connor et al. 1996).

Box 1.11: Dolphin Sexual Development (Mann and Smuts 1999)

Bottlenose dolphins exhibit preferential same-sex petting and rubbing. In a study by Mann and Smuts observing the development of bottlenose dolphins from newborn to juvenile, it was observed that 2-week-old male and female infants engaged in sociosexual rubbing (involving the genitals). Infant females were observed to engage in a keel-rub, a kind of rub common between male and female adults where the female swims belly-up under the male while rapidly flapping her tail, with older non-maternal females. Infant males did not keel-rub, but preferred rubbing of the erect penis, mounting, and even intromission with the mother. There was little contact between adult males and infants. As male dolphins grew older, they became more sexually active, mounting males and females of their own age as well as adults. Juveniles began to form same-sex alliances of peers and spend less time with their mothers, while females remained close to the mother-group (Mann and Smuts 1999).

1.3.3 Alliance Relationships

Affiliative interactions increase bonding among members of a group. Male bottlenose dolphins in first and second order alliances engage in petting, where they rub each other with their pectoral fins (Connor 2007). One male may move his fin against the other or may provide a stiff fin on which the other dolphin may move. Petting is thought to reduce tension, caused by competition, among males (Connor et al. 2006).

Members of alliances often are synchronized in their breathing, coming up for air within 80-120 milliseconds of each other (Connor 2007). Within secondary alliances, synchrony is more common between primary pairs or trios. Connor et al. hypothesized that synchrony is a measure of alliance unity, meaning that more united alliances surface synchronously (2006). Synchrony is also a form of bonding and stress reduction visible in a decreased heart rate during contact (Connor et al. 2006).

1.3.3.1 Kin selection

Why do males cooperate when resources, namely females and conceptions, are scarce and hard to secure (Krutzen et al. 2003)? Hamilton introduced the idea that related individuals may increase their inclusive fitness by cooperation, even if the increased reproductive benefits only apply to one of the individuals in his theory of kin selection (Hamilton 1964).

Box 1.12: Hamilton's Rule (Hamilton 1964)

In 1964, W. D. Hamilton published two papers titled The Genetical Evolution of Social Behavior in the Journal of Theoretical Biology to explain the theory of kin selection. He formulated a mathematical relationship that could explain how individuals could increase their own fitness by helping their relatives. An actor will only perform a costly action if the relationship $\mathbf{C<R*B}$, where $\mathbf{C}$ is cost in fitness to the actor, $\mathbf{R}$ is genetic relatedness of the actor to the recipient, and $\mathbf{B}$ is the fitness benefit to the recipient, holds true. This relation explains the driving force for many seemingly altruistic behaviors of related organisms and is the basis for the kin selection theory.

To test whether alliance formation in male bottlenose dolphins was influenced by kinship, Krutzen et al. tested relatedness in primary, secondary, and super-alliances. It was found that males in primary and secondary alliances were more closely related than expected by chance. However, super-alliance members were not significantly related. Relatedness of primary and secondary alliances may be explained by the theory of kin selection. Since super-alliances are not based on genetic relatedness, a large group must present other advantages for members. It is highly probable that super-alliances can compete more strongly against smaller primary and secondary alliances to secure more females (Krutzen 2003). Figure 1.17 shows a high correlation between association coefficient and relatedness in bottlenose dolphins ($p<0.01$), which supports the idea that alliances are related.

1.3.3.2 Reciprocal Altruism

In bottlenose dolphins, alliances form to help each other in foraging, predation, consorting females, and caring for young. This system of mutual assistance can be described by the theory of reciprocal altruism

(Connor & Norris 1982).

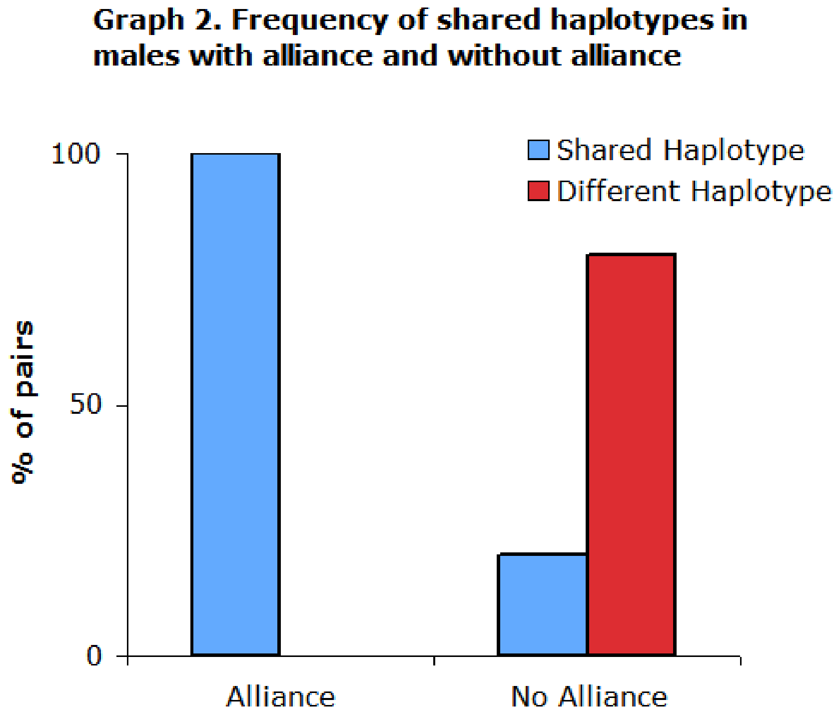

Figure 1.17: Reproduced from data in Parsons et al.

Reciprocity can occur independent of genetic relatedness (Trivers 1971). The model of reciprocal altruism consists of two parties, X and Y. X performs an altruistic act for Y, expecting that in return Y will perform an altruistic act for X. This increases the inclusive fitness of X (Connor & Norris 1982). However, what happens if X helps Y, but Y does not reciprocate? In order to prevent this situation of cheating, there must be a method for discriminating against a cheater (e.g. a partner who will not reciprocate). In a social society, like that of bottlenose dolphins, individuals communicate about the altruistic and cheating tendencies of other individuals. In a study by Marino et al., it was shown that dolphins demonstrate social knowledge, showing awareness of the behaviors and identities of others (2007). Because of the size of the society and the intermingling of individuals, dolphins must be able to recognize a high volume of individuals and identify them as ally or cheat. By sharing information on cheaters, bottlenose dolphins are able to discriminate against them. Consequently, the cheater's inclusive fitness decreases and the cheating gene will be selected against.

1.3.4 Conclusion

The bottlenose dolphin is an excellent example of how social alliances can benefit the fitness of individuals. Both direct and indirect fitness benefits are derived from social alliances which males use to acquire mates, dolphins use to gather food, and females or others use for defense. The direct fitness is derived from the improved opportunity for mates, food, or protection, but because certain members of the group get a disproportionate amount of these resources, related individuals are often allied to allow for indirect fitness benefits in which a relative is benefitted by additional resources. The specific dynamics of the dolphin alliances shed light on how and why they are evolutionarily advantageous while also providing interesting insight into the daily lives of these complex organisms.

1.3.5 Discussion Questions

1. What are some factors that may have allowed the specific types of alliances in dolphins to be selected for?
2. How does kin selection by dolphins satisfy Hamilton's Rule?

1.3.6 Glossary

- **Affiliative interaction**- interactions that occur to increase a sense of bonding among members of a group, such as contact swimming, petting, or rubbing in dolphins
- **Consort**- (n) a spouse or companion; (v) to habitually associate with
- **Conspecificity**- organisms that belong to the same species
- **Equivalence rule**- a theory that animals group things into classes of equivalent value and treat all members of a certain class as interchangeable
- **Estrus**- a period of time when females are sexually receptive and fecund
- **First-order alliance**- an alliance consisting of two or three males working together to consort a single female
- **Fission-fusion grouping pattern**- a form of social organization in which a large social group partitions into subgroups that change size and composition often
- **Haplotype**- alleles at multiple loci transmitted together on the same chromosome
- **Kin selection (Hamilton's rule)**- Genes should increase in frequency when rB>C, where r is the genetic relatedness of the recipient to the actor, B is the benefit gained by the recipient, and C is the cost to the actor
- **Inclusive fitness**- the sum of direct fitness (the individual's fitness) and indirect fitness (impact on fitness of social partners) weighted by the relatedness between the actor and the recipient
- **Labile**- tending to alter quickly and spontaneously
- **Male-biased**- the overrepresentation of males in a given population
- **Nested alliance**- an alliance within an alliance
- **Reciprocal altruism**- a form of altruism in which one organism provides a benefit to another and expects the benefit to be returned in the future
- **Second-order alliance**- an alliance consisting of males in first-order alliances working together to steal females from other alliances or to defend their own females
- **Triadic interaction**- interactions that occur in a group of three (A, B and C) where individuals attempt to band against an individual in the alliance (e. g. A and B versus C)

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1.3.8 About the Author

Figure 1.18

I am a sophomore Biochemistry and Cell Biology major from Dallas, TX. I enjoy drawing, painting, baking, and spending time with friends. In studying animal behavior, I am fascinated by learning about the motivation of organisms to behave in certain ways and how seemingly different behavior can be driven by similar principles. Most of the time, studying animal behavior proved easy mostly because it is interesting and applicable. I found myself often trying to relate what we learned in class to humans and trying to observe certain behaviors in my friends and myself.

1.4 The Evolution of Intergroup Coalitionary Aggression in Humans[4]

Author: Rachel Mis

1.4.1 Introduction: Human Aggression in Evolutionary Context

Warfare has often been interpreted as a sign of the perversion of human nature, a by-product of modern civilization, and absent from the balance of the natural world. However, it is now known that several species other than humans, including chimpanzees and even wolves, engage in **coalitionary acts of aggression** against other same-species groups, akin to human war (Wrangram 1999). This observation suggests that such behavior is in actuality an evolutionary **adaptation**, genetically passed on because it increases a perpetuator's **fitness** ((Durham 1976; Van Schaik, Pandit, and Vogel 2004; etc.). An understanding of the human behavior of intergroup coalitionary aggression would therefore benefit from the application of evolutionary behavioral theory (see Box 1.13 (What is Sociobiology)).

Evolutionary theories for intergroup coalitionary aggression center on the hypothesis that coalitionary aggression is an adaptive means of acquiring the resources of other groups, including territory, fresh water, food, tools, and even reproductive-age women (Buss 1997). The major perpetuators of coalitionary aggression are males, leading to the hypothesis that a major prerequisite for the occurrence of intergroup coalitionary aggression is an abundance of young males. Demographic studies indicate that males aged 15 to 29 years are most correlated with intergroup and interstate hostilities (Mesquida 1995, etc.).

This chapter will then explore the resource competition theory in humans with data from **anthropological** studies, as well as cross-species **comparisons with chimpanzees**, a close biological relative of human beings who also exhibit the behavior of intergroup coalitionary aggression (Wrangram 1999). In both cases, perpetuators may increase their fitness by co-opting resources of competing groups. Such evidence would support the hypothesis that human coalitionary aggression exists because under certain circumstances, the benefits gained by the young male perpetuators in resources and access to reproductive-aged females outweighs the potential costs suffered in the form of injuries and death, in line with the imbalance of power hypothesis. The chapter concludes with the implications of evolutionary theory and possible areas for future study.

Box 1.13: What is Sociobiology

Sociobiology involves the application of Darwinian theories of natural and sexual selection to the study of social behavior. Popularized largely by E.O. Wilson in his 1976 book *Sociobiology: The New* Synthesis, he describes the filed as “the systematic study of the biological basis of all forms of social behavior, including sexual and parental behavior, in all kinds of organisms, including man” (Wilson 1978). It relies on an interdisciplinary approach, drawing on fields as diverse as **anthropology**, zoology, evolutionary biology, population genetics, archaeology, and others. Though Wilson's work was met with controversy in regards to his application of his theory to human behavior, scholarship on the subject continues. Today sociobiology continues on as the fields of human behavior ecology, **evolutionary psychology**, evolutionary anthropology, and their subsets.

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[4] This content is available online at <http://cnx.org/content/m34750/1.3/>.

A young Maasia warrior-in-training (left) and American soldiers in Iraq (right).


(a) (b)

Figure 1.19: Coalitionary aggression, otherwise known as warfare, is found in varying forms across human cultures throughout history.

Available [5]

1.4.2 DEMOGRAPHIC PROFILES: Who engages in coalitionary aggression?

In his 1968 paper "Youth as a force in the Modern World," Herbert Moller observed that instances of violence in a society correlate with a large population of young adults within that society, and proposed that the presence of young people is thus a precursor to societal-level violence (Moller 1968). However, Moller failed to differentiate between the presence of young males and young females since males are the major perpetuators of coalitionary aggression; in fact, no historical or anthropological records exist of females forming groups to commit violent acts against other groups of females (Buss 1997). Theories now suggest that sexual selection explains the differences in aggressive behavior between the sexes (Archer 2009; Geary, Byrd-Craven, Hoard, Vigil, and Numtee 2003; etc.). Researchers Mesquida and Wiener expanded upon Moller's hypothesis to account for sex differences in acts of intercoalitionary aggression, proposing that it is the ratio of young *males*, aged 15 to 29 years, to *males* over the age of 30 years, within a society that can better account for occurrences of intergroup violence (Mesquida and Wiener 1995, Mesquida and Wiener 1999).

In a 1995 study, Mesquida and Wiener use data for 88 countries comparing the 1986 population ratio of males aged 15 to 29 years to males aged over 30, versus severity of conflict, measured as the number of conflict-related deaths from the period 1980 to 1993 (see Figure 1.20). The researchers found a significant relationship between the two variables (F = 79.25, p = .0001, r^2 = 0.47) (Mesquida and Wiener 1995). In addition, the researchers examined population and severity data from 15 republics during the dissolution of the Soviet Union, and again found a significant relationship (r = 0.63, p = .0112) (Mesquida and Wiener 1995) (see Figure 1.21). The researchers concluded that the presence of a large number of young males represents a situation in which engaging in coalitionary aggression is an advantageous strategy for this demographic (Mesquida and Wiener 1995). A later study offers additional support for this conclusion. By analyzing population and conflict-death data from additional samples, both from national and tribal levels, the researchers found that the prevalence of young men may account for approximately one-third of the variance in conflict-related deaths (Mesquida and Wiener 1999).

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[5] http://www.flickr.com/photos/72092071@N00/680459255 Available http://www.defense.gov/dodcmsshare/homepagephoto/2008-10/hires_081025-A-6851P-005b.jpg

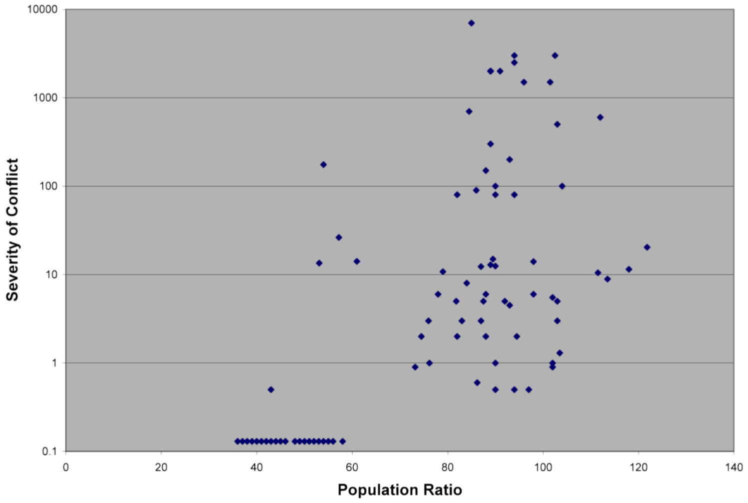

Figure 1.20: The relationship between population ratio (males aged 15 to 29 years per 100 males aged over 30 years) and conflict severity (death toll per million population per year) from 1980 to 1993 on a logarithmic scale. (*Adapted from Mesquida and Wiener 1995*)

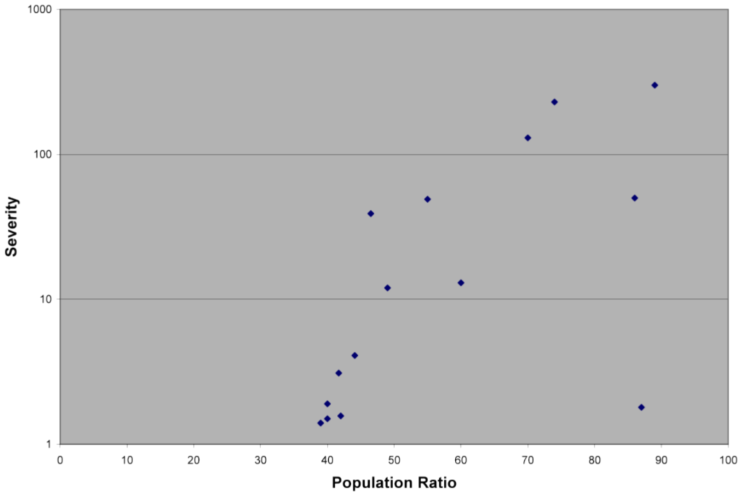

Figure 1.21: The relationship between the 1989 population ratio (males aged 15 to 29 years per 100 males aged over 30 years) and severity of conflict (total death toll per million population) from 1989 to 1993 on a logarithmic scale. (Adapted from Mesquida and Wiener 1995)

Box 1.14: How does testosterone affect aggression?

Although this chapter focuses on **ultimate causes** of human warfare, it is just as important to examine **proximate causes** in order to fully understand the nature of human aggression, such as the relationship between **testosterone** and aggression. Testosterone is the sex androgen believed to be responsible for masculine characteristics, and since females tend to have lower levels of testosterone as well as aggression, testosterone is assumed to have a causal relationship with aggressive behavior. In non-human animals, the hormone is known to be related to aggressiveness, and some studies have found a weak, positive relationship between testosterone levels and aggressiveness in humans as well (Book, Starzyk, and Quinsey 2001; Archer 1991). Testosterone levels have been shown to rise in males before engaging in competitive sports (Mazur and Booth 1998), and levels of testosterone can predict aggression in preschool boys (Sanchez-Martin, Fano, Ahedo, Cardas, Brain, and Azpiroz 2000). However, since studies in humans have largely been corrlational (Archer 1991), the exact nature of the relationship of testosterone in aggressive behavior in humans remains unclear.

1.4.3 Resource Competition Theory: Why do males commit coalitionary violence?

The **resource competition theory** of coalitionary aggression posits that individual male participants involved in coalitionary acts of aggression gain fitness through an increased access to fitness-enhancing resources, as women prefer to mate with men who are able to provide themselves and potential offspring with these resources (Buss 1989). In this model, aggressive acts may increase fitness either when resources are under the control of a competitor, wherein an aggressor would increase fitness by gaining access to the resource, or when access to a resource is threatened by a competitor, wherein an aggressor avoids a fitness loss by limiting competition (Durham 1976; Buss and Shackelford 1997). Additionally, coalitions of men may also directly compete for access to women; for example, among the Yanomamo tribes have been recorded to raid neighboring groups and kidnap reproductive-aged females (Chagnon 1983 cited by Buss and Shackelford 1997).

In order to determine whether groups of males are more likely to compete over resources or females, researchers Manson and Wrangham hypothesized that when resources are easily monopolized, conflict will likely occur over these resources. However, in circumstances where essential resources are not easily monopolized, conflict will likely occur over females themselves. To ensure that resources are in fact related to reproductive fitness, the researchers also hypothesized that in situations where resources are easily monopolized, the accumulation of wealth will be associated with **polygyny**, whereas when resources are not easily monopolized, polygyny will correlate with other factors, such as social ranking or ability to defend family. To test this theory, the researchers analyzed the anthropological literature for ethnographic accounts of autonomous societies dependent on hunting and foraging that at least occasionally engaged in warfare. The researchers recorded whether the societies fought over resources or females, whether resources were easily monopolized, and whether polygyny and wealth were related. Results were consistent with predictions (see Figure 1.22 (The relationship between cause of warfare and ability to monopolize resources. (Data from Manson and Wrangham 1991)) and Figure 1.23 (The relationship between polygyny and ability to monopolize resources. (Data adapted from Manson and Wrangham 1991))) (Manson and Wrangham 1991).

The relationship between cause of warfare and ability to monopolize resources. (Data from Manson and Wrangham 1991)

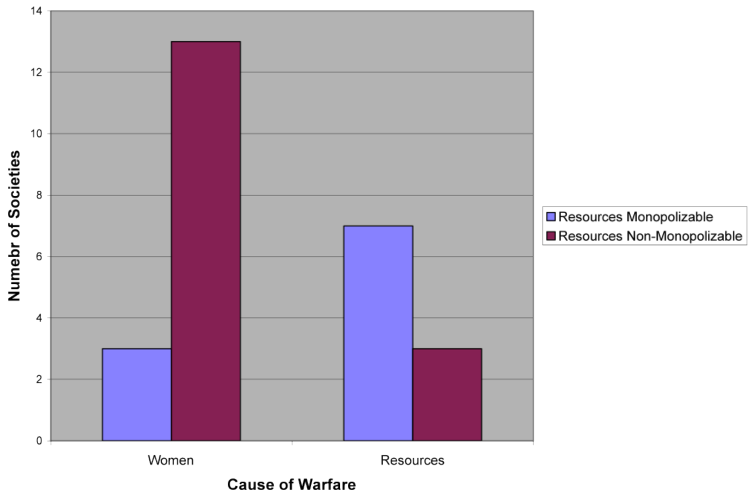

Figure 1.22: When resources are monopolizable, societies are more likely to go to war over resources. When resources are not easily monopolizable, societies are more likely to go to war in order to capture women.

The relationship between polygyny and ability to monopolize resources. (Data adapted from Manson and Wrangham 1991)

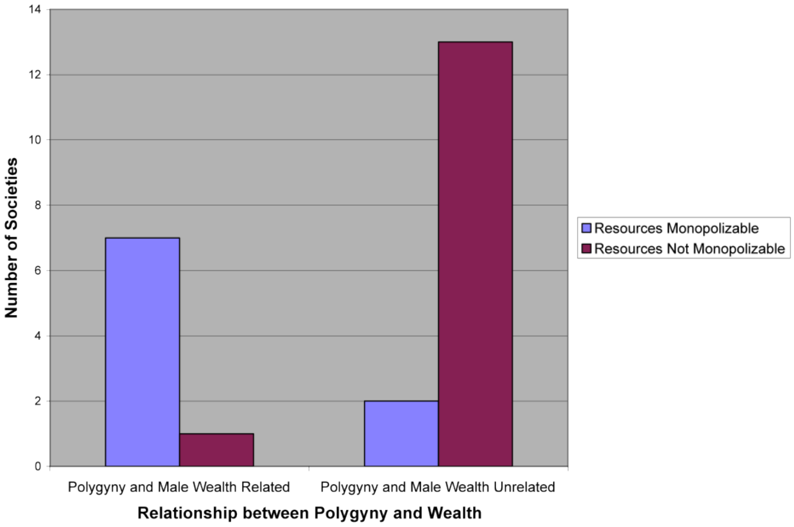

Figure 1.23: In societies where resources are easily monopolized, polygyny and male wealth are related. In contrast, in societies where resources are not easily monopolizes, polygyny is not related to male wealth.

The patterns of availability of resources also appear to correlate with occurrences of warfare. Outbreaks of war correlate with food shortages; war prevalence also correlates with the *threat* of food shortages or resource-depleting natural disasters (Ember and Ember 1992). In contrast, more peaceful interactions would be favored in conditions where resource supply is sufficient to exceed demand, groups are unlikely to come into contact with each other frequently, or an alternate resource is available to fulfill the same purpose (Durham 1976). Additionally, in regions where resources are generally very scarce, and availability differs between regions over time so that groups are forced to migrate in order to survive, cooperation with out-groups is favored over aggressive interactions. For example, Eskimos in more arctic areas migrate with the game, and seldom engage in aggressive behavior with passing neighbors. Groups that reside further south in areas which have a more consistent supply of game are far more likely to engage in violent conflict (Durham 1976).

However, in order for the aggressor to gain in fitness and outweigh the costs of violent behavior, the resource must sufficiently contribute to an increase in fitness, while the aggressor also must be sufficiently likely to defeat the competitor without suffering overwhelming reproductive costs (Durham 1976). Expanding upon this hypothesis, individuals would gain from joining groups to commit acts of aggression either in situations where the aggressive individuals themselves have access to the acquired resource sufficient to outweigh the potential fitness costs, while those who did not participate in the collective aggression do not benefit from increased access to the resource, or alternatively in situations where the aggressive individuals do not necessarily have direct access to the acquired resource, but do enjoy some other form of benefit from within the group sufficient to outweigh the fitness costs.

Factors contributing to Fitness Benefit	Factors contributing to Fitness Cost
Quality of resource	Size of competitors
Availability of resource over time	Strength of competitors
Distribution of resource in space	Technological state of competitor weapons
Possible uses of resource	

Table 1.2: In order for aggressive behavior to be favored, the fitness benefits must outweigh the costs incurred by the individuals involved (Durham 1976).

Box 1.15: Are other forms of aggression evolutionarily favored?

Evolutionary theory may also be applied to additional forms of human aggression. Buss and Shackelford propose seven situations in which aggression may have evolved as a possible situation, two of which – acquiring resources and preventing loss of resources – lead directly to intergroup coalitionary aggression. Other situations include:

- *Reduce fitness of same-sex rivals:* Members of the same sex often compete for access to the same resources as well as mates. By inflicting a cost on a same-sex opponent, an individual's relative fitness may increase. For example, both men and women engage in verbal derogation of the same sex in order to increase their own attractiveness to potential mates (Buss and Dedden 1990).
- *Increase social status within a group:* In some social contexts, men who expose themselves to greater physical danger in battle enjoy an increase in social status, which can translate into greater fitness (Geary and Bjorklund 2000). For example, among the Yanomamo of Venezuela, men who have killed other men are more likely to have more wives and children than men who have not killed (Chagnon 1988).
- *Discourage future aggression:* By promoting a reputation of aggressiveness, potential same-sex rivals may be discouraged from confronting an individual.
- *Discourage mates from cheating:* Jealousy by husbands or boyfriends is thought to be a leading cause of abuse by men against women. Men who are lower in relative mate value than their wives are more likely to commit aggression against their wives, in an attempt to prevent the woman from leaving (Buss and Shackelford 1997).
- *Prevent resource expenditure on unrelated offspring:* Parents are more likely to abuse step-children, who potentially may deprive one's own biological children of valuable resources (Buss and Shackelford 1997).

This evidence suggests that aggression is not a "monolithic" or "unitary" phenomenon; but instead is dependent upon context (Buss and Shackelford 1997).

1.4.4 Imbalance of Power Theory and Chimpanzees: When do males engage in coalitionary aggression?

Although controversial, many scientists believe that an understanding of human behavior may be augmented by the comparison of human behavior with that of other primates, particularly chimpanzees (*Pan troglodytes*). Humans and chimpanzees share many genetic similarities, and thus are believed to share a common evolutionary history (Manson and Wrangram 1991). While human intergroup coalitionary aggression was once considered unique in that humans will intentionally target and kill another human being, chimpanzees are now also known to target **conspecifics**. Termed lethal male **raiding**, groups of male chimpanzees sometimes invade neighboring territory belonging to a rival **community** and violently attack out-group chimpanzees, leading to serious injury or even death of the victim (Fukuyama 1998). This pattern of aggression is similar to that exhibited by small-scale human societies in raids, one of the most popular forms of coalitionary aggression (Manson and Wrangham 1991).

Similarities between Human and Chimpanzee Raiding
Conducted by groups of males
Victims unaware of impending attack
Aggressors intentionally seek opportunities to harm members of rival community

Table 1.3: Data from Manson and Wrangram, 1991

Figure 1.24: Both humans and chimpanzees engage in a similar pattern of intergroup aggression known as raiding.

Lethal raiding is hypothesized to occur in chimpanzees due to extremely low fitness costs compared with potentially large fitness benefits, consistent with the **imbalance-of-power hypothesis**. According to researchers Manson and Wrangham, this hypothesis predicts that attacks will occur in situations where the aggressor is unlikely to be harmed due to an advantage in force. Consistent with this prediction, the researchers found that, in a number of observational studies, no male aggressors suffered physical harm. Male aggressors only attacked solitary out-group individuals, or male-female pairings if the aggressor coalition consisted of at least three males; in other words, in situations where the aggressive individuals were unlikely to suffer injury (Manson and Wrangham 1991). The imbalance-of-power theory further postulates that chimpanzees will benefit from remaining in large groups in order to avoid potential attack. In border areas between communities, chimpanzees have been observed to travel in larger groups than when in the interior of the territory. Similarly, a highly popular strategy in human warfare, both between tribes or between nations, is also to overwhelm the opposing group in strength to avoid suffering as much injury as possible (Manson and Wrangham 1991).

Additional support for the idea that coalitions of chimpanzee males compete for reproductively-essential resources derives from research into territorial defense patterns (Williams, Oehlert, Carlis, and Pusey 2004). Chimpanzee males defend a group territory, within which live females and their offspring, as well as the resources sustaining the community. Food availability correlates with territory size, supporting the hypothesis that males defend a group territory in order to maintain an adequate supply of resources, most especially food. Females residing within larger territories - which correlate with higher resource supply - reproduce at shorter intervals, reinforcing the notion that higher resource supply enhances reproductive fitness. Additionally, males are less likely to attack out-group females who are reproductively-receptive, likely because it is more adaptive for the males to directly enhance their fitness by mating with these females (Williams, Oehlert, Carlis, and Pusey)

1.4.5 Conclusions

Throughout human existence, coalitions of people have engaged in violence for a myriad of social, political, and economic reasons. The evolutionary analysis of human behavior in no way implies that these methodologies are irrelevant, nor that evolutionary and social scientific methodologies are mutually exclusive. Each seeks to explain the same human behavioral phenomena from a different perspective. However, as revealed by evolutionary analyses, human societies engaged in intercoalitionary aggression do appear to share intriguing commonalities that can serve to further our understanding of the causes of human warfare.

> **Box 1.16: Are humans innately violent or peaceful?**
> Studying human aggression from an evolutionary perspective by no means implies that humans are innately violent. Cooperation is just as much a part of human social interactions as competition, and may also be approached from an evolutionary perspective (Fuentes 2004). For example, reciprocal altruism is ubiquitous among human societies and is also subject to evolutionary theory (Trivers 1971). As stated in this chapter, aggression must meet certain conditions before it is considered adaptive to the individual, which stated differently, means that there are conditions in which peaceful behavior is the adaptive strategy. Rather than thinking of human nature as inherently violent or inherently peaceful, it is perhaps more accurate to consider the situations and environmental stimuli that favor aggressive or cooperative behavior.

Research on warfare from an evolutionary behaviorist perspective using modern theories of individual natural selection appears to be limited. A complete and coherent view of the evolutionary nature of human coalitionary aggression remains elusive, and the field would benefit form an increased understanding of the evolutionary factors that lead humans into warfare. Human aggression is highly dependent upon social cues as well, so learning to understand these can help to reduce instances of aggression by making other, more peaceful options favorable (Lore and Schultz 1993). Any person, whether politician, scientist, or layperson, who seeks to understand human warfare and prevent further violence, can benefit from an increased understanding of the evolutionary basis of intercoalitionary aggression.

1.4.6 Discussion Questions

- From an evolutionary perspective, why would human females be less likely to engage in physical aggression?
- In what ways is intergroup coalitionary aggression an adaptive strategy for human males? For chimpanzee males?
- Under what circumstances are human males unlikely to engage in intergroup coalitionary aggression?

1.4.7 Glossary

- **Adaptation** – A trait that increases an individual's fitness.
- **Anthropology** – The study of human beings and ancestral species. It is frequently divided into the subfields of cultural anthropology, archaeology, linguistic anthropology, and physical anthropology.

- **Intergroup coalitionary aggression** – Violent behaviors committed by one group of humans against members of another group.
- **Community** – Term used to describe a group of chimpanzees.
- **Conspecific** – A member of the same species as another individual.
- **Cross-species comparison** – Method of study in evolutionary biology completed by comparing two species that exhibit a similar trait or behavior.
- **Evolutionary psychology** – The study of human psychological processes as products of evolutionary selection.
- **Fitness** – The genetic contribution of an individual to the next generation.
- **Imbalance of Power Hypothesis** – This theory posits that intergroup coalitionary aggression will only occur if the risk of costs to the aggressors is sufficiently low.
- **Polygyny** – Type of marriage system in which a man may have multiple wives.
- **Proximate Cause** – An explanation for a behavior or trait involving the biological mechanisms that result in the behavior or trait.
- **Raiding** – Type of coalitionary aggression in which one group invades the territory of another group in order to obtain resources or harm members of the rival group.
- **Resource Competition Theory** – This theory posits that male intergroup coalitionary aggression evolved as a strategy for obtaining resources. According to this theory, greater control of resources results in an increase in fitness.
- **Sociobiology** – A field, developed largely by E.O. Wilson, attempting to study social behavior in terms of evolutionary theory.
- **Testosterone** – Male sex hormone essential to the development of male reproductive organs. Testosterone is hypothesized to play a role in aggressive behaviors in humans, though the precise nature of the relationship remains unclear.
- **Ultimate Cause** – The evolutionary explanation for the existence of a behavior or trait.

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Van Schaik, Carel P., Pandit, Sagar A., Vogel, Erin R. 2004. A model for within-group coalitionary aggression among males. Behav Ecol Sociobiol. 57: 101-109. This article explores the formation of coalitions among primate males. It examines the conditions under which coalitions may form, and proposes a model for the formation of ranks and rank-changing within these coalitions. It then applies this model to non-human primate examples.

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42: 1-30. This article proposes an explanation for the presence of intergroup coalitional aggression, called the "imbalance-of-power hypothesis." This hypothesis suggests that intergroup coalitional killing, observed in species such as humans, chimpanzees, and wolves, is an evolutionary adaptation to achieve dominance over one's neighbors. This paper will likely provide essential information in the form of an evolutionary explanation for the presence of intergroup aggression in humans.

1.4.9 About the Author

Rachel Mis will graduate from Rice University in May 2010 with a BA in psychology, after which she hopes to travel the world before attending graduate school in psychology. She loves dogs, coffee, silly conversations, and attempting to unravel the mysteries of the human mind.

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Photo by friend of the author

Chapter 2

Sexual conflict, and sometimes cooperation

2.1 The Role of Evolution in Mating Behavior of Lekking Species[1]

Author: Kirby Kempe

2.1.1 Introduction

The wide variety of mating systems and display behaviors in the animal kingdom today represents species' adaptation and co-adaptation to their environments. Mating behavior is determined both by ecological conditions and by differences in parental care and family organization. Mating behavior can be classified as monogamous or mating multiply, though there are multiple subsets of each broad classification. For example, in a polygynous species, one form of mating multiply, one male can mate with multiple females, whereas in a polyandrous species, one female mates with multiple males (Box 2.1 (Mating Systems)). Whenever individuals of one sex can mate with multiple individuals of the other sex, it follows from sex ratio arguments that some to many individuals of the multiple mating sex will not get to mate at all. Species that mate multiply, as opposed to monogamous species, are far more common in the animal kingdom and life-pairs are extremely rare. In fact, the most common system is one in which no bond is formed whatsoever and there is no care by either parent, known as promiscuity. However, even among only multiply-mating species, mating behavior varies widely. Natural selection has worked to favor elaborate courtship rituals and complex mating displays that underline the process of **sexual selection**, giving rise to species that spend much of their time and energy attracting a mate. Perhaps the most puzzling of these displays, known as a lek, is the large aggregation of displaying males that females interact with solely for the purpose of procreation (Kokko 1996).

Box 2.1: Mating Systems

Monogamy: Research suggests monogamy occurs when there is no potential for polygamy or for taking advantage of limited polygamy potential. It is estimated that over 90% of avian species are monogamous, but monogamy is very rare among mammals (Emlen et al. 1977). It is hypothesized that monogamy is advantageous when male territories are small and equal and the cost of mating is high, so polygynous females are at a disadvantage, and where male assistance is necessary to raise offspring so the male rears more successful offspring more by assisting one female than by mating multiply (Clutton-Brock 1989).

Polygyny: Polygyny occurs in situations where behavioral and/or environmental conditions cause females to clump together, where males either monopolize them directly or by hoarding

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[1] This content is available online at <http://cnx.org/content/m34752/1.3/>.

resources and mate with the same group multiple times (Emlen et al. 1977, Clutton-Brock 1989). Polygyny is seen in many marsupials, carnivores, and rodents (Clutton-Brock 1989). Polygyny is most common when male home ranges overlap with those of several females as opposed to monogamous ranges overlapping with that of only one female (Clutton-Brock 1989).

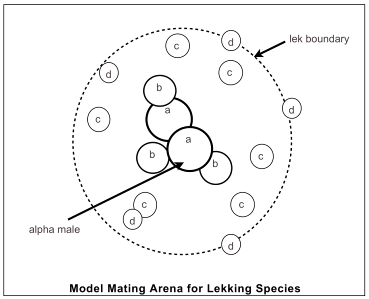
Polyandry: Females can monopolize males if resources are congregated and able to monopolize or by defending and directly controlling males (Emlen et al. 1977).

While these are the main systemic classifications, some species alternate between variations of these while some mate in different arrangements altogether.

Scientists have studied lekking behavior intently, as it appears paradoxical at its very foundations. The **epigamic** displays often result in significant escalations, leading to the formation of a dominance hierarchy, which serves to establish a rough predictor of mating success in the next generation (Dastagir 1997). Males in the lek defend individual territories, but these territories contain no resources or other benefits to the females (Isvaran 2003). Female choice among the males of the lek is easily observed, but traditional evolutionary approaches and natural selection principles would predict that female choice would eliminate the variation in the traits for which they are selecting, eliminating the great diversity that characterizes a lek. Additionally, the tendency of competing males to establish and defend territories in such a cluster seems paradoxical, as the density of these territories would traditionally escalate the cost of aggression among the males in addition to adding the cost of attracting predators (Isvaran 2003). The growth of female choice alongside the stability of male variation has given this mating behavior the title of the "lek paradox" and has forced scientists to propose various models to explain the behavior (Hamilton 2006). This chapter will address the strengths and shortcomings of the "hotshot," "hot spot," and '"preference" models, which are the most common explanations for lekking behavior in animal species, as well as evidence for other possible explanations of lekking behavior.

2.1.2 Overview of Lek Organization

The organization of a lek sets the foundation for the behaviors demonstrated by lekking species. Within the boundary of the lek, each male displaying holds his own display territory, but individual dominance displays vary (Westcott 1994). In an extreme lekking species, multiple males share an area inside which they compete for individual success. On the other extreme, males simply divide the lek into territories and any disruption in mating activities is limited to that between neighbors (Gibson 1987).



Model Mating Arena for Lekking Species

Figure 1 - This shows the basic organization of territory distribution for males in a lek. Alpha males (a) have the largest territories, with territory size decreasing with position in the hierarchy. Figure adapted from Starr, Hall.

Figure 2.1

The organization of a lek sets the foundation for the behaviors demonstrated by lekking species. Within the boundary of the lek, each male displaying holds his own display territory, but individual dominance displays vary (Westcott 1994). In an extreme lekking species, multiple males share an area inside which they

compete for individual success. On the other extreme, males simply divide the lek into territories and any disruption in mating activities is limited to that between neighbors (Gibson 1987).

When females visit the lek, they do so only for the benefit of copulation and choose their mate free from any coercion from the male (Westcott 1994). The allocation of territories and the lack of economic benefit to the female that could have been derived from the male's land do not seem to have any role in mate selection (Reynolds 1990). The paradox of the lek enters in discussing the preferences of the female. Often on lek, females will show strong preference for and consensus in mate choice, regardless of the fact that the male she is choosing contributes nothing more than genes to her offspring, and the genes that correspond to the traits selected for don't contribute to the fitness of her offspring to a significant extent (Reynolds 1990). In other instances, the desperate displays of the males have no significant influence on the female's choice and do not benefit him at all.

The original three proposed models to account for lek formation are the "preference," "hotspot," and "hotshot" models. The preference model hypothesizes that leks persist because they are more advantageous for males and/or females than mating at isolated sites, in ways such as decreasing the costs associated with searching for a mate or giving honest signals as to the strength and fitness of the males on lek (Westcott 1994). The hotspot model suggests that female movement patterns and behaviors are the cause of lek formation and males lek in areas of highest female density (Westcott 1994). The hotshot model proposes that, due to the inherent variation in mating success, less successful males tend to cluster around successful males in order to intercept some of the females that are attracted to the "hotshots" (Westcott 1994). To date, scientists have been unable to solve conclusively the lek paradox. Evidence of varying strength and reproducibility for and against these models has been found in various species of lekking animals, and additional hypotheses have developed through observation. For example, some scientists have proposed kin selection as an explanation for the formation of leks, while others support the importance of networking within the lek as a predictor of alpha male fecundity.

Breakdown of Hypotheses and Supporting/Refuting Sources

Hypothesis	Species	Overview	Literature Cited
Preference	Black grouse	Females visit larger leks more often	Alatalo et. al, 1992
	Topi antelopes	- Central males are significantly larger- Females choose to mate more when other estrous females are present	Bro-Jørgensen et. al, 2002
	Blue-crowned manakins	- Mating based on display patterns and vocalizations- No mating bias toward larger leks- Prefer males that display more	Durães, 2009Durães et. al, 2009

continued on next page

	Mathematical model	Mating bias manipulations had greatest effect on males	Isvaran et. al, 2003
	Moor frogs	Males no more closely related than expected by chance	Knopp et. al, 2008
	Cichlids	- Average female encounter rate increases with size- Preference for males on larger leks determined indirect choice rather than direct assessment	Young et. al, 2009
Hotspot	Manakins	- Correlation between female home range and male clustering- Males settle at sites with high female traffic	Théry, 1990
	Neotropical birds	- Hotspots initiate and determine location of aggregation and other factors (predators, resources, etc.) modify size	Westcott, 1994
Kin Selection	Black grouse and ruff	- Number of copulations, per capita, increases with lek size- Small lek: inclusive fitness is high as new males increase lek size/attractiveness- Large lek: negative as alpha males can no effect longer monopolize females	Kokko et. al, 1996

continued on next page

	Manakins	- No more related than by chance- Relatedness and distance found inversely related- Mean relatedness is negative	Loiselle et. al, 2007McDonald et. al, 2009

Table 2.1

2.1.3 The Preference Hypothesis

Perhaps one of the most widely supported models, the preference hypothesis attributes lek formation to the benefits that accrue to either males or females, or both, by mating in a lek as opposed to mating individually, the traditional approach to reproduction in the animal kingdom (Dastagir 1997). Among the benefits to females proposed as explanations are size, i.e. the ability to compare more males at a lower cost, preference, i.e. the ability of females to compare and then to mate only with males that display most vigorously, and “good genes,” i.e. the ideal that only males with well-adapted genes will be able to control and win all of the escalations that occur in order to maintain status as the alpha male (Alatalo et al. 1992, Durães et al. 2009, Young et al. 2009). Other research has shown lek formation being driven by benefits that accumulate for males in the natural pattern of male clustering at sites of high female traffic (Théry 1990).

2.1.3.1 Support

2.1.3.1.1 THE MANAKIN

Support for the preference hypothesis as an explanation for lek formation has come from studies on a very diverse array of species, from mammals such as the topi antelope to amphibians such as moor frogs. A study conducted by researchers at the University of Missouri-St. Louis followed blue-crowned manakins (*Lepidothrix coronata*) at a site in Ecuador to monitor the behavior of the organisms and determine patterns between and within leks (Durães et al. 2009). Part of the preference hypothesis proposes that females choose mates based on the size of their lek and that the females strongly prefer mating with males on larger leks. The study established male to female ratio between leks as an accurate indicator of this aspect of the hypothesis for a high ratio of females to males at larger leks would indicate that the females either actively or passively chose to mate with males on larger leks.

Figure 2.2: Blue-Crowned Manakin
http://farm4.static.flickr.com/3253/2537888503_94b7b41b23.jpg

Support for the preference hypothesis as an explanation for lek formation has come from studies on a very diverse array of species, from mammals such as the topi antelope to amphibians such as moor frogs. A study conducted by researchers at the University of Missouri-St. Louis followed blue-crowned manakins (*Lepidothrix coronata*) at a site in Ecuador to monitor the behavior of the organisms and determine patterns between and within leks (Durães et al. 2009). Part of the preference hypothesis proposes that females choose mates based on the size of their lek and that the females strongly prefer mating with males on larger leks. The study established male to female ratio between leks as an accurate indicator of this aspect of the hypothesis for a high ratio of females to males at larger leks would indicate that the females either actively or passively chose to mate with males on larger leks.

The study also used relationships within leks to test the hypothesis that females choose mates that will maximize **heterozygosity** of their offspring. The theory of heterozygosity stems from the fact that sexual reproduction is costly because it carries with it the potential of accumulating in the offspring the parents' inferior recessive alleles (Brown 1997). If females were able to choose mates to increase heterozygosity, this would decrease the chance of their offspring suffering from recessive homozygosity. Another benefit of heterozygosity is that it diversifies the genes of the offspring, increasing potential for adaptation to the environment, should it change. Thus, studies have shown that heterozygous males tend to have progeny that are more successful than the average in a fluctuating environment. Studies across many species have determined heterozygosity to be advantageous in areas such as pathogen resistance, growth rate, and developmental stability (Brown 1997). Thus, the University of Missouri-St. Louis study also controlled for among-lek variations and looked at mate choices within individual leks to determine whether females chose mates that were able to maximize heterozygosity in progeny. The study used vocal signaling as an indicator of heterozygosity, as it is costly and easily accessible as an honest signal to females (Durães et al. 2009). The quantifiable objective of this party of the study, then, was the correlation between vocal display and fitness in number of offspring, with the predation that more vocal males will produce more offspring because vocalizing is an honest indicator of heterozygosity (Durães et al. 2009).

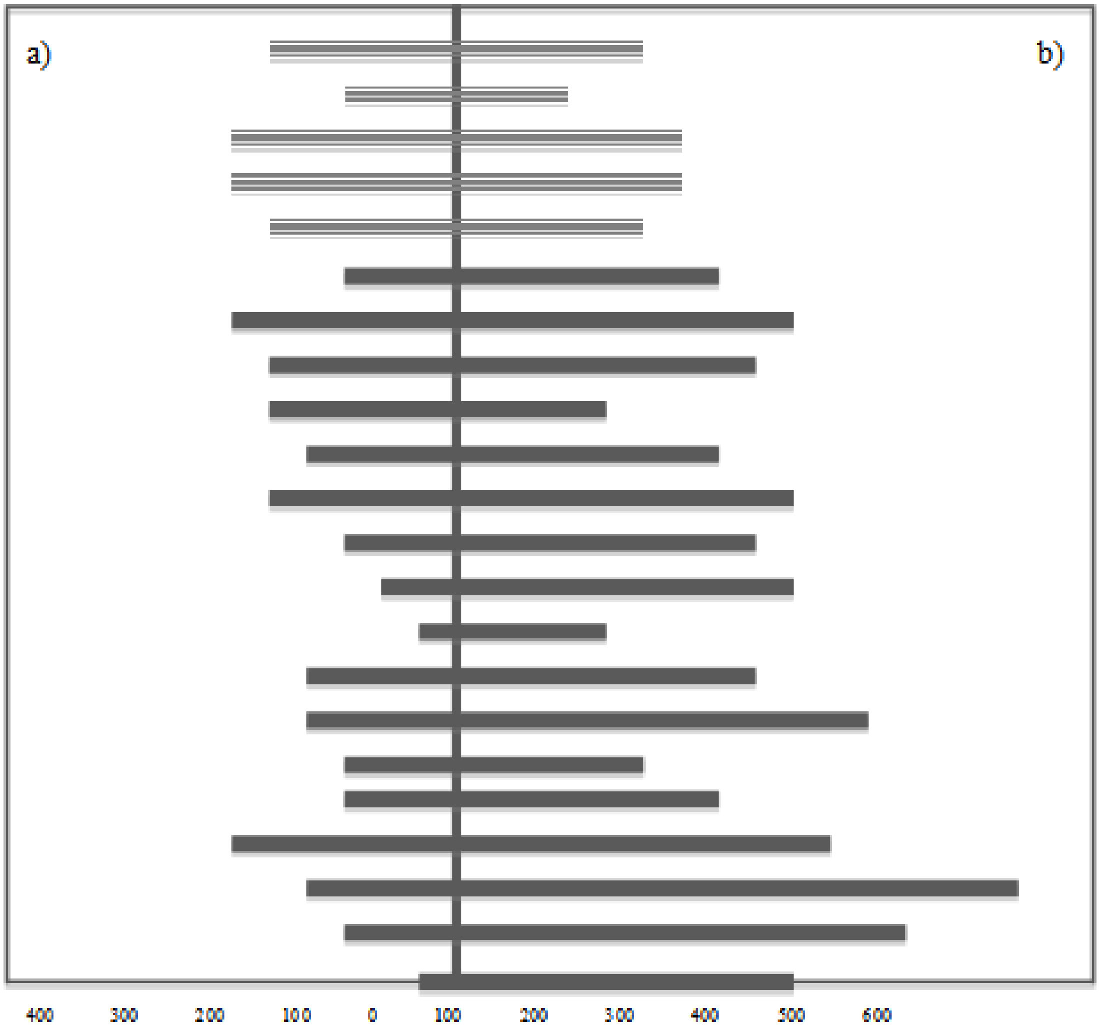


Figure 2.3: Side a) represents the distance between the females' nest and the edge of the nearest lek. Side b) represents the distance between the nest and the lek of the male with which the female mates. The top striped bars represent females nesting at the closest lek.

The evidence of female preference was found in the distance the female manakins traveled in order to mate. If females had no preference of lek, they could be expected to mate at the lek closest to their current location in order to minimize search costs. However, the results of this study found that only 33% of females mated at the nearest lek and most mated at leks located significant distances from the lek nearest to their nest (Durães et al. 2009). This shows that females did, in fact, have a preference for where they mated, and the preference seemed to be based on size of the lek. Females that passed up the nearest lek to mate elsewhere were located close to a lek that was significantly smaller than the one at which they chose to mate. In other words, the lek closest to the female's nest was very small so the females chose to travel a greater distance in order to mate at a larger lek. However, females that were nesting in close proximity to an average-sized lek were no more likely to visit a larger lek than the one nearest them.

In determining whether heterozygosity was a factor in the mating choices of females, the researchers found that the male manakins increased vocal displaying on larger leks but that the rate of vocalization did not reflect heterozygosity of the male or of his offspring (Durães et al. 2009). However, the males that females chose to mate with did vocalize more than non-siring males on a given lek. This indicates that the investment of vocalization is effective in increase a male's probability of producing offspring and that male success is limited by the extent to which they are able to increase display (Durães et al. 2009).

Box 2.2: Fisherian Model of Female Preference

The Fisherian model proposes that female preference is rooted in selection for traits that yield reproductive advantage in males and male progeny. Fisher holds that these traits are distinct from those acted upon by natural selection and only confer advantage in sexual selection by female preference (Kodric-Brown 1984).

The overall conclusion of the study supports a subset of the preference model called the "best-of-n" hypothesis (Durães et al. 2009). The "best-of-n" males is a model describing female mating behavior that describes female behavior as choosing the best of n males she encounters (Janetos 1979). This model is unique in that it requires the assumption that females have a memory capacity, and the capacity may be measured by the size of n. Additionally, in the case of leks, a female might encounter the first of n males on one lek and the last in another lek. If the best of n is in the first lek, the model requires that the female is able to return to the first lek and mate with that organism (Janetos 1979). The results of this study support the best-of-n model over strict female preference because while female preference is a main condition for determining which organism is "best," the females who were able to encounter n males at a nearby lek visited only that lek, whereas females who were nesting close to a lek of smaller size than n were forced to travel until they came upon another lek in which to find the best. Strict female preference, on the other hand, indicates that the act of being at a larger lek benefits males.

The preference indicated by this study is consistent with the Fisherian model (Box 2.2 (Fisherian Model of Female Preference)) of female preference, first proposed by Fisher in 1930 (Kodric-Brown 1984). Because the vocal displays of the males are sexually selected and heritable, the Fisherian model predicts that females who mate with the dominant males may actually increase the fitness of their offspring by other indirect means such as "attractive" genes that caused the female to mate with the male on lek. Because the display behavior of the males is determined at least in part by the males' natural abilities and instincts, female preference for males that show this behavior serves to increase the fitness benefits and mating success of the offspring (Durães et al. 2009).

2.1.4 The Hotspot Hypothesis

Another theory on lekking behavior is known as the "hotspot" hypothesis. This theory proposes that leks form as an aggregation of males each settling in an area where females are most likely to pass by (Théry 1991). Thus, male clusters are expected to occur in regions of high female density or in regions determined likely to encounter females based on studies of female dispersion patterns (Westcott 1994). While perhaps less supported than the preference model, the hotspot model is appealing to many scientists as a result of its congruity with generally-accepted knowledge of the fundamentals of mating systems. Leks provide an opportunity to study mating fundamentals, because in leks, males contribute only sperm and are therefore able to act solely out of concern for maximum reproductive success without the confound of providing parental care to offspring. Logically, then, the hotspot hypothesis of leks is a natural phenomenon of male behavior as a function of female behavior, which is to be expected in a mating system where males are focused solely on genetic distribution (Westcott 1994).

2.1.4.1 Support

2.1.4.1.1 MANAKINS

Figure 2.4: White-crowned manakin

The manakins (Pipridae) are a group of approximately 40 different Neotropical bird species characterized partially by their lekking behavior (Prum 1990, Théry 1991). **Sympatric** manakin species demonstrate various distributions of clustering, but lekking display to some degree is present in all manakin species (Théry 1991, Prum 1990). Manakins are noted and selected for their bright plumage displays, and thus **sexual**

selection has led to strong **dimorphism** in male characteristics (Prum 1990). Male birds are selected for bold, bright patterns of black and white with very bright colors while females are more camouflaged in greens and yellow. Manakins are traditionally **frugivorous**, feeding on fruits similar to other tropical birds. Manakin displays tend to vary among species. Some display on tree branches and limbs while others perform their mating dances on fallen logs or in cleared patches. Behaviors also vary in complexity, which many species demonstrating simple callings and flights while others show orchestrated wing noises, postures, flights, and patterns (Prum 1990).

Figure 2.5: Golden-headed manakin

A study by Marc Théry in French Guiana followed six species of manakins, white-crowned (*Pipra pipra pipra*), golden-headed (*P. erythrocephala erythrocephala*), white-fronted (*P. serena serena*), white-bearded (*Manacus manacus manacus*, white-throated (*Corapipo gutturalis*), and thrush-like (*Schiffornis turdinus wallacii*) for 3 years, banding them and studying mating and breeding behaviors as well as movement patterns (Théry 1991). The researchers found that the female manakins stayed within their **home ranges** when courting and visiting males. Additionally, the location of the leks was always near regions of climaxing feeding activity of females. When studying the ranges of different females, researchers noted that females visiting males on the same lek showed overlapping home ranges and the male manakins were found to settle in regions of high resource density, where female traffic was highest. These observations show strong support for the hotspot theory, with males aggregating in "hotspots," or regions that attract high densities of females (Théry 1991).

This study also demonstrates the importance of fluctuations in food supply on the breeding season of manakins (Théry 1991). Females tended to favor certain nutrient resources over others, and males congregated around these regions of fruit density during breeding seasons. Thus, breeding success is positively correlated with fruit supply and resource distribution shows itself to be a driving force in communal displays (Théry 1991).

2.1.4.1.2 NEOTROPICAL BIRDS

Researchers at the University of British Columbia in Canada conducted another study supporting the role of hotspots in lekking behavior. They followed four neotropical bird species, the ochre-bellied flycatcher (*Mionectes oleaginous*), red-capped manakin (*Pipra mentalis*), blue-crowned manakin (*Pipra coronata*), and long-tailed hermit hummingbird (*Phaethornis superciliosus*) (Westcott 1994). The researchers monitored annually male displaying behavior and location of lek center in canopy trees in Corcovado National Park in Costa Rica. The lek distributions were also analyzed for any correlation with geographic qualities of the area that would have an influence on them, such as waterways and drainage.

The results determined an underlying factor that affects the lek location distributions of all four species, and the researchers propose the geographic features as probable causes. The four species all demonstrate similar movement through the canopies and therefore are expected to show the same effects of the influence of the geography. The features of the land focus the movements of the females, causing males to cluster in these areas (Westcott 1994).

The potential influence of predators on lek distributions was overruled because, in 500 hours of study, only two instances of predation were noted. If the males were congregating to take advantage of the ability of clusters to fare better against predators, the other leks should be expected to notice the attacks. Contrarily, however, the calling of the other leks had no correlation with predation. It did not stop in response to the predation of neighbors and it did not increase to signal the arrival of a predator (Westcott 1994).

The study concluded in support of the hotspot hypothesis under certain conditions. Because an area of higher female density, where males are likely to visit, is likely to be very large to accommodate all of the females, many proclaim that it is unlikely to produce the clustering of males that characterizes a lek. However, the researchers at the University of British Columbia claim that if other factors are severe enough to constrain the movement of females, hotspot explanations alone may be sufficient to explain the leks (Westcott 1994).

2.1.4.2 Opposition

A study conducted by Jakob Bro-Jørgensen and other researchers from the Institute of Zoology in London refuted the hotspot hypothesis in a study on topi antelopes. Antelopes lek similarly to manakins, with this study focusing on leks of between 11 and 14 males each, visited by groups of up to 40 females (Bro-Jørgensen 2002). The hotspot hypothesis predicts that resource density would be greatest on lek as benefit to the females, which, in turn, attracts the lekking males. Instead, the results of the study determined the land on leks to be nutritionally deficient. The ground was bare and females grazed off lek close to 7 times more often than they grazed on lek (Bro-Jørgensen 2002). This indicates that the females gained no benefit in resources from the location of the lek, which refutes the hotspot hypothesis.

2.1.4.3 The Hotshot Hypothesis

While the preference model suggests that females are biased towards aggregated males in general, the hotshot model proposes that females show a preference for particular individual males (Young 2009). The theory claims that leks form as aggregations of inferior males around the preferred "hotshots" in attempts to increase their successes in attracting females by intercepting the females attracted to the hotshot. This theory leads to the logical prediction that preferred males should display in central territories with inferior males aggregated about them (Young 2009).

Figure 2.6: Lake Malawi Cichlids

2.1.4.3.1 Opposition

2.1.4.3.1.1 CICHLIDS

A study performed in Africa by Kyle Young followed the behavior of a species of **bower**-building cichlid fish, *Nyassachromis cf. microcephalus* (Young 2009). Male bowers are volcano-shaped nests that males defend and territorialize in their courtship of passing females. This species is native to Lake Malawi, Africa, and demonstrates many characteristics that suit it for studying lek behavior. The male cichlids build bowers that are easily quantified in size and their reproductive behaviors are easily assigned cost and benefit figures. Additionally, researchers can easily study female choice, as males of this species do not actively pursue females but rather court them as they pass the males' bowers. Variation in courtship rates is therefore a result of female, rather than male, choice because the males play no role in the coordination of a partnership. Finally, the series of mating behaviors in this species relies first on indirect female choice, in swimming past a male's bower, then on direct female choice, as the female assesses the pursuing male and his bower and determines whether to proceed with the mating process (Young 2009).

Researchers followed three different leks for one week during peak mating season, documenting every instance of a male beginning courtship with a female, acting out of aggression toward a male of the same species, acting aggressively toward a male of a different species, building his bower, and engaging in foraging behavior. The researchers then created a correlation matrix relating the position and size of the bower, male behaviors, and female interest.

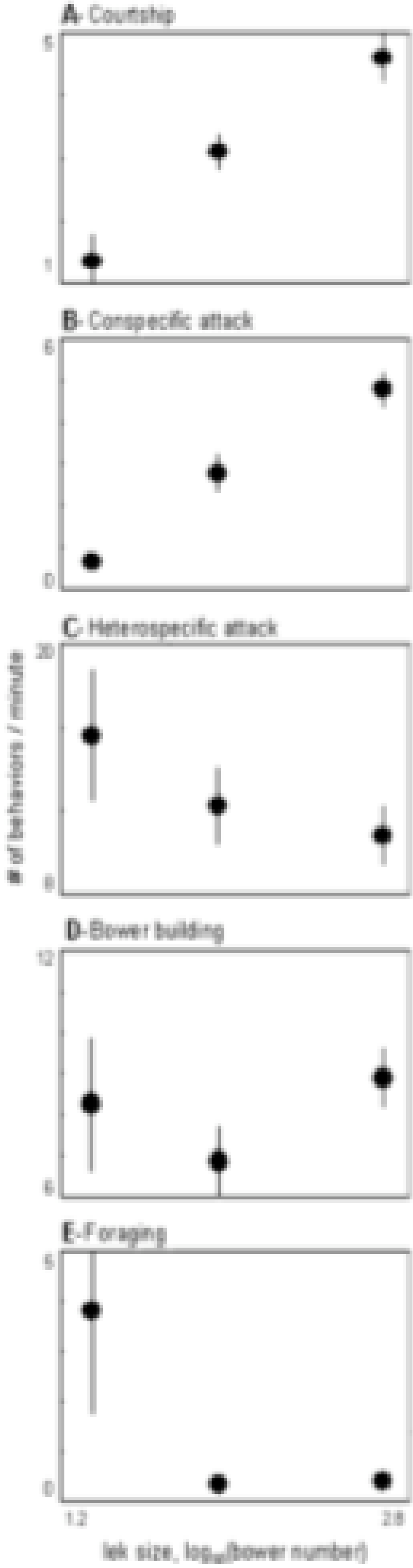


Figure 2.7: Results showing courtship, conspecific attack, heterospecific attack, bower-building, and foraging behaviors as a function of lek size Young 2009

The results of the study, however, did not show support for the hotshot hypothesis. Researchers determined a negative correlation between **conspecific** attack rate and bower location, which suggests that there is, in fact, an added cost that the hotshots must bear to hold the central lek territory, but this did not affect their encounter rate with females (Young 2009). In other words, lek position, bower size, and attack rate had no correlation to courtship initiation by females. Additionally, none of these factors correlated significantly with the reproductive success of the cichlid males either. In further evidence against the hotshot theory, once courted, females did not show any direct preferential selection for males holding territories in the center of the lek.

2.1.5 The Kin Selection Hypothesis

This chapter will conclude with a brief analysis of the support and opposition for kin selection as a mechanism of lek creation and persistence. Although kin selection is not a distinct hypothesis in itself, it can play a role in any of the mechanisms proposed to explain lek behavior. Kin selection is a common evolutionary explanation for the basis of many animal behaviors. At heart, the theory proposes relatedness as an explanation for behaviors that would otherwise prove disadvantageous for an organism. An organism can pass on its genes directly, through traditional reproduction, or indirectly, by increasing the reproductive fitness of its relatives who share its genes (Hamilton 1964). Thus, it is oftentimes more advantageous for an organism to forgo reproduction in order to assist in the reproductive efforts of his kin. Researchers see potential for the explanation of the group mating structure of leks in terms of kin selection and increased relatedness between members. One of the biggest conundrums of the lek system comes from trying to understand the role of lesser males on the lek. Numerous studies have shown a positive correlation between lek size and frequency of female visits to the lek (see The Preference Hypothesis), which indicates that these lesser, unsuccessful, males are actually increasing the fitness of their more successful counterparts (Petrie 1999). When considering full benefit to the organism, including indirect benefits, this behavior can be understood if the successful males are closely related to the unsuccessful males. Because lower ranking are very unlikely to successfully copulate, theoretical evidence predicts that they join leks where the dominant male is closely related so that they receive indirect benefits (Loiselle 2006).

Box 2.3: Hamilton's Rule

Hamilton's Rule is a simple and effective method for analyzing indirect benefits and inclusive fitness. The rule states that a behavior with benefit b and cost c to an organism, with relatedness r between organism and partners in the act, is evolutionarily favored if

$rb - c > 0$

(Hamilton 1964)

2.1.5.1 Support

2.1.5.1.1 PEACOCKS

Peacocks establish their permanent display areas in the lek during their fourth year and return to this site every year, where they remain for the duration of the mating season (Petrie 1999). Peacocks are traditional lekking organisms in that the males play no role in reproduction once copulation is complete. On lek, the males are oftentimes as close as 2.5m from one another. Peacock leks demonstrate many characteristics of any classic lekking species. The peacocks congregate in large display arenas and call together, as a group, to attract the peahens. A peahen's arrival at the lek signals the males to stop calling and instead display their tail **coverts** in competitive display behavior. Like most leks, the success of the displaying males is very skewed and the majority of the peacocks receive no copulations in return for their elaborate calling and displaying.

Box 2.4: Multilocus Fingerprinting
DNA fingerprinting is used across a wide range of disciplines, such as ecology, population genetics, conservation, and breeding. Multilocus fingerprinting is often the preferred method for determining parentage and genetic variability. This method has also been used to "distinguish between... crops, between sexually reproducing... berry species, and to establish paternity in apples" (Bruford 1998).

Marion Petrie and researchers at the University of Newcastle, UK attempted to determine the relatedness of peacocks on leks to conclude whether relatedness plays a role in the persistence of group display behaviors in the species. They studied 4 peacock leks at Whipsnade Park, UK, totaling 21 organisms (Petrie 1999). They used **multilocus fingerprinting**as a method of determining relatedness among the peacocks, as closely related individuals share a greater number of bands. Petrie and team compared the degree of relatedness in peacocks within the same lek to peacocks between leks and found the organisms on the same lek to be more closely related, to about the degree of half-siblings (Petrie 1999).

Figure 2.8: Peacock
http://s0.geograph.org.uk/photos/08/39/083993_a0152c68.jpg

Because the males do not assist in the rearing of young, birds have no opportunity to learn the identity of their father, which makes Petrie's results surprising. One possible explanation could be that the peacocks simply don't disperse far from their nests, but the results of Petrie's study refuted this by showing that the birds need not even be born in the park for them to show preference in displaying with kin. In fact, "when the birds established their permanent adult display sites several years after their release there was a clear tendency for known brothers or half-brothers to display close together" (Petrie 1999).

Another possible explanation for this behavior is that the related birds have a genetically based preference for a particular type of display site. In other words, they don't actually choose the site based on the fact that relatives are there but indirectly lek with relatives because they all prefer the same type of location. However, this, too, can be refuted because the male peacocks showed no preference in lekking on the sites at which their fathers lekked. If the genetic basis of preference is true, it can be expected that they would share the preference with their father as well. Because this is not seen in the data, the explanation can be rejected (Petrie 1999). The researchers then concluded that kin selection is a viable explanation of the results, with the benefits of inclusive fitness due to relatedness outweighing the costs of forming a lek and displaying communally.

2.1.5.2 Opposition

2.1.5.2.1 MANAKINS

Two separate studies on manakins, one headed by Bette Loiselle at the University of Missouri-St. Louis and the other by David McDonald, oppose the findings of Petrie. The Loiselle study covered 4 manakin species (*Pipra filicauda, Pipra pipra, Lepidothrix coronata,* and *Chiroxiphia pareola*) in Ecuador. In these species, the males lek at essentially the same location annually. The leks were monitored for activity and genetic samples were taken to study relatedness (Loiselle 2006). The results of the study found that "in no case were males within leks more related than expected by chance" (Graph 3). The data showed that the male manakins appeared to join leks randomly and without correlation to relatedness (Loiselle 2006). The McDonald study, also covering manakins, found that the "mean relatedness among network males was less than zero." Because of this and the fact that neither direct nor indirect relationships preferred kin, the manakin networks showed no evidence of the kin selection hypothesis (McDonald 2007).

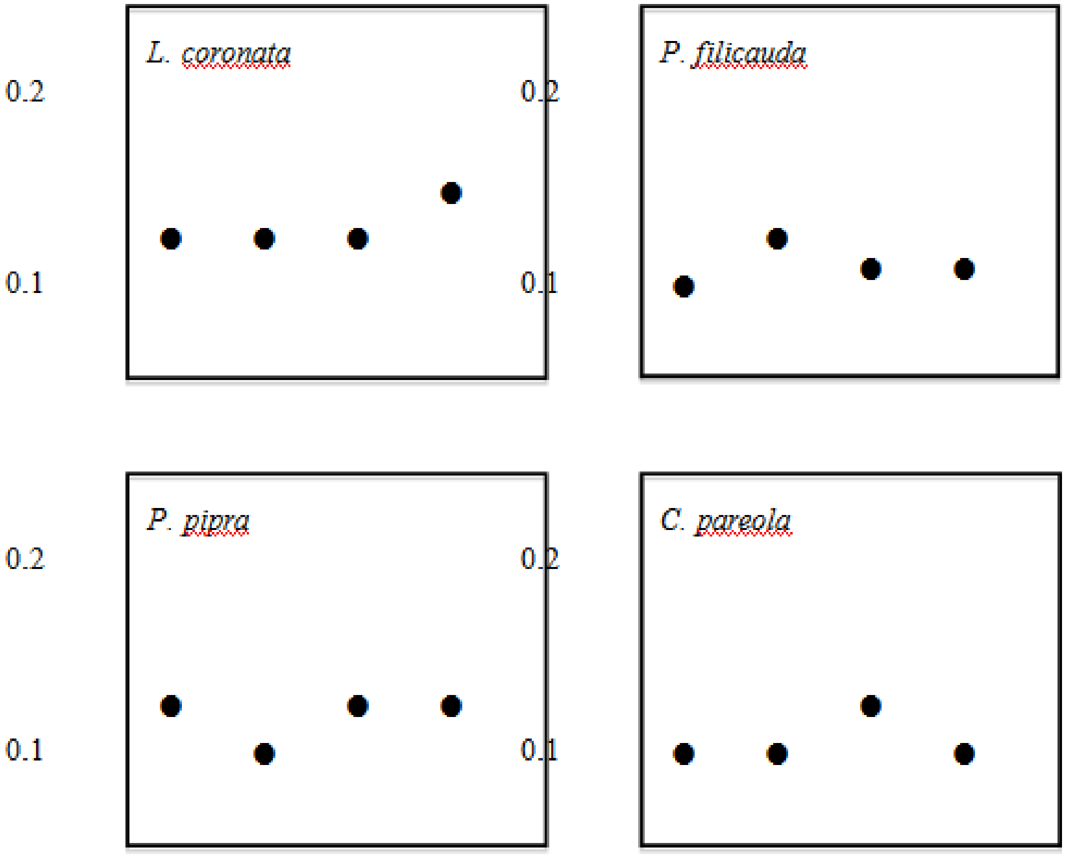


Figure 2.9: Displaying Relatedness Among Members of Manakin Leks

This graph shows the relatedness coefficients of organisms in leks of different species of manakin. The average relatedness is 0, which led Loiselle and team to conclude that relatedness did not have an effect on lek formation and persistence (Loiselle 2006).

McDonald concludes that while some studies have shown kin selection to play a role in lekking, the results of this study demonstrate that kin selection is unlikely to be the driving evolutionary force in lek formation (McDonald 2007). To completely rule out kin selection as a mechanism for lek formation in manakins, however, the relationship between male status and reproductive success within lek must be analyzed. Additionally, future experiments must be done to determine whether or not males can recognize unfamiliar kin (Loiselle 2006).

2.1.6 Conclusion

The study of lekking animals has led to important hypotheses and explanations for their paradoxical behavior, but a conclusive explanation has yet to be drawn. The preference, hotshot, hotspot, and hypotheses are all attempts to explain the peculiar behavior of this classification of animals, but no theory accurately accounts for all of the observations observed across all lekking species. The diversity of animals that mate in leks further complicates the research and explanation process, as behaviors that can be explained in one species may persist for different reasons in organisms of another species, making it difficult for researchers to draw definite conclusions. The **phenotypic gambit** enables researchers to assume a genetic basis for lek behavior, but the exact mechanism is yet unknown.

2.1.7 Discussion Questions

1. Do you think lekking is selected for by similar or different selective forces in different species?
2. Why does lekking appear paradoxical from an evolutionary standpoint? How is this paradox overcome?

2.1.8 Glossary

- **Bower**- a shelter, dwelling, or nest
- **Conspecific**- referring to the same species as the organism in question
- **Coverts**- in birds, the small feathers that conceal the base of the animal's larger tail and wing feathers
- **Dimorphism**- often the result of sexual selection or disruptive natural selection, dimorphism refers to the existence of two distinct forms of the same species that differ in one or more characteristics such as size, color, pattern, etc.
- **Epigamic**- any mal characteristic, such as coloring, behavior, or patterning, that serves to attract the other sex during courtship
- **Fecundity**- having abundant offspring
- **Frugivorous:** having a diet consisting mostly of fruit
- **Gene**- the fundamental unit of inheritance and evolution; a hereditary unit that results in the expression of a phenotype through protein manufacture
- **Genotype**- the genetic makeup of an organism
- **Heterozygosity**- the state of being heterozygous, i.e. having more than one allele at a locus
- **Hierarchy**- a system of ranking determined by escalations between individuals of a species. Often, the hierarchy is determined by strength, fitness, and/or age.
- **Home range**- the limits to the area in which an animal lives the majority of the time
- **Hotspot**- an area characterized by high encounter rates with females of a given species. One explanation for lekking behavior is that male settlement is determined by these hotspots and, thus, leks are formed by the aggregation of individual males settling where they are most likely to be encountered by a female.
- **Inclusive fitness**- the fitness of an organism determined by taking into account not only its direct offspring but those of its kin as well. Because an organism shares many of its genes with its kin, certain cost-benefit tradeoffs increase its fitness by helping its kin reproduce rather than reproducing itself.
- **Kin selection**- an evolutionary theory that posits some behaviors, though they may not directly improve an individual's fitness, improve the fitness of relatives that share their genes and thus are selected for. Kin selection can be explained by Hamilton's Rule.
- **Lek**- an area in which males of a certain species gather together in competitive sexual courtship and mating displays. Leks themselves are small and are composed of the individual territories of many males. Leks are often characterized by a lack of resources and by a clear hierarchy among males.
- **Monogamy**- the practice of having only one sexual partner throughout a period of time; males mate with the same female for multiple attempts during a period of time.
- **Obligate monogamy**- monogamy that occurs across an organisms life span; a life-pair
- **Multilocus fingerprinting**- a form of DNA analysis designed to identify polymorphisms at multiple loci
- **Natural selection**- the process, defined by Charles Darwin, by which animals best suited for their environment are the most successful in reproduction and thus pass on their adaptive genes in a greater percentage to the next generation
- **Networking**- male-male social interactions, as seen in coordinated displays

- **Phenotype**- observable, physical expression of a trait
- **Phenotypic gambit**- the assumption that, because genes control the expression of phenotypic characteristics and behaviors, evolution of characteristics/behaviors can be assumed to have a genetic basis, even if the genes are unknown. This enables researchers to study the persistence of traits without having to determine the exact chemical mechanism by which they persist.
- **Polyandry**- the state of having more than one male mate at a time
- **Polygyny**- the state of having more than one female mate at a time
- **Sexual selection**- behaviors or characteristics that are not necessarily of adaptive advantage but increase the likelihood of successful mating of an organism
- **Sympatric**- of or relating to the same geographic region (without interbreeding)
- **Variability**- the description of deviation between individuals in genetic characteristics in a population; the potential of a genotype to diverge when subjected to environmental pressures

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2.1.10 Author's Biography

Figure 2.10

Kirby Kempe is a first-year Economics major and first-time city dweller at Rice University in Houston, Texas. Originally from Florida, Kempe grew up on the beach and quickly fell in love with the outdoors, taking the phrase "tree hugger" to the extreme. In those rare moments of tranquility hiding in the life of a college student, Kempe enjoys reading, laughing, photographing, Houston highways, loose-leaf tea, and

StumbleUpon. She has dreams of becoming a neonatologist, and is most frequently seen on shift for EMS on the ambulance or in the Emergency Rooms of Houston's local hospitals.

2.2 To Eat or to Mate? Sexual Cannibalism in Mantodea and Arachnid Species[2]

Author: Rachel Carlson

2.2.1 Introduction

Mating interactions are frequently marked by conflict. Males and females have asymmetric goals in optimizing reproductive fitness, but they must rely on each other to produce offspring in sexual species (Box 2.5 (Intersexual Conflict with Respect to Paternal Investment)). A dramatic example of intersexual conflict is sexual cannibalism, in which the female consumes the courting male before, during, or immediately after copulation (Buskirk et al. 1984). The male appears to be victimized, a hapless casualty of the female's selfish drive to increase her nutrient store. However, examination of sexual cannibalism in the context of spider and mantis species reveals that these sexual selection pressures are accompanied by a host of costs and benefits to females as well as males

Box 2.5: Intersexual Conflict with Respect to Paternal Investment

Intersexual conflict occurs when individuals in a mating interaction jockey for the greatest reproductive benefit at the lowest cost. Though individuals must cooperate at least during the mating act to produce viable offspring, their investment in the common young is often highly asymmetrical (Schneider and Lubin 1998). This fact is founded on the anisogamy of the sexes. Female eggs are significantly more nutrient-rich and exacting to produce than male sperm. The female also has fewer eggs than males do sperm. Since the donation of an egg is costlier than that of a sperm, females are immediately more committed to the offspring produced than males. Embryonic food demand places restrictions on the amount of offspring a female can produce in her lifetime, while male reproductive potential has a very high internal upper limit (Schneider and Lubin 1998). There are some rare species (sea horses, jacanas, for example) where males care more for progeny than females, reversing these strategies.

These conditions have created divergent optimum reproductive strategies between the sexes. Males are driven to mate as many times, and with as many females, as possible in order to maximize the number of eggs he fertilizes. Simultaneously, however, females seek to offset the disproportionate costs of reproduction by obtaining a paternal investment from the male, which can come in the form of food, protection, defense of resources, or other energetic expenditures. The female may select mates based on secondary sexual trait indicators of "good providers." Inducing the male to bear a greater share of the reproductive burden allows the female to store resources for future offspring (reduces her parental investment) (Schneider and Lubin 1998).

Female selection for paternal investment may impose a suite of costs not directly associated with resource provision, such as elaborate male courtship costs (Schneider and Lubin 1998). In species of arachnids and insects, females often guard the ootheca before it hatches, but males do not directly provide parental care. Thus, parental investment and sexual conflict chiefly occur within the context of mating (Schneider and Fromhage 2005).

Life-history parameters such as the timing of sexual maturation and oviposition, expected number of matings, body size, maturity, and generation length are likely to influence the degree and outcome of intersexual conflict (Buskirk et al. 1984). Dynamics of functional morphology and ecology may also limit or enhance mating costs/benefits, impacting intersexual conflict (Andrade 2003).

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[2] This content is available online at <http://cnx.org/content/m34755/1.3/>.

Several hypotheses explain ways in which sexual cannibalism can occur by natural selection. This chapter first discusses the interpretation of sexual cannibalism as a case of **paternal investment**: females require substantial nutrients to produce their eggs, and extract food from the male's own biomass. This **"foraging strategy" hypothesis** is based on experiments with mantises since male self-sacrifice drastically increases the reproductive yield of the female (Barry et al. 2008). Enhancing female fecundity improves the male's direct fitness because he can pass on more of his genes through healthy offspring. This chapter also reviews corroborating evidence from redback spider males, who initiate their own cannibalism to maximize reproductive benefit in a hostile environment that opposes repeated mating (Andrade 1996). An outwardly brutal mating interaction may ultimately be adaptive for members of both sexes.

This chapter proceeds to examine the limitations of, and alternatives to, the above hypothesis. Many male spiders and mantises are not complicit in self-sacrifice, indicating that cannibalism is not adaptively favorable to males (Liske and Davis 1987; Wilder and Rypstra 2008). Additionally, sexual cannibalism is prominent in **size dimorphic** spider species, in which males are too small to substantively feed females. These observations give rise to claims that cannibalism in the context of mating is actually a non-sexual, predator-prey interaction (Wilder and Rypstra 2008b). Alternatively, a sexual selection hypothesis suggests that females discriminately eliminate undesirable mates by devouring them (Elgar and Nash 1988). Overall, the examination of sexual cannibalism reveals the variable influences of species morphology and environmental conditions on a behavior's evolutionary significance. Also, since both reproductive and mortality considerations are inherent in sexual cannibalism, examining its adaptive value offers intriguing insight into the fitness dynamics of sexual interactions

2.2.2 The Organisms

Sexual cannibalism has been observed in 30 arthropod species, and occurs in all arachnids and three orders of insects [Figures 10-12]. One of these orders is Mantodea, which is comprised of about 2,000 mantis species worldwide, mostly within the family mantidae (Yagar and Svenson 2008). Mantises are highly predatory organisms, employing an ambush technique in which they camouflage themselves to wait for prey, then strike rapidly once food approaches. Most mantis species have spiked, muscular forelegs called raptorial legs, which are designed for gripping a range of prey, including lizards, frogs, birds, snakes, rodents, insects, and, of course, mates (Yagar and Svenson 2008).

Between sexually mature adults, attraction typically occurs via visual cues and the use of pheromones, which the females release during the nighttime (the organisms' prime mating period) (Robinson and Robinson 1979). In order to mate, the male approaches the female, leaps onto her back, and uses his forelegs to grip her thorax and wings. Males transfer sperm from their abdomen into a chamber at the tip of the female's own abdomen. Mothers can be polyandrous, mating with several males during a reproductive season (the number of males varies with the mating season). Eventually, she deposits as many as 400 eggs in a frothy mixture secreted by abdominal glands, which hardens into a clumped egg mass called an ootheca. After oviposition, mantis mothers almost always abandon the ootheca, increasing the importance of the nutrients and protective protein coat she originally invests in the egg mass.

Figure 2.11: A deposited ootheca from a praying mantis (Mantis religiosa). Egg clusters are typically abandoned after oviposition by female mantises (Robinson and Robinson 1979). *Image :TarynMarie http://www.flickr.com/photos/tarynmarie/233251370/* .

Mantises exhibit moderate **sexual size dimorphism** (*Iris oratoria* males, for example, are 49% the size of females), which improves the female's ease of cannibalizing the male (Barry et al. 2008). An estimated 63% of the diet of female Chinese mantises (*Tenodera sinensis*) is derived from cannibalized mates (Fox 1975b). Even in species that rarely exhibit sexual cannibalism, the behavior can be a major source of population mortality if it occurs in a specific seasonal or life cycle frame (Fox 1975b). Thus, sexual cannibalism is a crucial component of mantis behavior.

Figure 2.12: A praying mantis (*Mantis religiosa*) clutches the head of a cannibalized mate. Female mantises may substantially improve reproductive output by engaging in sexual cannibalism before, during, or after copulation (Barry et al. 2008). *Image :TarynMarie http://www.flickr.com/photos/tarynmarie/233251370/* .

A wide range of spider species also engage in sexual cannibalism, including wolf spiders, orb-weaving garden spiders, and Australian redback spiders. Though mating tactics, insemination techniques, and oviposition timing vary depending on the species, several common factors affect spider reproduction. Firstly, high sexual size dimorphism is common in spiders, and females can be over 100 times bigger than males (Schneider and Lubin 1998). Secondly, female spiders are typically polyandrous, though wide population dispersal and harsh environmental conditions can limit mating opportunities. When they do find mates, male spiders use **palpal emboli (pedipalp)** to inject sperm into female storage organs, and their confidence in paternity can be affected by the number of palpal insertions (Andrade and Snow 2005). However, as a tradeoff to trying to ensure paternity, males may incur physical damage from either cannibalism or the loss of their palpal emboli tips during insertion.

This is a concise description of some sexually cannibalistic species, but provides sufficient background to understand the conditions for sexual cannibalism's adaptive value.

2.2.3 A Parental Investment Hypothesis for Sexual Cannibalism

In order to produce viable offspring, females must first obtain and process huge amounts of nutrients (Box 2.6 (The Impact of Diet on Fecundity in Mantises and Spiders)). Females have evolved a variety of adaptations for efficient food acquisition, including increased consumption rate, selective consumption of certain food types, and dietary mixing (Wilder and Rypstra 2008a). Some researchers argue that, from a female perspective, sexual cannibalism is simply one in a litany of strategies for gaining more food. This foraging strategy hypothesis states that sexual cannibalism has adaptive value for both sexes, since the male soma provides a female with nutrients that increase her **fecundity** (Figure 2.13; Barry et al. 2008). Though the male loses lifetime survivorship, he gains overall fitness from passing on genes to more vigorous offspring. Male self-sacrifice is therefore considered a beneficial form of **paternal investment**.

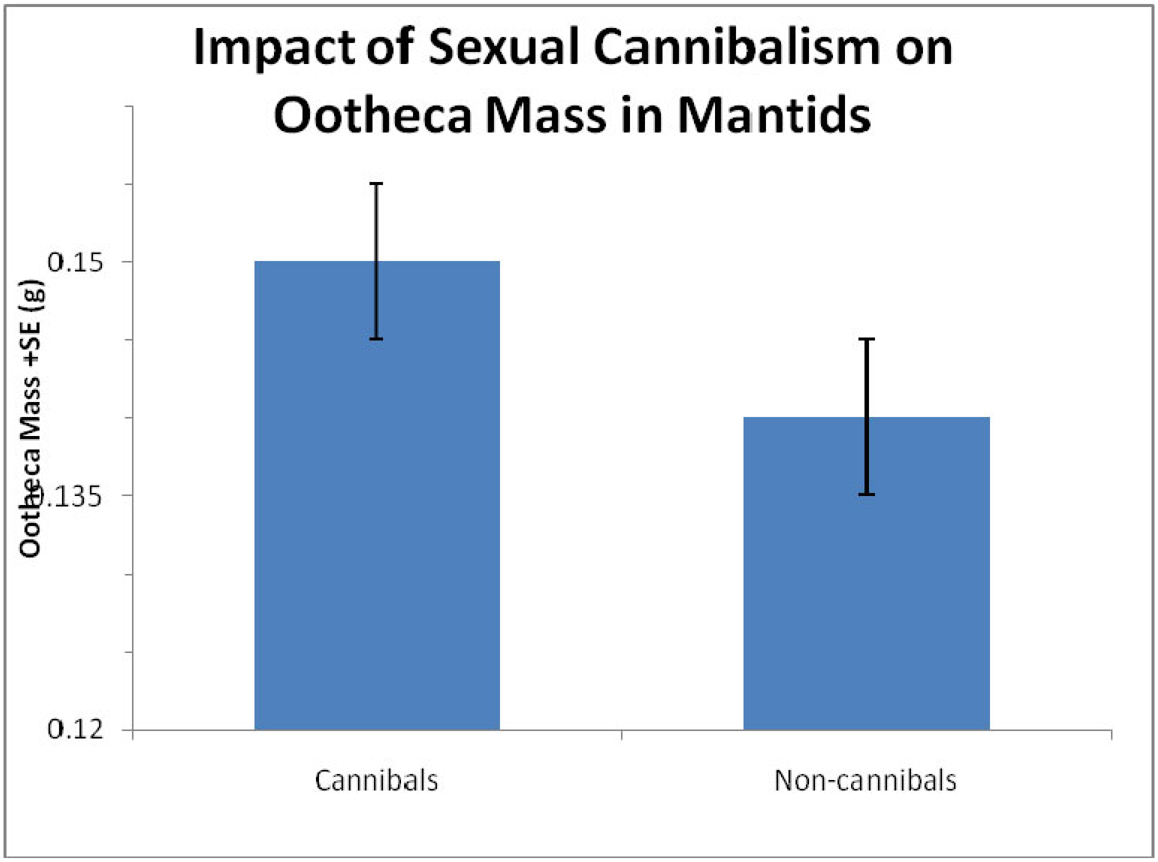


Figure 2.13: Mass of first ootheca from females who cannibalized and did not cannibalize their mates. Cannibals had more massive ootheca (p=.017) than non-cannibals (Barry et al. 2008).

Box 2.6: The Impact of Diet on Fecundity in Mantises and Spiders

Research on praying mantis species shows that females' diet impacts two distinct phases of their development. Firstly, the diet of juveniles determines how long their body becomes as they mature. Length is a limiting factor for weight, so the adult's initial body condition restricts its potential for weight gain throughout its life, which in turn impacts fecundity (Eisenberg et al. 1981). Mantises' food intake is positively related to the female's maximum attained mass, the mass of her first and second ootheca, the rate of ootheca production, and the number of total young produced (Birkhead et al. 1988).

Similar studies in orb-weaving and wolf spiders indicate that spider females achieve a higher body mass when fed with a high-quality diet (Hebets et al. 2007). Well-fed wolf spiders also mature at a faster rate, which is important for fecundity since females must produce ootheca within a seasonal time frame (they can produce more offspring if they reach the adult stage earlier). Thus, food acquisition is fundamentally linked to fecundity of mantises and spiders, supporting the hypotheses that it is adaptive to engage in sexual cannibalism, especially when the male can provide a nutritive meal.

In order to test this hypothesis, researchers regulated the diets of three groups of *Pseudomantis albofimbriata* (mantis) females, feeding them with crickets on low to high frequency schedules to produce low to high body conditions (Barry et al. 2008). The foraging hypothesis predicted that sexual cannibalism would be motivated by the female's drive to acquire food (and, on the ultimate level, increase her fecundity), so hungrier, needier individuals were expected to cannibalize more mates. Indeed, females of poor initial body condition, who were starved for nutrients, cannibalized their mates more often than robust females. Additionally, results showed that cannibalistic females most significantly improved their body condition and produced heavier ootheca than non-cannibalistic subjects, due to food gained from the mate's biomass (Figure 2.14; Barry et al. 2008). Similar evidence exists in tests involving wolf spiders (Wilder and Rypstra 2008a; Hebets et al. 2008; Hurd et al. 1994). Overall, the incidence of sexual cannibalism appears to be positively related to reproductive output, so the behavior can increase the fitness of both sexes.

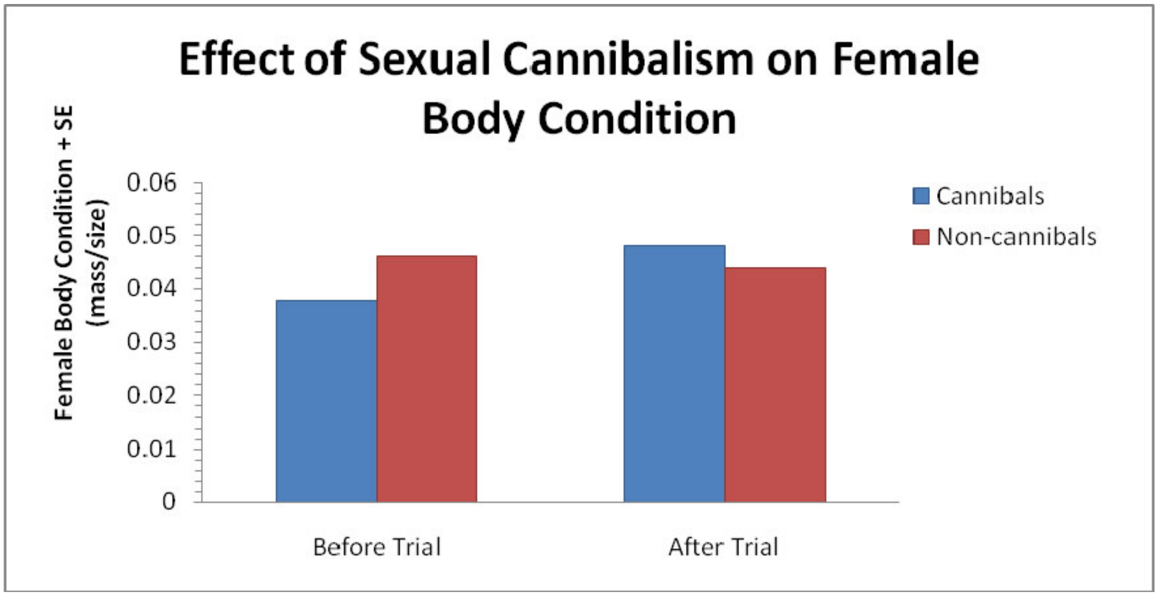


Figure 2.14: Female body condition before and after a trial in which females either cannibalized or did not cannibalize mates. Cannibalistic females were in poorer condition initially, but their body condition improved more than that of non-cannibals throughout the test ($p < 0.001$) (Barry et al. 2008).

Conflict of Interests

If the foraging strategy hypothesis adequately explains sexual cannibalism, then one would expect male mantises and spiders to be complicit in their own self-sacrifice. Since males can improve fitness by investing their body as their mate's food source, evolution should select for a willingness to be consumed (Lelito and Brown 2006). The advantage of complicit self-sacrifice is especially apparent in mantis species, because the male's decapitation often triggers a mechanism that increases the rate and effectiveness of sperm transfer (Liske 1991).

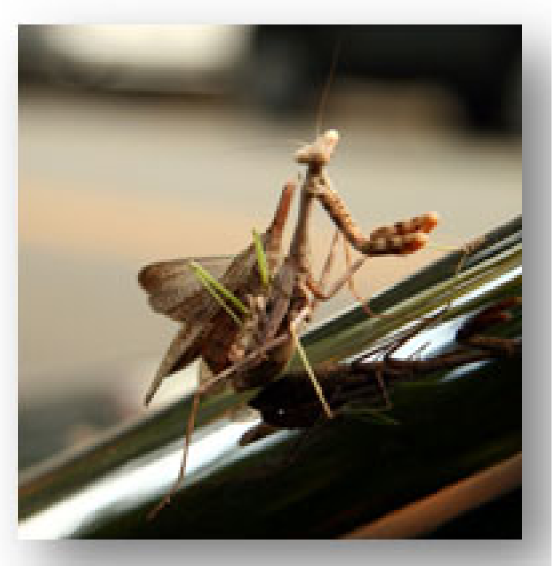


Figure 2.15: A female mantis is mounted by a male who she has already decapitated. In mantises, insemination can occur during or after cannibalism. Decapitation may even increase the rate of copulation (Liske 1991). *Image :Taurusaficionado http://www.flickr.com/photos/* .

Nonetheless, in several species, male compliance does not occur. Males of both mantis and spider species have evolved various precautionary behaviors designed to thwart female attack.

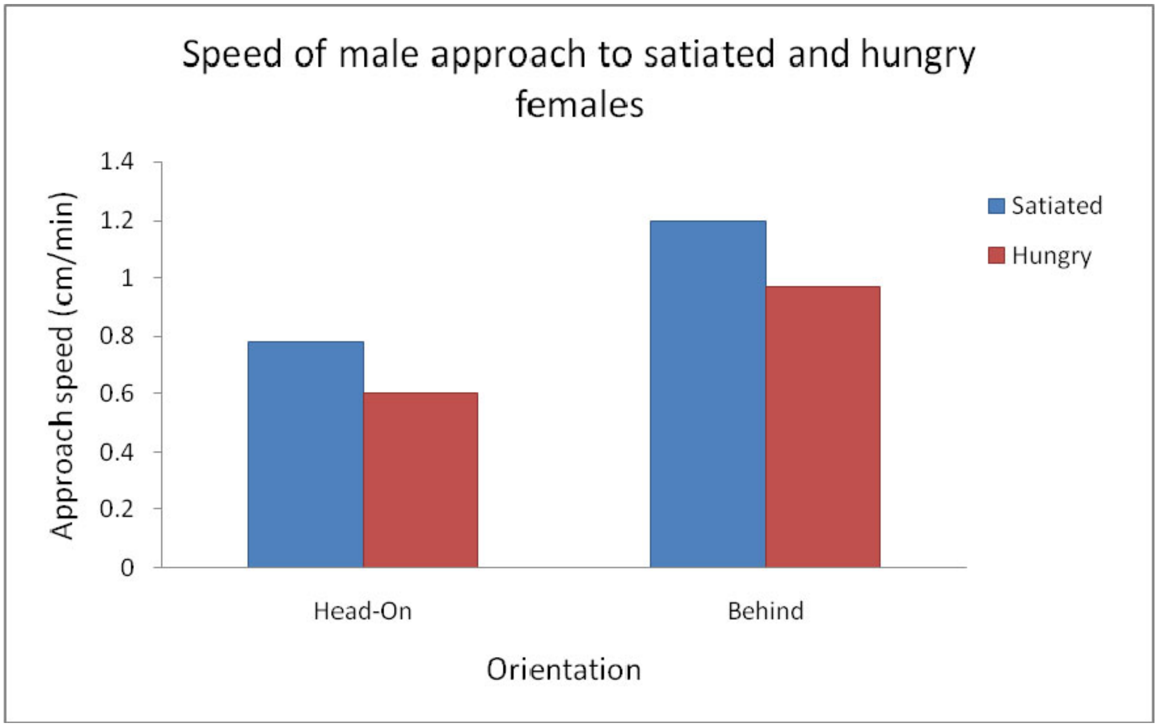


Figure 2.16: Relationship in *Tenodera sinensis* between female hunger treatment, male orientation of approach, and speed with which males approached females. Males approached females more quickly from behind (not in female's direct line of sight), and approached satiated females more quickly ($P < 0.0001, P_{adj} < 0.00055$).

For example, in one study, praying mantis males tended to mount females from low-risk positions (out of the female's range of mandible reach) (Birkhead et al. 1988). Also, *Hierodula membranacea* mantis males approached females more actively (with fewer hesitant pauses) when experimental conditions imitated a cover of nighttime darkness (Birkhead et al. 1988). Finally, male Chinese praying mantises neared females in a crouching stance, approached them only when they were turned away, and mounted them in a sudden leaping motion that left little opportunity for pre-copulatory cannibalism (Liske and Davis 1987)

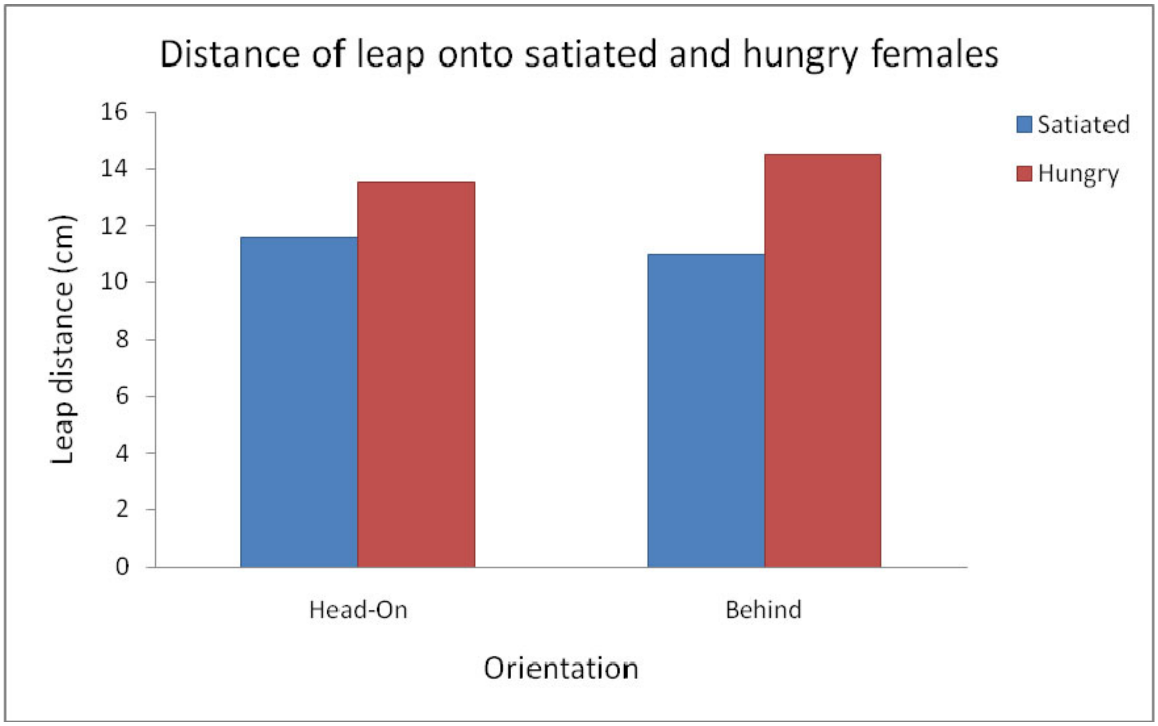


Figure 2.17: Relationship in *Tenodera sinensis* between female hunger treatment, male orientation of approach, and distance from which males leapt onto the backs of females. Males leapt onto hungry females from a longer distance away ($P < 0.001, P_{adj} < 0.0044$)(Lelito and Brown 2006).

These diverse and often sophisticated protection mechanisms would not have evolved if males gained ultimate fitness benefit from self-sacrifice (Box 2.7 (Counteradaptations and Cryptic Female Choice)). Females may increase the vitality of a male's offspring by consuming him, but evidently not enough to offset his cost in death. The functional design of male mating behavior displays noncompliance, exhibiting a conflict of interest between male and cannibalistic females (Lelito and Brown 2006).

Box 2.7: Counteradaptations and Cryptic Female Choice

Conflicts between interacting organisms can drive adaptation and counteradaptation. Individuals evolve traits that provide them with the greatest benefit possible from social interactions, even at the cost of another organism. Thus, two organisms may steadily interact through a system of "one-upmanship," as each develops counteradaptations to exploit, and avoid being exploited by, the other.

Mating interactions are prime arenas for adaptation/counteradaptation, since they often involve a conflict of interest between the sexes. Males evolve traits that promote their confidence in paternity and sperm viability, while females develop mechanisms for selecting only optimum sperm (sexual selection)(Siller 2001). While sexual selection is easily recognized before mating (females choose to mate with males who display attractive characteristics and/or fitness indicators), it can also occur post-insemination through sperm ejection or a mechanism called cryptic female choice-the differential selection at the hidden level of the gamete(Eberhard 2000). Cryptic female choice can be passive, as when eggs are fertilized by sperm that win the "race" to the gamete. Or, the choice can be active: a female's sperm storage system can be designed to give priority to the last sperm she receives, allowing her to annul the representation of previous mates if she meets a superior male

(Eberhard 2004).

One intriguing example of cryptic female choice exists in Australian redback spiders. The female redback has developed multiple sperm storage sites, which promote post-copulatory sperm management by the female. The male has two palpal emboli, so he could potentially inseminate both sites (the fitness optimizing strategy for males), but the larger female can physically control where the male injects sperm (in one or two sites, or in an empty site versus one occupied by previous males' sperm) (Andrade and Snow 2005).

The male redback thus appears at a disadvantage for two reasons. Firstly, if he manages the rare deal of finding a mate, his control over paternity is minimal. Also, if takes more time to inseminate two sites as opposed to one, and females usually cannibalize doubly inserting males before copulation is complete (Andrade and Snow 2005). Thus, the male redback has developed an important counteradaptation: a constriction of the abdominal exoskeleton during mating that protects male organs from wounds inflicted by the female mandible. In one study, males displaying constriction had improved survival, heightened physical endurance, and greater mating success with new males (Andrade and Snow 2005). Multiple sperm storage units in females and the constriction mechanism in males illustrate how mating interactions can disproportionately benefit a single sex, driving a progression of counteradaptations.

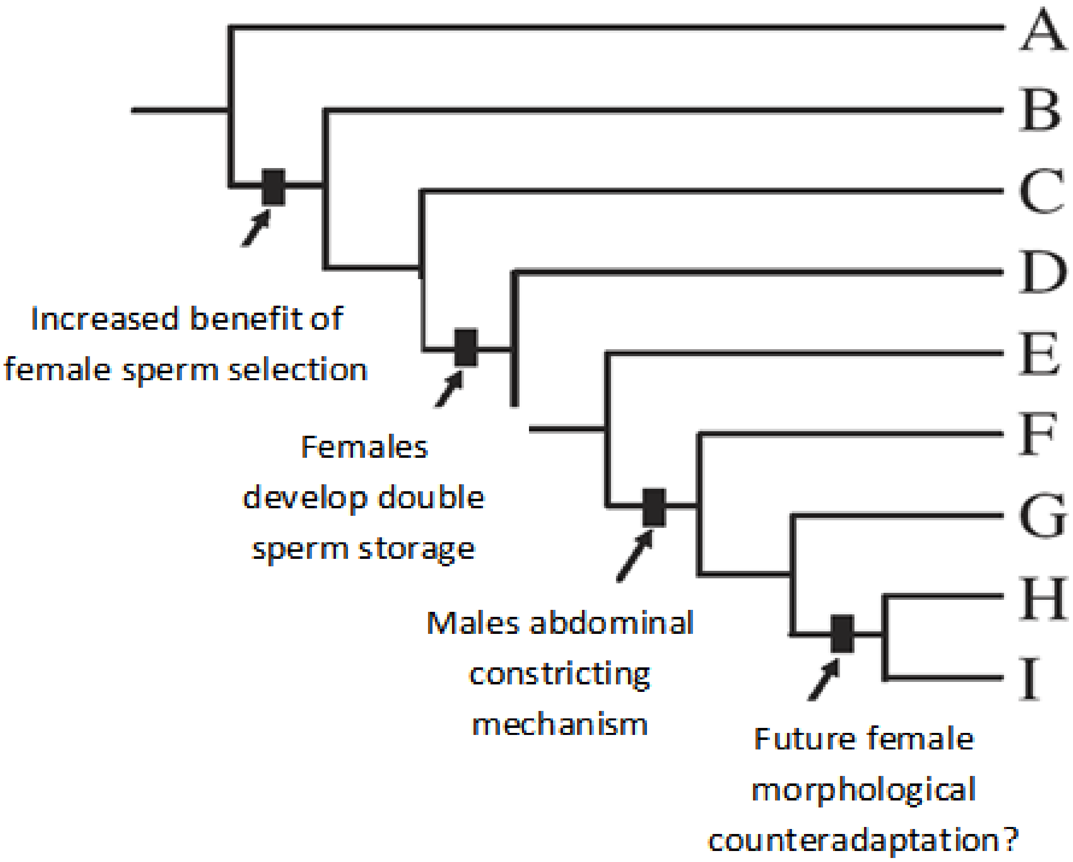


Figure 2.18

The Question of Female Fecundity Benefit

Even a conflict of interest hypothesis, a claim that females gain disproportionate benefits from eating males, is insufficient to explain the majority of sexual cannibalism cases. The behavior is prominently observed in spider species that are highly **sexual size dimorphic**, such as wolf spiders. In contrast with mantises, male spiders are frequently diminutive compared to females. The consumption of male bodies can contribute little substance to the mother's nutrient store, so cannibalism does not measurably increase female body condition or ootheca mass (Wilder and Rypstra 2008). If female fecundity does not increase from sexual cannibalism (which obviously precludes the male from gaining fitness), then how can this behavior have evolved? Perhaps there is a context in which males alone profit from their own self-sacrifice.

Does a male ever really present himself to be eaten? In fact, such complicity is blatantly displayed in Australian redback spider mating, wherein the male grabs the female and somersaults directly into her mouthparts (move this up to the non compliance section). Without halting his acrobatics, the redback transfers his sperm into female storage organs by inserting one or both emboli into her (Andrade 1996). As a result, 65% of redback mating interactions end in sexual cannibalism (Andrade 2003). The male Australian redback's biomass is miniscule, so his sacrifice has no apparent impact on the female spider's reproductive output.

Discussion Question:

Why could males have evolved such exaggerated willingness for self-sacrifice?

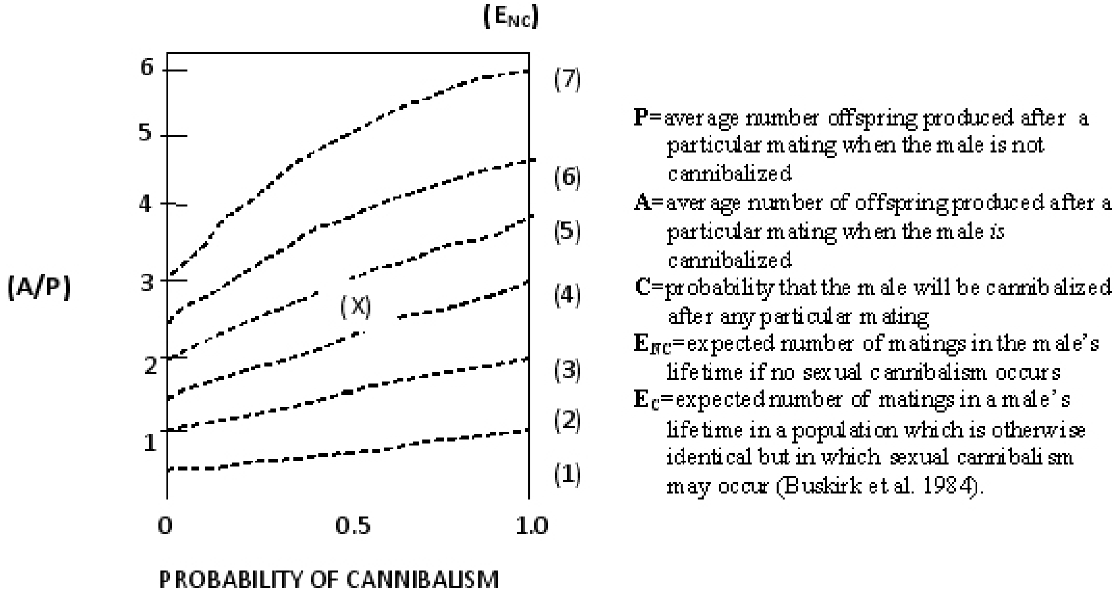
2.2.4 The Tradeoffs: Economic Models for Sexual Cannibalism

In an attempt to develop an adaptionist description of sexual cannibalism, several researchers have devised mathematical **cost-benefit** models that address both the foraging strategy hypothesis and observations of redback self-sacrifice.

The Male Perspective

Male complicity in sexual cannibalism is interpreted by the economic model of Buskirk et al. Buskirk posits that a male should permit himself to be eaten only if he increases his inclusive fitness more in that manner than by surviving to inseminate other females (Buskirk et al. 1984). Two factors impact the male's inclusive fitness in sexual cannibalism: the number of times a male may be expected to mate during his lifetime and the proportional increase in the male's offspring resulting from self-sacrifice. The first factor is based on several conditions, including the ability of males to locate other females (often through the use of pheromones), as well as the time and effort required to court and defend the female. Other constraints are posed by male morphology, such as the length of reproductive lifetime, the time and energy needed to produce sperm, and (in spiders) the detrimental loss of pedipalpal tips to previous mates (Schneider and Lubin 1998). The second factor, offspring increase, is dependent on the female's food supply and the male's **confidence of paternity**. In turn, confidence of paternity is contingent on the extent of a female's polyandrous behavior, as well as copulation duration, sperm storage methods, and the nearness of copulation to oviposition (Box 2.7 (Counteradaptations and Cryptic Female Choice)) (Buskirk et al. 1984).

Based on these parameters, the adaptive value of cannibalism for males can be mathematically modeled (Figure 2.19).



P=average number offspring produced after a particular mating when the male is not cannibalized
A=average number of offspring produced after a particular mating when the male *is* cannibalized
C=probability that the male will be cannibalized after any particular mating
E_{NC}=expected number of matings in the male's lifetime if no sexual cannibalism occurs
E_C=expected number of matings in a male's lifetime in a population which is otherwise identical but in which sexual cannibalism may occur (Buskirk et al. 1984).

Figure 2.19: Buskirk et al.'s model for the evolution of sexual cannibalism, based on the mathematical formula $\frac{A}{P} > \frac{E_{NC}}{\left[1-(1-C)^{ENC}\right]} - \frac{1}{C}$

This theoretical graph shows the relationship of A/P to C for different values ENC. For organism X, C=0.5 and A/P=2.5, and ENC=4. That is, if a male has a 50% chance of being cannibalized and can produce 2.5 times more offspring by being cannibalized than not, then self-sacrifice is advantageous until the male's expected number of lifetime matings exceeds four (in other words, until being cannibalized causes him to forgo three or more matings). The graph suggests that, as the number of expected matings increases, male self-sacrifice must greatly enhance his mate's fecundity in order to offset his cost of neglecting future mates (Buskirk et al. 1984).

Notice what happens to the equation when it is certain that the male will be cannibalized (ENC=1 and C=1): the right side of the inequality becomes zero. Any value of A/P greater than zero (that is, any increase in number of offspring due to sexual cannibalism) thus conveys a selective advantage to sexual cannibalism (Buskirk et al. 1984). This relatively simple model organizes the costs and benefits of male complicity into comparable mathematical terms, describing the conditions by which sexual cannibalism favors male fitness.

The Female Perspective

Newman and Elgar supplement Buskirk's hypothesis with an economic model from the female perspective, drawing on evidence from the orb-weaving spider. Specifically, these researchers address pre-copulatory cannibalism, in which the female consumes the male before sperm transfer is complete (post-copulatory cannibalism is assumed to never harm the female, unless the species raises young and requires future male aid). The mathematical description of Newman and Elgar involves complex dynamic programming, and will not be detailed here. However, it essentially illustrates that females are more likely to engage in pre-copulatory cannibalism if they can encounter several males during a season and have both a low and inconsistent food intake rate from non-mate sources (Newman and Elgar 1991). This model resonates well with the foraging strategy hypothesis, which also emphasizes the nutritional utility of sexual cannibalism for females.

The intersection of the two economic models illustrates the possibility for intersexual conflict in sexual cannibalism. There is a discrepancy between parameters of fitness benefit from the female and male perspectives (Newman and Elgar 1991). For example, consider a mating season in which males encounter many females, and females also frequently meet males. In these conditions, males will incur high costs from sexual cannibalism because they forgo ample mating opportunities. Simultaneously, females will be more inclined to consume mates before copulation because they have many chances to accept sperm later. The discord between male and female perspectives drives some level of conflict of interest in mating interactions. Depending on ecological conditions and species traits, members of the opposite sex experience different costs and benefits that determine the extent to which cannibalism is adaptively favorable.

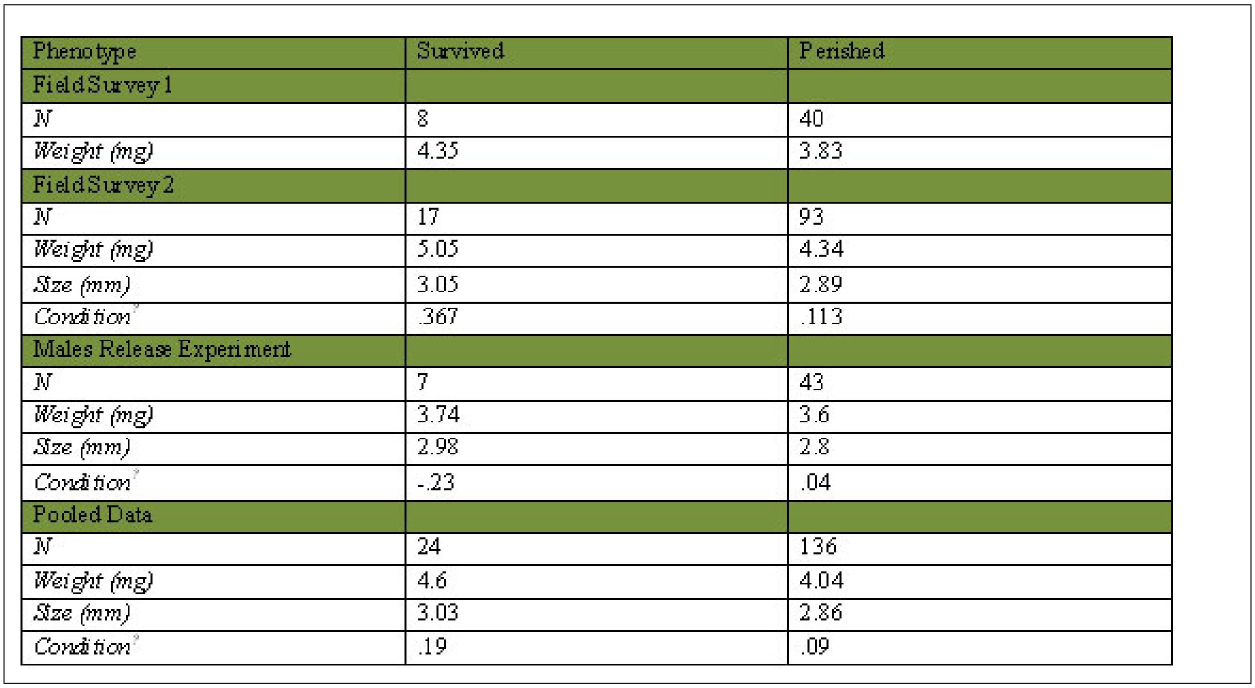
2.2.5 Applications of economic models to mantises and spiders

The economic models of Buskirk; and Newman and Elgar help explain previous observations, including male mantises' non-cooperation in sexual cannibalism. For most mantises males, the likelihood of finding a second mate is high, which increases the cost of self-sacrifice by Buskirk's model. Even if the male's biomass improves female fecundity, the resulting viability of the male's offspring must not be great enough to overcome the cost to his future mating opportunity. (Gemeno and Claramunt 2006). Sexual cannibalism in mantises must be adaptive solely from the female perspective (conflict of interest).

Economic models are also readily applied to the behavior of Australian redback spiders. Experiments consistently show that when a male somersaults into the female's mouth (thus inducing cannibalism), the length of the copulation period doubles (Andrade 2003). Male redbacks, like many organisms, can sexually function long after females start to consume them. While females are occupied with their meal, the male profits from 15-20 minutes extra insemination time. Studies show that cannibalized males usually insert emboli twice, and in one experiment, self-sacrificing redbacks fertilized twice the number of eggs as non-eaten males (Andrade 1996). Self-sacrifice also gives males an advantage in terms of **sperm competition**, because females tend to spurn other males directly after they copulate with, and cannibalize, their first mate (Andrade 2003). In economic terms, the male redback reaps high paternity benefit from increasing the proportion of offspring he sires in the female's brood. Meanwhile, the cost inherent in redback self-sacrifice is extremely low, because males live in a hostile environment that often precludes them from second matings. In fact, there is an 85% mortality rate for males after they leave natal webs [Chart 1], so each male is destined to encounter very few females during his lifetime (Andrade 2003). Therefore, the fitness benefit to post-copulation survivorship is low (Andrade 1997). Based on economic models, male complicity in redbacks makes sense.

Success at finding a mate in male Australian redback spiders: surviving versus perishing on

trip to find mate (modified from Andrade 2003).



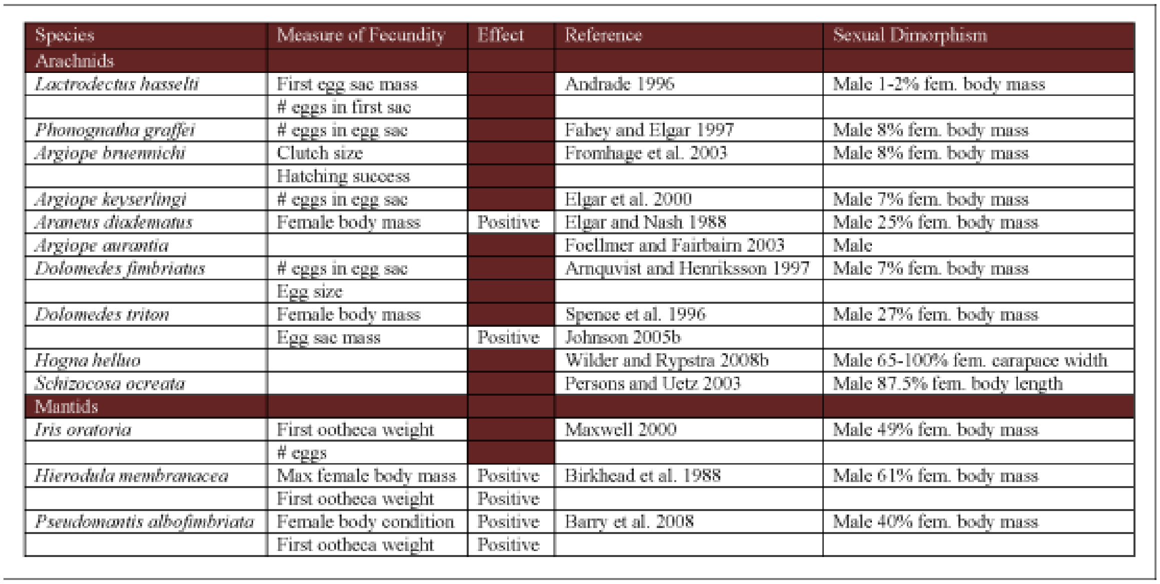
Phenotype	Survived	Perished
Field Survey 1		
N	8	40
Weight (mg)	4.35	3.83
Field Survey 2		
N	17	93
Weight (mg)	5.05	4.34
Size (mm)	3.05	2.89
Condition[y]	.367	.113
Males Release Experiment		
N	7	43
Weight (mg)	3.74	3.6
Size (mm)	2.98	2.8
Condition[y]	-.23	.04
Pooled Data		
N	24	136
Weight (mg)	4.6	4.04
Size (mm)	3.03	2.86
Condition[y]	.19	.09

Table 2.2: Weight and size values are mean. n represents total number of organisms monitored in given trial. “Residuals from a regression of male weight on size. Weight/size regressions were highly significant ($p < 0.001$) (Andrade 2003)

Economic models are further verified by evidence from the orb-weaving spider. Males of the genus *Argiope* often die directly after copulation, regardless of female cannibalism (Sasaki and Iwahashi 1995). In the species *Argiope aurantia*, mating triggers the inflation of the male’s second palp when increased haemolymph pressure causes its distal bulb to expand. Palp swelling catalyzes a cascade of reactions that culminates in the male’s death 15 minutes later (Foellmer and Fairbairn 2003). Since the male willingly engages in mating and evolution has not selected against the spontaneous death mechanism, terminal reproductive investment appears ultimately beneficial. It is unusual to think of dying as a prime fitness strategy, but two morbid processes actually benefit males. The first is familiar: the male soma provides nutrients to the female and increases the quantity and quality of her offspring. Additionally, the dead male can prevent female polyandry. Several male spiders often wrestle vigorously for access to a mate, and even try to dislodge males already in the copulatory position. If the mating male’s pedipalp is in the inflated state, he is more difficult to remove, so his corpse serves as a genital plug to block his rivals’ access to the female (Foellmer and Fairbairn 2003). Thus, evidence from the orb-weaving spider indicates that the costs of foregoing future mating opportunities can be overcome by the direct benefit of increased female nutrition and the male’s **confidence in paternity**.
Discussion Question:
Do female redbacks benefit from being monopolized by the male? What are the costs and benefits of polyandry in this situation?

2.2.6 Sexual Cannibalism and Sexual Selection

Though these economic models are enticingly straightforward, they still do not explain all incidences of sexual cannibalism. **Sexual size dimorphic** species (prominently spiders) pose a problem when males are not complicit. Because their males are too small to provide a nutritionally substantive meal for females, these species elude the foraging strategy hypothesis. Consuming diminutive males may even be costly to the female if she neglects hunting larger food items while busy consuming her tiny mate (Elgar 1991). Since many male spiders are not willing self-sacrificers like the redback, cannibalism appears to be unfavorable to male fitness as well (Wilder and Rypstra 2008). How can non-complicit sexual cannibalism in **mate size dimorphic** couples be considered adaptive?



Species	Measure of Fecundity	Effect	Reference	Sexual Dimorphism
Arachnids				
Lactrodectus hasselti	First egg sac mass	🟥	Andrade 1996	Male 1-2% fem. body mass
	# eggs in first sac	🟥		
Phonognatha graffei	# eggs in egg sac	🟥	Fahey and Elgar 1997	Male 8% fem. body mass
Argiope bruennichi	Clutch size	🟥	Fromhage et al. 2003	Male 8% fem. body mass
	Hatching success	🟥		
Argiope keyserlingi	# eggs in egg sac	🟥	Elgar et al. 2000	Male 7% fem. body mass
Araneus diadematus	Female body mass	Positive	Elgar and Nash 1988	Male 25% fem. body mass
Argiope aurantia		🟥	Foellmer and Fairbairn 2003	Male
Dolomedes fimbriatus	# eggs in egg sac	🟥	Arnquvist and Henriksson 1997	Male 7% fem. body mass
	Egg size	🟥		
Dolomedes triton	Female body mass	🟥	Spence et al. 1996	Male 27% fem. body mass
	Egg sac mass	Positive	Johnson 2005b	
Hogna helluo		🟥	Wilder and Rypstra 2008b	Male 65-100% fem. carapace width
Schizocosa ocreata		🟥	Persons and Uetz 2003	Male 87.5% fem. body length
Mantids				
Iris oratoria	First ootheca weight	🟥	Maxwell 2000	Male 49% fem. body mass
	# eggs	🟥		
Hierodula membranacea	Max female body mass	Positive	Birkhead et al. 1988	Male 61% fem. body mass
	First ootheca weight	Positive		
Pseudomantis albofimbriata	Female body condition	Positive	Barry et al. 2008	Male 40% fem. body mass
	First ootheca weight	Positive		

Table 2.3: Relationship between sexual cannibalism incidence, sexual size dimorphism, and fecundity in arachnid and mantis species (modified from Barry et al. 2008).

One hypothesis for this quandary claims that the cannibalistic behavior is an extreme form of mate selection, in which females reject miniscule, undesirable males by consuming them. According to the sexual selection hypothesis, the female is not driven to cannibalism by a proximate, nutrition-related cause, but instead by the function of ultimately beneficial sexual selection. Females may prefer larger males because body size reflects foraging skill: males who are able to obtain higher mass may be more capable of constructing and placing their webs, as well as capturing trapped prey (Wilder and Rypstra 2008b). If foraging abilities are heritable, then females can use male size as an indicator of the fitness of her offspring. Though sexual size dimorphic females may not obtain survival benefit from cannibalism, they use is as a mechanism of choosing males to sire fitter sons. This strategy is only costly if females are too selective and cannibalize all potential mates.

Testing the sexual selection hypothesis

In order for the argument to be supported, pre-insemination (non-mating) cannibalism in sexual size dimorphic species should target smaller males (Elgar and Nash 1999). One means of testing the hypothesis is through **observation within a species**, wherein researchers observe mating interactions involving same-species males with different levels of **secondary sexual characteristics**. Wilder and Rypstra monitored *Hogna helluo* (wolf spider) males in 90-minute mating trials within a laboratory setting, and found that larger male *Hogna helluo* were less frequent victims of sexual cannibalism (Wilder and Rypstra 2008b). In another investigation, *Araneus diadematus* females (1.89 female/male body length ratio) preferred to mate with, not consume, larger males (Elgar and Nash 1999). Furthermore, *Schizocoas ocreata* virgin females (1.26 female/male body length ratio) attacked smaller males of poorer body condition that displayed small, asymmetrical tufts of bristles, as opposed to voluminous tufts (Persons and Uetz 2005). Experimental evidence has consistently suggested that, in species with high sexual size dimorphism, predatory mating behavior targets smaller males. Thus, sexual cannibalism may indeed serve as a mechanism of sexual selection favoring larger males.

2.2.7 Gould's Spandrel: a Non-Adaptionist Hypothesis

Though experimental results appear to support a sexual selection hypothesis, some researchers present an alternate interpretation. Female spiders may consume smaller males because, quite simply, it is easier to do so (Wilder and Rypstra 2008). Though tiny males may not be nutritionally substantive, it is possible that female predatory behavior is ingrained and non-discriminatory (a female is willing to catch any prey around). In size dimorphic species, sexual cannibalism may have arisen incidentally from the condition of sexes' size divergence.

The non-adaptionist hypothesis is composed of a simple argument:

1. High levels of size dimorphism is an attribute of typical predator-prey interactions. Sexually cannibalistic spider species often display high sexual size dimorphism (Wilder and Rypstra 2008)
2. There is no feasible explanation for how sexual cannibalism could have selected for high sexual size dimorphism. If females consistently selected against smaller males, there would be lower dimorphism than spider species exhibit. Instead, sexual size dimorphism must have evolved first, driven by external factors. Fecundity selection favored greater female size because massive females could produce bigger ootheca, and more surviving offspring. Conversely, scramble competition promoted smaller size among males.
3. Since size dimorphism is conducive to predator-prey interaction (see premise 1), sexual cannibalism emerged subsequently (Wilder and Rypstra 2008).

Thus, the non-adaptionist hypothesis argues that the phylogenic distribution of sexual cannibalism in some spiders is a by-product of selection for sexual size dimorphism in other contexts. Stephen J. Gould terms such incidental cross-trait associations "spandrels," after an architectural term for the space between two arches (Gould 1997). In a **spandrel**, a behavior may not be beneficial at all, but inevitably arises out of external survival pressures.

A corollary to the "spandrel" explanation is another, "spillover" hypothesis. According to some researchers, sexual cannibalism is a consequence of generalized female aggressive behavior. The trait of female rapacity is favorable for juveniles, promoting their survival in a stage that demands high food consumption. Rapacity is less important after females attain maximum size and sexual maturity, but the aggressive trait cannot be extricated by that point (even if it drives away a fecund female's potential mates). Thus, sexual cannibalism is non-adaptive, but sustained because rapacity helps juveniles survive (Arnqvist and Henriksson 1997).

Discussion Question:

Given the analysis regarding how sexual cannibalism could be adaptive, how are these non-adaptive theories and to what extent are they contradictory? Which do you think is more likely?

2.2.8 Conclusions and Future Directions

Several well-developed hypotheses arise to explain the peculiar and dramatic behavior of sexual cannibalism. Models based on fitness economics, sexual selection, and non-adaptive "spandrels" or "spillovers" provide viable descriptions of cannibals' evolution. These various hypotheses are not mutually exclusive, and may apply differently to species based on organisms' unique morphology and environmental pressures. A common vein in several hypotheses is that sexual cannibalism is a manifestation of conflict of interest between the sexes. Intersexual conflict is succinctly expressed by cost/benefit models for males and females, in which parameters for the benefit of cannibalism contrast. This conveys the divergent nature of reproductive behaviors. Sexual cannibalism demonstrates that, even when organisms have the common goal of producing quality offspring, they interact through selfish and often antagonistic tactics.

Sexual cannibalism also exhibits an intriguing interplay between sexual and natural selection pressures. Depending on the timing of cannibalism (pre or post-mating), it can be either the process by which genes are selectively favored, or the instrument of their elimination. The relationship between female mate choice and natural selection through cannibalism may not be static, but contingent on the shifting value of the male as mate or prey item (Persons and Uetz 2005). Further research into the timing of sexual cannibalism could expand an awareness of this dynamic.

2.2.9 DIVERSE SEXUAL CANNIBAL SPECIES

Spiders and mantises are the basis of most research on sexual cannibalism, but the behavior has been anecdotally and experimentally observed in a variety of organism orders.

Figure 2.20: The horned nudibranch *Herminssenda Crassicoris* will consume members of its own species while mating if the male is small enough to be ingested (Megina and Cervera 2002). *Image :Lemurdillo http://www.flickr.com/photos/lemurdillo/2650327503/in/set-72157607190457016/.*

Figure 2.21: Copepods, small marine arthropods that include many species of plankton, occasionally exhibit sewual cannibalism. *Image :Ethan Hein http://www.flickr.com/photos/ethanhein/2250890367/.*

Figure 2.22: Sexual cannibalism is rare in scorpions, but males have still developed the behavior of rapidly backing away from the female after copulation has terminated. *Image :Andres N. Hayes http://www.flickr.com/photos/26432312@N06/2845311259/.*

Box 2.8: Nuptial Gifts, Why don't males offer a proxy?

Males of some species provide **"nuptial gifts,"** or alluring food items, to females during a mating interaction (Choe 1995). The purpose of the gift is to entice females to accept the aspiring mate, and often his success is contingent on the size of the gift procured. The donation of foraged prey before mating is prominently seen in birds and insects, though one spider, Pisaura mirabilis, displays this courting ritual as well (Stalhandske 2001). Some insects, centipedes, and onycophorans offer nuptial gifts in the form of seminal secretions. When sexually cannibalized males offer their own body parts or soma as nourishment, they may also be viewed as extending a nuptial gift (Stalhandske 2001). But why don't male mantises and spiders offer a "cheaper" version of the nuptial gift (a prey item, a nonessential body part, etc.), instead of opting for total self-sacrifice?

One study uses an **experimental method** of hypothesis testing to determine the value of the nuptial gift and its effectiveness as a proxy for the male suitor. Stalhandske summarized three hypotheses for gift giving:

- The nuptial gift could represent a paternal investment. If the nutrients of the "gift" increase female fecundity and, subsequently, the fitness of the male's own offspring, the offering has adaptive value. According to this hypothesis, nuptial gift giving arose from natural selection (Stalhandske 2001).
- The gift could represent a male mating effort. Its primary purpose is to tempt the female to mate, distract the female while the male assumes a copulatory position, and maximize ejaculate transfer. According to this hypothesis, gift giving is derived from sexual selection.
- Gift giving could be a mechanism for protecting the male from sexual cannibalism. By this hypothesis, the nuptial gift promotes male survivability and thus is a consequence of natural selection (Stalhandske 2001).

Stalhandske performed 82 trials in which male Pisaura mirabilis were given no gift, or small, medium, or large size gifts to offer females. For hypothesis 3 to be supported, males without gifts would be expected to approach females, and females to act more aggressive toward mates without a gift. Results showed just the opposite. Males without gifts attempted copulation, and the presence of gifts enhanced female aggression (they were violent only towards males with gifts) (Stalhandske

2001). However, females only mated readily with males procuring gifts (90% mated) and avoided coupling with non-gift givers (40% mated). Additionally, gift size was positively correlated with sperm transfer duration and confidence in paternity (Stalhandske 2001). Thus, sexual cannibalism is an ingrained part of the mating interaction. It occurs when mating occurs, and is not offset by a nutritional proxy. Instead of offering protection, nuptial gift giving represents male mating effort, a tactic for tempting the female, accessing the copulation site, and increasing copulation time (Stalhandske 2001).

2.2.10 Glossary

- **Observation Within a Species Hypothesis Testing**- A method of testing a hypothesis in which organisms of a single species are monitored, often in a field setting, to determine if differences between individuals have adaptive significance. This method demands extensive knowledge of the organisms' habits and attributes.
- **Confidence in Paternity**- When females mate with more than one male in a breeding season (polyandry), the sperm donated by a single male is in danger of being supplanted by that of a later rival. A male's confidence in fathering the offspring of the female decreases as her number of mates increases. Male spiders may try to increase their confidence in paternity by allowing themselves to be eaten, which may increase time of sperm transfer (Andrade 1996).
- **Cost-benefit approach**- An adaptively valuable trait must have a higher ratio of fitness benefits to fitness costs than alternate versions of that trait. This approach acknowledges that phenotypes are associated with varying costs and benefits to the individual as their genes interact with their environment (Humphries 2003).
- **Experimentation Hypothesis Testing**- A method of testing a hypothesis in which a researcher methodically varies an environmental factor (explanatory variable) and observes its effects on animal behavior (responding variable). This technique only applies to behaviors that can alter in response to manipulated external variables. Experimentation is used on behaviors that are immediately traceable; it is a short-term method that does not track the evolutionary response to change.
- **Fecundity**- An individual's reproductive capacity. The number of viable, surviving offspring a female produces is a function of her fecundity.
- **Foraging Strategy Hypothesis**- The evolution of sexual cannibalism in some species is explained by its fitness benefits to females. Females of species having low to moderate sexual size dimorphism improve their fecundity and reproductive yield through eating the male soma (Barry et al. 2008).
- **Intersexual conflict**- Reproductive strategies of males and females usually differ due to incongruence in gamete size and number (females inherently invest more gamete resources in the common young). Each parent wants to produce the greatest number of surviving offspring while minimizing costly resource investment. This imposes asymmetric costs of reproduction on the sexes, resulting in conflict within mating interactions (Schneider 1998).
- **Mate size dimorphism (MSD)**- Difference in size between a pair of male and female individuals (Wilder and Rypstra 2008).
- **Natural Selection**- The process that occurs when members of a species vary in their traits due to genetic differences, and an individual's unique traits cause them to have more surviving offspring than others in the population. Surviving offspring inherit parents' favorable traits, which are then sustained or evolved in future generations.
- **Nuptial Gift**- Nutrient resources supplied to females by courting males prior to, during, or shortly after copulation (Stalhandske 2001). See Box 2.8 (Nuptial Gifts, Why don't males offer a proxy?) for further information.
- **Pedipalp**- A pair of extremities located posterior to the fangs that serves as a copulatory organ in spiders. Each pedipalp inserts into one of the females paired genital openings and injects sperm into a female storage organ (Foellmer and Fairbairn 2003).

- **Paternal Investment**- Activities conducive to producing and rearing surviving offspring which are costly to the female or male parent and reduce their ability to produce offspring in the future. Include nutrient (food), energy, time, and risk-taking forms of investment (Schneider and Lubin1998).
- **Proximate cause**- An immediate cause, based on the operation of an individual's physiological mechanisms. Proximate causes concern the biological structure of an animal that enables it to behave in a particular way.
- **Secondary Sexual Characteristics**- Traits that are unique to a particular sex in a species, but are not used directly in mating and reproduction. These characteristics are often the result of sexual selection for traits that improve the desirability or competitiveness of the mate.
- **Sexual Cannibalism**- The consumption of a male by a female in the context of mating. Females consume courting males before, during, or immediately after mating. Occurs prominently in arachnids, insects, and amphipods (Wilder and Rypstra 2008).
- **Sexual Dimorphism**- A difference between traits of males and females in a species.
- **Sexual Selection**- The process that occurs when members of a species vary in their ability to compete with others for mates or attract individuals of the opposite sex. When this variation is due to genetic differences, sexual selection drives genetic changes in the population. It is a form of natural selection.
- **Sexual size dimorphism (SSD)**- Mean difference in size between males and females for a species (Wilder and Rypstra 2008).
- **Spandrel**- When selection in one context has implications for another context. A trait is viewed as an incidental by-product of selection on suites of correlated traits. The concept of spandrel is invoked as an alternative to adaptionist explanations for the evolution of traits (Gould 1997). Originates from an architectural term meaning a space between two arches, or between an arch and a rectangular enclosure.
- **Sperm Competition**- When a polyandrous female has accepted sperm from multiple males, sperm competition determines the portion of her eggs fertilized by each male. The extent of the male's paternity is positively related to the amount of sperm he transfers. A male can increase his chances in sperm competition through behaviors like mate guarding (seen in harems of elephant seals, for example), increasing copulation time, or doubly inserting palpal emboli. See Box 2.7 (Counteradaptations and Cryptic Female Choice) for more information.
- **Scramble Competition**- Polygynous males (that is, males who fertilize several females' eggs in a given reproductive season) compete for widely dispersed, more sedentary females by "scrambling" over long distances to find them first (Vollrath and Parker 1992). The successful male is determined more by his fortune to be in the right place at the right time, than by particular male characteristics.
- **Ultimate cause**- Evolved causes that are based on the past and current usefulness of the behavior in promoting lifetime fitness and reproductive success. Contrasts with **proximate causes** which are the physiological mechanisms resulting in an act.

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2.3 Violent Mating: Traumatic Insemination in Bed Bugs and other Cimicids[3]

Author: Christine Sun

2.3.1 Introduction

In the animal kingdom, mating interactions are frequently marked by conflict (Johnston & Keller 2000). In sexually reproducing organisms, both the male and the female have conflicting strategies in optimizing reproductive fitness (Morrow et al. 2003). Although male fitness increases with the number of matings, female fitness is not increased and is often lowered. At the same time, however, the two sexes must meet somewhere in the middle to be able to successfully produce offspring. As a result, **sexual conflict** often leads to an **evolutionary arms race** between males and females (Rice & Holland 1997; Morrow et al. 2003; Lessells 2006). As Dawkins and Krebs phrased it, "as swords get sharper, so shields get thicker, so swords get sharper still"(Dawkins & Krebs 1979). One organism that displays sexual conflict is the common bed bug, *Cimex lectularius*.

The bed bug, which belongs to the Cimicidae family, has been known to parasitize humans for more than four million years (Reinhardt & Siva-Jothy 2007). While the organism itself is relatively common, the bed bug's particular mating behavior is rarely found in other species. Although bed bugs have fully functional reproductive tracts, they reproduce solely by traumatic insemination (Usinger 1966 as cited by Reinhardt & Siva-Jothy 2007).

During traumatic insemination, the male pierces the female's abdomen with his knifelike intromittent organ and injects his sperm through the wound into her **hemocoel**, the cavity that contains the **hemolymph**. The sperm travels throughout the female's hemolymph and eventually reaches the ovaries, resulting in fertilization (Carayon 1966 as cited by Reinhardt & Siva-Jothy 2007).

Although its evolutionary origins are not clear, traumatic insemination most likely evolved in order to bypass the mating plug and overcome female resistance during mating (Arnqvist & Nilsson 2000). Keeping in line with the evolutionary arms race theory, female bed bugs have evolved a spermalege, a special sperm-receptacle organ in the abdomen that helps absorb trauma and reduce the damaging effects of traumatic insemination (Reinhardt et al. 2003).

Even though traumatic insemination is rare among vertebrates, there are a handful of insect species that reproduce by this mating practice. Traumatic insemination has also been observed in fruit flies, plant bugs, spiders, bat bugs, and bean weevils, to name a few (Crudgington & Siva-Jothy 2000; Wigby & Chapman 2004; Tatarnic & Hochuli 2006; Kamimura 2007; Ronn *et al.* 2007; Hotzy & Arnqvist 2009; Rezac 2009; Polak & Rashed 2010). While traumatic insemination occurs in these organisms, this form of mating behavior is most highly adapted and thoroughly studied in bed bugs. For this reason, this chapter will focus mostly on

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[3] This content is available online at <http://cnx.org/content/m34756/1.3/>.

sexual conflict in *C. lectularius*. The following sections will detail the mechanisms of traumatic insemination, female adaptations, paternity of offspring, and evolutionary significance of this mating practice in bed bugs.

Box 2.9: Bed Bugs Outside of the Research Laboratory

The bed bug is one of the world's most widely recognized insects in human history. Usually considered a pest, it has been associated with humans for more than 4 millennia (Panagiotakopulu & Buckland 1999).

Bed bugs are found in temperate environments and are found all over the world. Thus, they thrive in human environments, where they have easy and convenient access to food. When bed bugs feed on human blood, they release a type of anesthetic produced from their saliva. The itching and discomfort associated with bed bug bites is caused by an allergic reaction to this anesthetic in bed bug saliva. A small percentage of people have severe reactions to bed bug saliva, going through anaphylactic shock (Goddard & deShazo 2009).

Although bed bug bites cause discomfort and allergic reactions in humans, that seems to be the extent of their health repercussions. Studies have indicated that bed bugs are unlikely to transmit diseases from one person to another (Goddard & deShazo 2009).

2.3.2 How does Traumatic Insemination Work?

Before this chapter delves into specifics about the evolutionary significance of traumatic insemination in cimicids, it is necessary to understand the mechanics of this violent mating behavior. As mentioned earlier, traumatic insemination is rare, and occurs in only a few species of bugs. Insects and other various bugs have open circulatory systems, in which blood and lymph circulate together, and mix to form a substance called hemolymph. This means that in organisms with open circulatory systems, all organs, including reproductive organs, are surrounded by hemolymph, which carries oxygen and nutrients.

The fact that invertebrates have open circulatory systems is important in the reproductive function of traumatic insemination. When the male copulates with a female, he punctures the female's abdominal region with a **paramere**, and injects sperm into the abdominal cavity through the wound. Because the sperm comes into direct contact with hemolymph, the sperm can travel through the hemolymph to the female's ovaries. However, the insemination is only successful if the sperm fertilizes an ovum (Carayon 1966 as cited by Reinhardt & Siva-Jothy 2007).

Box 2.10: Homosexual Traumatic Insemination

Strangely enough, traumatic insemination is not just limited to female-male couplings. In the African bat bug *Afrocimex constrictus*, both sexes are subject to traumatic intromission from males. In this species, both males and females have ectospermaleges, but only females have mesospermaleges. Although the ectospermaleges of each sex differs, male bat bugs have shown symptoms of suffering from traumatic inseminations. Not only were there characteristic mating scars on the males, but there were also foreign sperm found throughout the bodies of the homosexually mated males. There is debate as to whether these same sex traumatic inseminations are a result of sexual competition or just carelessness.

Furthermore, some females in *A. constrictus* have developed these male spermalege structures. Males, as well as females that had the male genitalia form, experienced fewer traumatic inseminations than the typical female that had the female genitalia form. Scientists believe that females mimic the male condition in order to reduce the frequency of the costly traumatic inseminations. (Reinhardt et al. 2007).

2.3.3 Traumatic Insemination in C. lectularius: an Overview

In male bed bugs, the intromittent organ is highly specialized for traumatic insemination (see Figure 2.23). The organ is not only **sclerotized**, but also curved and needle-like, perfect for puncturing the exoskeleton (Usinger 1966 as cited by Reinhardt & Siva-Jothy 2007).

However, males do not just intromit their parameres anywhere on their partners (Reinhardt et al. 2003). In C. lectularius, females have a unique organ called the spermalege, which is thought to have evolved as a counter adaptation to the antagonistic traits of the male (see Figure 2.24). The spermalege consists of both the **ectospermalege** and the **mesospermalege**. During traumatic insemination, a male bed bug inserts his intromittent organ into the ectospermalege, a groove in the right-hand posterior margin of the fifth sclerite, and pierces the pleural membrane (Stutt & Siva-Jothy 2001). The sperm is then injected into the mesospermalege, which contains hemocytes. Once the wound at the injection site heals, a melanized scar forms (Usinger 1966 as cited by Reinhardt & Siva-Jothy 2007).

An interesting point to note is that bed bugs copulate exclusively by traumatic insemination. This may seem odd because female cimicids possess a fully functional female reproductive tract. In the past few decades, not once has a male bed bug ever been observed copulating by placing his paramere into a female's vagina (Carayon 1966 as cited by Reinhardt & Siva-Jothy 2007, Reinhardt et al. 2003) In fact, females only use the genital tract for **oviposition** (Carayon 1966 as cited by Reinhard & Siva-Jothy 2007).

Figure 2.23: Scanning electron micrograph of the male intromittent organ (paramere) of *Cimex lectularius*. Males bed bugs have evolved a needlelike penis that they insert directly into the abdomen of their mates during traumatic insemination. Photo courtesy of A. Syred (Siva-Jothy 2006).

2.3.4 Reducing the Cost of Traumatic Insemination in Females

While advantageous to the reproductive success of the individual male, traumatic insemination imposes a cost on the females. When the female is ready to mate, as demonstrated by her large post-feeding body volume, she receives an average of five traumatic inseminations, not necessarily from the same male (Reinhardt et al. 2009a). The frequent wounding of female bed bugs during copulation has been shown to result in reduced lifespan and decreased reproductive output.

The evolution of the spermalege in female bed bugs is a possible counteradaptation to the harmful male traits (see Figure 2.24, Figure 2.25). It has been suggested that the ectospermalege serves to alleviate the female's costs associated with the physical piercing trauma of the male's paramere, and that the mesospermalege restricts diffusion of the sperm within the female, thereby minimizing the female's costs of receiving male ejaculates (Stutt & Siva-Jothy 2001).

Box 2.11: Inter-species Traumatic Insemination

Traumatic insemination between different species has also been documented. For example, researchers have observed male *Cimex hemipterus* traumatically inseminate *Cimex lectularius*, a different cimicid species. Traumatic insemination between these two different cimids prompts an immune response in the female; the female will swell up at the site of the wound in response to the ejaculates. This swelling further reduces the female's lifespan, and there are even some cases where the swelling reaction causes immediate death. In addition to reduced longevity, fertile egg production in a female *C. lectularius* is also reduced when she mates with a male *C. hemipterus*. Among a population consisting of both *C. lectularius* and *C. hemipterus*, most of the female *C. lectularius* lay only sterile eggs when *C. hemipterus* make up more than 75% of the group. Scientists are unsure as to the exact reason why inter-species traumatic insemination occurs, but some have hypothesized they may occur out of carelessness or inter-species competition. (Newberry 2008).

Furthermore, there is support for the evolution of the spermalege resulting at least partly from selection to reduce the costs of mating-associated infection (Morrow & Arnqvist 2003; Reinhardt et al. 2003). Bed bugs spend the majority of their lifetime in dark and cramped crevices in the walls. These small spaces not only house many bed bugs, but they also contain their feces and dead bed bugs, making the bed bug's living area very unsanitary. Therefore, when a male bed bug pierces the female with his paramere to deliver his sperm, he also introduces pathogens, which have potential to cause infections in females (Reinhardt et al. 2005).

Researchers have demonstrated that the spermalege has adaptive value in relation to traumatic insemination because female bed bugs that have been stabbed in the spermalege with a needle contaminated with bacteria have greater egg production and longevity than those stabbed elsewhere on the abdomen (see Figure 2.26). Because egg production and longevity are indicators of an individual's fitness, the greater the egg production and longevity in a female, the higher the fitness is for that same female.

These findings demonstrate that the spermalege serves as an organ with immune function. The source of this protection comes from the abundance of spermalege dwelling phagocytic hemocytes, which can kill the pathogens that enter the female's body during traumatic insemination (Reinhardt et al. 2003; Siva-Jothy 2006).

In *C. lectularius*, competition among males for mates is thought to have led to the evolution of traumatic insemination by males, followed by the evolution of the spermalege in females, which in turn selected for cooperation by the male with regards to pierce the spermalege, where it would do the least amount of harm. It is not in the interest of the male bed bug to do unnecessary harm to his partner. Given that male fitness also depends on female survival, male bed bugs want the female to live long enough to lay at least some eggs fertilized with his sperm (Reinhardt et al. 2003).

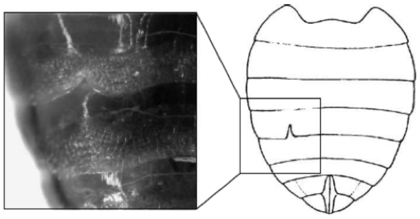

Figure 2.24: Drawing of an abdomen of a typical female *C. lectularius* with an enlarged photograph of the ectospermalege, the site of traumatic insemination. Photo courtesy of M. T. Siva-Jothy (Siva-Jothy 2006).

Fig 2. Traumatic insemination (mating) in *C. lectularius*. The bed bugs are placed upside down to show the point where the female is pierced by the male during sperm transfer.

Figure 2.25: Traumatic insemination in *C. lectularius*. The male only inseminates the female at the spermalege, which is most likely a counteradaptation that reduces the damaging effects of male sexual behavior. Photo courtesy of R. Ignell.

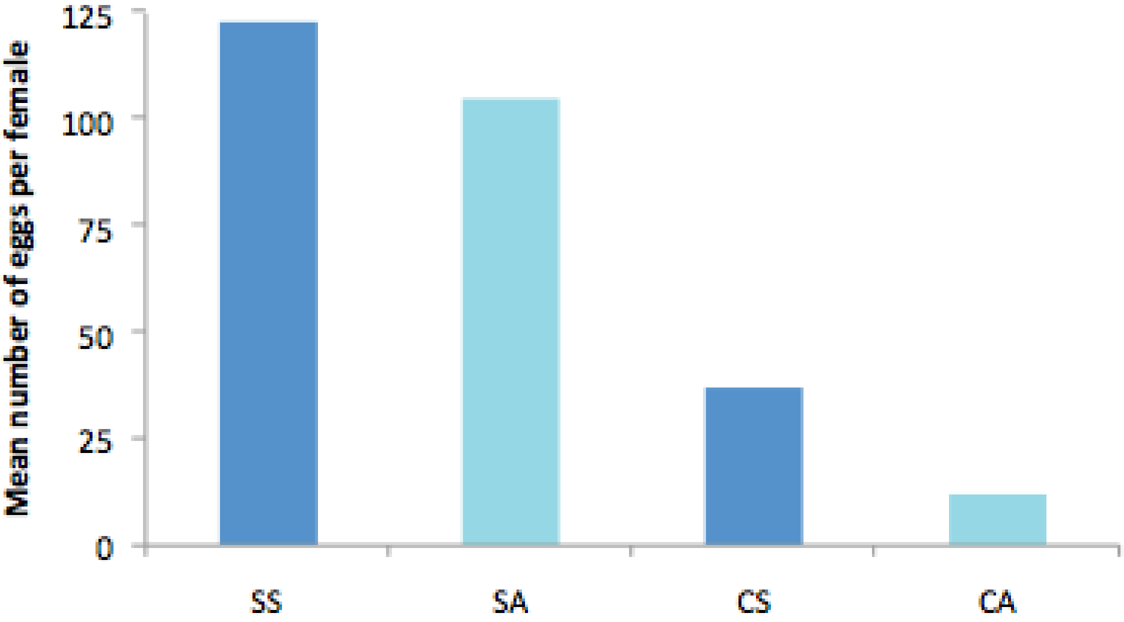

Figure 2.26: Female bed bugs have evolved a specialized organ, the spermalege, in the abdominal region that receives sperm injected into them during traumatic insemination. Females that are pricked in the spermalege with a contaminated needle produce more eggs than those penetrated with a contaminated needle elsewhere. SS= sterile needle in spermalege, SA= sterile needle in abdomen, CS= contaminated needle in spermalege, CA= contaminated needle in abdomen. After Reinhardt *et al.* 2003.

2.3.5 Paternity of Offspring Produced by Traumatic Insemination

The males of many animals adjust their ejaculate size according to the probable mating status of females because relative sperm numbers can determine paternity outcomes in a system of **polyandry**, in which one female copulates with multiple partners (Simmons 2001 as cited by Siva-Jothy & Stutt 2003; Parker 2008). Male bed bugs are no exception to this phenomenon. They can detect the mating status of females through chemoreceptors located on their intromittent organs. These receptors allow the male bed bug to sense the presence of ejaculates in the female. If a male bed bug perceives that he is not the first male to mate with a female bed bug, he will copulate for a significantly shorter amount of time than if he were the first male (see Figure 2.27) (Siva-Jothy & Stutt 2003).

Box 2.12: Protecting Sperm: Bacteriolytic Activity in Male Ejaculate

As mentioned in the chapter, the spermalege contains phagocytic hemocytes that provide immunity by killing pathogens foreign to the female bed bug. Thus, as a male bed bug ejaculates are introduced to the female's hemocoel, many components of his semen, including sperm, are under threat of attack from the female's immune system (Reinhardt *et al.* 2003; Siva-Jothy 2006). Furthermore, contact with microbes during traumatic insemination can also damage sperm and reduce male reproductive success as well (Otti *et al.* 2009).

Thus, in *C. lectularius*, males have been selected to protect their sperm. Research has shown that male med bugs have bacteriolytic activity (lysozyme-like immune activity [LLA]) in their ejaculates.

While LLA is found in the seminal fluid of male bed bugs, its antimicrobial effects may be beneficial to both the male and the female, given that the female is introduced to potentially harmful microbes during sexual transmission (Otti *et al.* 2009; Reinhardt *et al.* 2000b).

However, what is interesting to note is that while a male who mates with a virgin female bed bug has a significantly longer copulation duration and ejaculate size than a male who mates with the female afterwards, the latter actually has a higher fertilization success, with a 68% last-male **sperm precedence** in *C. lectularius* after two matings (Stutt & Siva-Jothy 2001). One explanation for the longer copulation duration between a male and a virgin female is that it is possible the first male's ejaculate is subjected to disproportionate phagocytic attack from hemocytes in the female's spermalege. Therefore, selection via sperm competition may favor first males who have a large ejaculate size (Siva-Jothy & Stutt 2003).

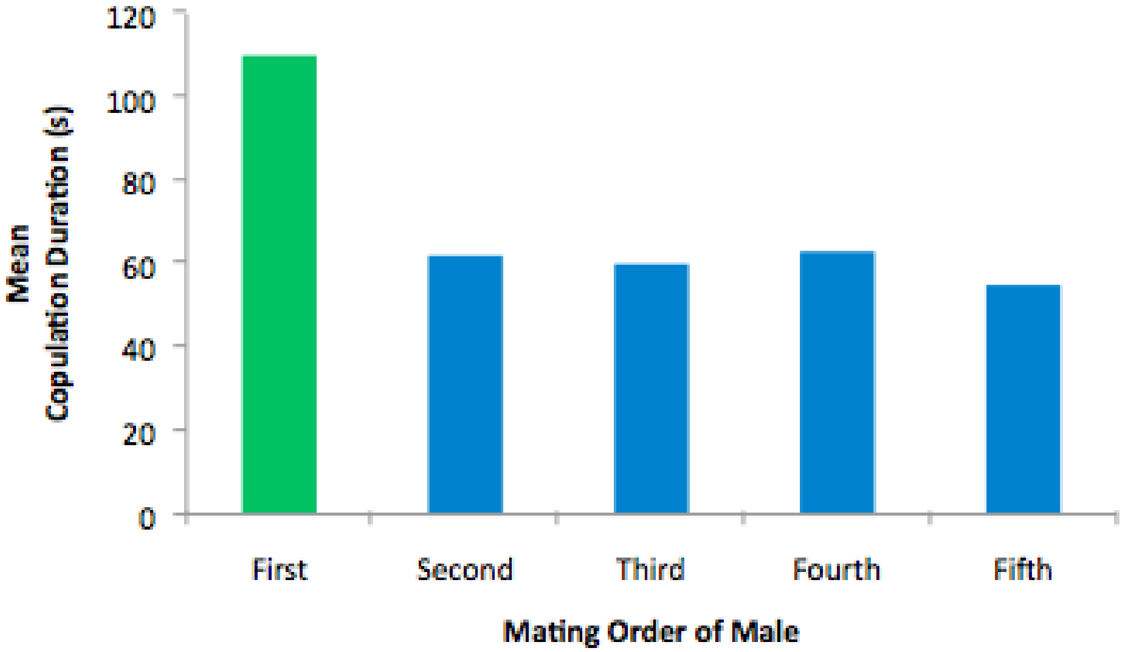

Figure 2.27: Mean copulation durations for virgin males sequentially mated to females. The female's first copulation in a bout of copulations last significantly longer than subsequent copulations. ($p < 0.0001$) After Siva-Jothy & Stutt 2003.

2.3.6 Conclusion: Evolutionary Significance of Traumatic Insemination

Consistent to the evolutionary arms race theory, both male and female bed bugs have evolved certain adaptations and counter-adaptations against each other in order to optimize their own reproductive fitness (Morrow et al. 2003). Although the origins of traumatic insemination are unclear, many hypotheses have been proposed, including bypassing the mating plug and overcoming female resistance during copulation, which would be reproductively advantageous to males (Parker 2008). Although we may never know its origins, the studies surrounding traumatic insemination in *C. lectularius* have truly provided valuable insight into sexual conflict and further research should be conducted to get an even clearer picture.

2.3.7 Discussion Questions:

1. Why is the spermalege considered a counteradaptation? In what ways does the spermalege benefit the female?
2. Can you think of a scenario in which the traumatic insemination and evolutionary arms race in the bed bug would be reversed due to selective pressures? In what scenario would increased matings benefit females?

2.3.8 Glossary

- **Evolutionary Arms Race**- The evolutionary struggle between competing sets of co-evolving genes that develop adaptations and counter-adaptations against each other.
- **Ectospermalege**- The cuticular groove that guides the male's intromittent organ into the mesospermalege (Reinhardt & Siva-Jothy 2007).
- **Hematophagous**- Feeding on blood.
- **Hemolymph**- Found in organisms with open circulatory systems, hemolymph is comparable to the blood and lymph of vertebrates.
- **Hemocoel**- The cavity found in insects that contains the hemolymph.
- **Intromittent organ**- Refers to an external organ of a male organism that is used for delivering sperm during copulation, also known as paramere.
- **Mating plug**- A gelatinous secretion deposited by a male into a female genital tract that later prevents the female from being successfully bred with later (Parker 2008).
- **Mesopermalege**- The hemocyte-containing bed bug organ into which sperm are introduced (Reinhardt & Siva-Jothy 2007).
- **Oviposition**- a term used for invertebrates and especially insects, oviposition refers to the act of laying eggs.
- **Paramere**- see intromittent organ.
- **Polyandry**- A mating system in which one female copulates with multiple males.
- **Sclerotized**- Hardened by the presence of substances other than chitin, such as scleroproteins, waxes, or calcium salts
- **Sexual conflict**- occurs when the male and female have conflicting optimal fitness strategies concerning reproduction, leading to evolutionary arms race between the two sexes.
- **Spermalege**- consisting of the ectospermalege and mesospermalege, the spermalege is a pair of sperm-receptacles which reduce damage to the female bedbug during traumatic insemination.
- **Sperm Precedence**- an indicator of male fertilization success in a polygamous mating system.
- **Traumatic insemination**- the mating practice in some species of invertebrates in which the male pierces the female's abdomen with an intromittent organ and injects sperm directly into the abdominal cavity.

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2.3.10 Biography

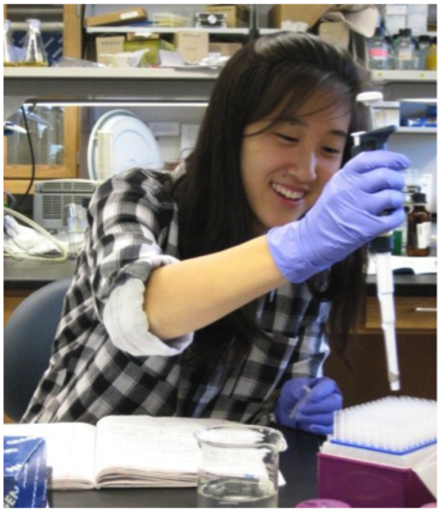

Figure 2.28

Christine Sun was born in Gaithersburg, MD and currently attends Rice University in Houston, TX. There, she is a sophomore double majoring in Biochemistry and Asian Studies. She loves to travel, and recently came back from a service trip to Taiwan. It was actually because of the numerous bed bug bites she received in Taiwan that compelled her to go to Wikipedia to research bed bugs in the first place. Although she does not think bed bugs are the most pleasant creatures, she finds their reproductive behavior fascinating.

2.4 Sexual Conflict and Forced Copulations Lead to the Co-evolution of Sexual Organs in Anas platyrhynchos[4]

Author: Allen Gu

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[4] This content is available online at <http://cnx.org/content/m34749/1.3/>.

Figure 2.29: *Anas platyrhynchos.* The male mallard with its distinctive green hood during mating season (left) along with its female mate (right).
Photo from: < http://www.flickr.com/photos/kjwcode/3416225985/sizes/m/>.

2.4.1 Introduction

Mallards, like most waterfowl, form seasonally monogamous **pair-bonds** during the fall or winter before breeding season. During this time, the male stays close to the female to guard her from predators and other males until she lays her eggs which allows her to spend more time feeding to cope with the increased energy requirements for producing her **clutch** (Losito 1996). When the breeding season arrives, the males' plumages changes noticeably so that **drakes** take on their distinctive green hood and begin to court the females, known as **hens**, see Figure 2.29. This ritual begins with head pumping and specific calls from the drake to which the hen responds and ends with the drake mounting her, grasping her neck feathers, and thrusting (McKinney 1983). Mating ends within a minute after which the two begin post-copulatory rituals (McKinney 1983). After the hens begin laying their clutch, the drakes, leave them and begin to attempt forced copulations with other females that are still fertile (Davis 2002). It can usually be assumed that males will not form new pair bonds because all other females have already bonded, (Goodburn 1984).

Box 2.13: Mallard Characteristics and Facts
The mallard is roughly 0.6m or 2 ft long and has a wingspan of 82-95 cm or 32-37 in. Its breeding season begins in late March or early April. The female builds the nest by herself, usually in a concealed area near the water, and has an average clutches have 9 eggs. The eggs are laid one a

day and incubated for 22-28 days. Down feathers from the female are shed to insulate heat. If a nest is destroyed the female can rebuild but is unlikely to lay as many eggs (Goode).

Mallards are primarily vegetarians that eat things like leaves, wheat, rice, and willows, but they will also feed on small fish, tadpoles, and snails. Mallards migrate in the winter to warmer areas in the central and southern United States (Goode).

Sexual conflict is the result of differing evolutionary interests between the sexes of a species (Adler 2010). This conflict is usually due to competition for greater **reproductive success** among members of the same sex but which often involves tactics that reduce the other sex's success. While this is uncommon in most birds, it is prevalent in *Anatidae*,the waterfowl family. In fact, recent studies by Brennan et al. have shown by comparative analysis that, in ducks with greater genital complexity there is more frequently forced copulation which provides strong evidence that the organs were developed due to sexual conflict (2007). These undesired and actively resisted extra pair copulation's (EPCs) are deemed forced copulations, and are the subject of debate in the field of animal behavior (McKinney 1983). This chapter will outline the mechanisms and specific reproductive interests at stake for each sex. Then, theories for the co-evolution of behaviors and sexual organs will be presented. At the end, some peculiar and intriguing alternative sexual practices of mallards will be given for the reader's edification.

2.4.2 The Male Intromittent Organ

Male waterfowl are some of the few birds that have well-developed **intromittent organs**(IO's), external organs that deliver sperm during copulation (Briskie 1997), which have been termed phalluses. These phalluses grow to full size in the mating season and regress afterwards until the next season (Johnson 1961). The phallus is kept inside the drake until mating begins, see Figure 2. Once the drake has secured his position upon the hen and the two are made contact with their genitalia, the phallus rapidly **everts**in a counter-clockwise spiral inside the female, allowing ejaculate to run along its length inside the vagina. Eversion can be likened to pulling one's finger out of a glove turning it inside out.

Some **phylogenetic evidence** shows that IO's were lost and redeveloped several times throughout evolutionary history. This is supported by the fact that IO's are mostly found in primitive birds, and there is evidence of IO's in some bird embryos that are reabsorbed before hatching (Briskie 1997). Several hypotheses exist as to why this occurred, but this chapter will focus on one reason mallards may have retained them, which is sexual conflict. To fully understand this, it is necessary to examine the female genitalia too.

2.4.3 The Female Genitalia

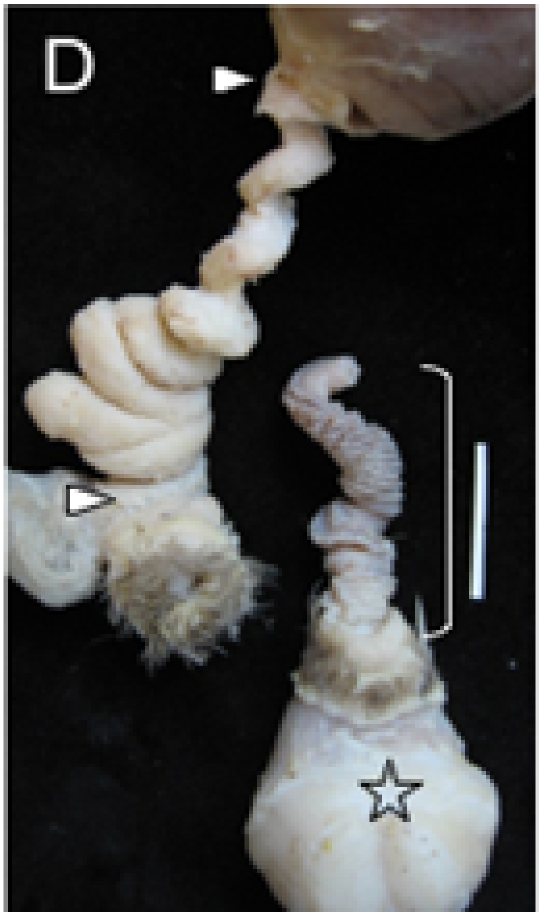


Figure 2.30: Figure 2. *Anas platyrhynchos* sexual organs. The female mallard's vaginal tract (left) spirals harshly clockwise from the cloaca to the uterus. The bracket on the right shows the drake's phallus along with a 2 cm white dash for scale. The arrows on the left indicate the beginning and end of the vaginal tract. The start indicates the testes. Photo taken from Brennan et al. (2007)

Surprisingly, it was only recently discovered that the female waterfowl genitalia were even more complex than the male genitalia and subsequently researched. Waterfowl have the only known coevolved, elaborate female genitalia in the avian family. In 2007, Brennan et al. published their findings: that many female waterfowl have vaginas that twist clockwise, opposite to the direction that male phalluses do, and frequently include dead-end pockets that trap semen (see Graph 2.32 & Graph 2.33). How could the female have sexual organs that are so elaborately designed to hinder insemination by males? It seems counterintuitive that female sexual organs would not be adapted to best fit male reproductive organs, but that kind of thinking is based on human anatomy.

Brennan argues that it is due to sexual selection and conflict that these adaptations arose in the female mallard's vagina (2007). Brennan produces some possibilities that it would not be including homology and natural selection (2007). She states that homology is impossible because the female oviducts begin from the Mullerian ducts whereas the male phallus comes from a ventral region of the cloaca and is homologous with the female hemi-phallus (2007). Natural selection to prevent water damage is also ruled out because of the extent to which the vagina specifically hinders the male phallus, and the similar phalluses that crocodiles have and use exclusively underwater (Brennan et al. 2007).

Box 2.14: How do other birds manage procreation?

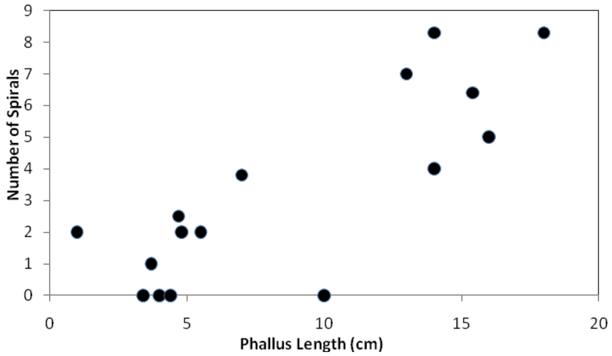
Figure 2.31

Birds that do not have phalluses use their cloaca, the opening used for urinating and defecating, to mate. The male occasionally has a stiffened pseudo-phallus developed during the breeding season which aids in his endeavors, and the two touch cloaca for a brief moment as sperm is transferred to the vagina in the so called "cloacal kiss" (Briskie 1997). In other birds, the female must evert her vagina into the male's cloaca to receive the sperm, which gives her far greater control over whose sperm she selects.

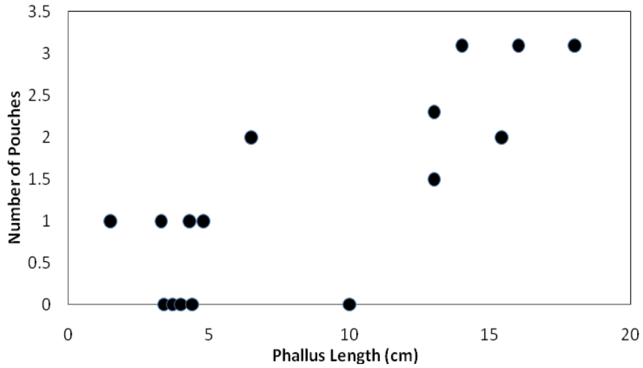
As seen above, arranging the cloacal kiss can be extremely difficult in waterfowl. The intense awkwardness of this arrangement in waterfowl (the birds pictured above are American Coots) triggered some of the theories for the prevalence of intromittent organs among *Anatidae* species. These include: water damage prevention, maintaining genital contact, minimizing flight costs, and sperm competition (Briskie 1997). These theories may all play a role in the maintenance of IO's, but currently, the strongest hypothesis is sexual selection. Photo from: <http://www.flickr.com/photos/kevcole/2499844531/>.

2.4.4 Forced Copulation

Recall that sexual conflict occurs when one sex obtains an advantage over the other. Mallards are socially monogamous, so females choose males during the breeding season and, quite surprisingly, attempt to remain faithful to them; however, males are polygamous despite their socially monogamous pairings, much like some humans (Adler 2010). In a purely monogamous society or one with fewer males than females, the male's reproductive success would depend on the health of the female. However, if males used their intromittent organs and larger size, they could forcibly inseminate females either if they had no mate of their own or outside of their mate pair to increase their own reproductive success. This is exactly what is seen in the frequent extra-pair copulations and "rape flights" that mallards have. Recent experiments have also shown that the sizes and spirals of phalli in waterfowl directly correlate with the complexity of the corresponding vaginas and the occurrence of forced copulations within the species, see Graph 2.32 & Graph 2.33 (Brennan 2007)



Graph 2.32: Comparison of average phallus length vs. the number of spirals in the corresponding female's vagina also shows a positive correlation and evidence of co-evolution (Adapted from Brennan et al. 2007).



Graph 2.33: Comparison of average phallus length vs. the number of pouches in the corresponding female's vagina shows a positive correlation. This provides evidence of co-evolution (Adapted from Brennan et al. 2007).

This provides comparative evidence for the sexual conflict between sexes in waterfowl, as species that do have elaborate genitalia have been shown to be more likely to practice forced copulation while those that do not are less likely to have convoluted genitals**.**

It has been suggested that perhaps these forced copulations are due to overcrowding and not a natural part of the mallard's reproductive tactics; however, research has concluded that the drakes practice forced copulation in normal population conditions in the wild (Evarts 1987). It would be uncertain whether or not the extra-pair drakes were copulating with the females when forcibly mounting the hens (see Figure 2.34), but because of the multiple parentage observed in mallard clutches, 17-25%, and the lack of **brood parasitism**, it was concluded that the actions were extra-pair copulations (Evarts 1987). Normally in birds, extra-pair copulations are consensual and initiated by the female leading to greater fitness in her offspring; however, in mallards this may be a direct loss of fitness for the female if these extra-pair chicks are actually from an inferior male. In this case, both the female and her mate have lost some amount of fitness while the extra-pair male has increased his own.

Figure 2.34: A group of drakes waiting to mount a female. Photo taken from <http://www.flickr.com/photos/26421824@N03/3413720963/sizes/m/>.

Forced copulations are distinct from regular copulations in that females show significant resistance to them by making displays, flying, hiding, diving, running, or swimming away (Evarts 1987). If the hen is mated, then her mate will peck at the aggressor(s) unless there are too many to deal with. Various studies have shown that in mallards, drakes will defend their own mates against other aggressors until she has laid her eggs. However, afterwards, the drake will join groups of other paired or unpaired males to attempt forced extra-pair copulations with fertile females that have yet to lay their clutches, which maximizes their own reproductive successes (McKinney 1983).

Therefore, female hens that have developed labyrinthine vaginas exert greater control over their reproductive fitness. Assuming that all drakes have elaborate phalluses, even the unfit ones would be able to forcibly inseminate hens that did not have this trait, so elaborate vaginas went to fixation. Bluhm and Gowaty describe this phenomenon well with the **constraints theory**: "[which] says that when individuals reproduce with nonpreferred partners, they will have offspring of lower viability than when individuals reproduce with preferred partners" (2004). They found by experimentation that this was true in mallard hens by controlling which partners the hens mated with and comparing offspring surviving to 45 days after hatching. This would support a **mate-choice hypothesis** for the co-evolution of mallard sexual organs wherein indirect benefits, the good genes of preferred males, would be what the females are selecting for (Adler 2010).

2.4.4.1 Proximate reasons for Mate Choice

Testosterone was positively associated with forced copulations in mallards, greater time spent near females, increased mate guarding, and mating success (Davis 2002). Females choose mates in the autumn that they can accurately predict will have higher levels of testosterone come breeding season, and the females that had mates with higher testosterone also had fewer lost feathers due to forced copulation, presumably because the mate was a better defender (Davis 2002). This may provide direct benefits that complement the **good genes hypothesis**(same as mate-choice hypothesis for indirect benefits). However, research also shows that increased testosterone increases the FEPCs that drakes perform, so it may just be that the females that chose the most aggressive drakes do not have to deal with FEPCs (Davis 2002).

2.4.4.2 How successful is it?

As a reproductive tactic, the success of the insemination matters greatly to unpaired males and slightly to paired ones. The action itself would not be worthwhile if it failed each time. The data for this are mixed. Brennan claims that successful forced copulations are rare and successfully blocked by the female hens' elaborate vaginas (2007). However, other studies show successful forced copulation rates of up to 50% (McKinney and Evarts 1998). Depending on the study, success rates vary; however, in general, it seems that forced copulations are successful enough to remain a viable reproductive tactic.

2.4.5 Why Have Unconditional Resistance?

Figure 2.35: Forced copulation in mallards.The female here has been caught by at least three persistent drakes that are pushing to mount her and shaking her by the scruff of her neck

However, as mentioned above, the hens have an uncanny desire it seems to remain faithful to their chosen mates (Adler 2010). The hen's struggles often attract groups of other drakes who will follow after her, see Figure 2.35 (Goodburn 1984). The hen's resistance is unusual as the cost of it is so high. In their excitement, males continually pile themselves on top of hens and grasp at their neck feathers to better position themselves for entry. This, along with her resistance, frequently causes injuries ranging from lost feathers to scratches, ruptured organs, and even drowning (Adler 2010). Many times it may be better to avoid this damage by accepting the forced extra-pair copulation (FEPC) as other species do. There are several hypotheses for this. The resistance may be related to maintenance of the pair-bond to assure that the mate will continue to guard the hen since he needs assurance of his reproductive success. It may be the **good genes hypothesis**, to ensure the best chicks survive as stated above. However, if this were the sole reason, then hens should engage in some extra-pair copulations (EPCs) with dominant males that have better genes which it is never seen doing.

Instead, Adler suggests that in spite of the high costs of resisting, the hen is filtering out the weak drakes that attempt FEPCs in favor of the fittest individuals (2010). She does clarify however, that this is to make the best of a bad situation, not to have a net benefit. In other words, this behavior is has the byproduct of selecting for forced copulation and complex phalluses to stay in the pool. Thus, the resistance provides indirect mate choice making it more likely that the male with the most adaptive genitals, that can bypass the vaginal labyrinth, would succeed. To clarify, the hen is not calculating the fitness profits and deficits from her actions, but gradual evolution has resulted in these behaviors being selected and working together optimally. This furthers the co-evolution of the two genitalia in a constant arms race as the fit males would be able to reproduce with greater success and the females should also evolve more elaborate vaginas that only the fittest could inseminate forcibly (Adler 2010).

There is still a great deal of controversy over these theories and more research is needed to establish one way or another which theory or theories best explains the co-evolution of mallard sexual organs. One way or another, sexual conflict is at the heart of why drakes have complex intromittent organs, and why females have developed elaborate defensive vaginas. Females invest far more in the offspring than the males do, and this trait preserves their ability to select for better mates. Better mates increase her own chances of survival directly, but more importantly, they give her offspring higher fitness. This ensures that her own genes will be more likely to spread throughout the population, even if she still had to do most of the work on her own.

Box 2.15: Sexual deviance in mallards

Did you know that mallards are one of the few species that have been observed practicing homosexuality and one of even fewer that have been noted to practice homosexual necrophilia?

In 2001, a researcher sitting at his desk at the Natuurmuseum of Rotterdam heard a loud bang and looked outside his window to find two mallard drakes; one was in full breeding plumage while the other in post-breeding moult. It was found that the breeding male was chasing the other drake in an attempted rape flight before the latter smashed into the building's wall instantly dying, but still not losing his undesired partner's interest (Moeliker).

What followed for the next 75 minutes was an unprecedented torrent of passion captured on camera by the researcher who eventually ended the scene by removing the mallard corpse. C.W. Moeliker would go on to publish his findings and earn one of the ten 2003 Ig Noble Prizes (Moeliker 2001).

Box 2.16: Free love in *Anatidae*

Homosexual behavior in animals has been documented but not well studied. Ducks in particular have often been observed practicing male homosexuality. Mallards in particular have been noted to have up to 19% of pairs be homosexual (Bagemihl 1999).

It's up to brilliant future researches like yourself to uncover the mysteries behind this act which seems to have no apparent fitness benefit, and in fact doomed one species to extinction. The blue duck species pictured below is now going extincti as the last three individuals, a female and two males, have chosen sterile relationship paths. The males have bonded while the female remains solitary. Future studies of this duck species will be impossible, so comparative methods with other duck species will have to be used to understand this bizarrre phenomenon.

Figure 2.36: From <http://en.wikipedia.org/wiki/File:Whio_(Blue_Duck)_at_Staglands,_Akatarawa,_New_Zealand.jpg>.

2.4.6 Discussion Questions:

1. Which gender do you think first began to evolve the complexity leading to sexual conflict?
2. What is the social monogamy in mallards like?
3. Why don't males in other species practice forced copulation?
4. Why would matching male and female genital complexity exist in certain species and how does this apply to mallards?
5. Why might the hen's unconditional resistance be selected for and how might this affect selection on the drake's phalluses?
6. Ethics bonus question: Can mallard drakes be held morally responsible for forced copulation?

2.4.7 Glossary

- **Brood Parasitism**- when members of the same species surreptitiously place their own eggs in another's nest so that the parenting costs are placed on the host. Evidence for this would include above average clutch sizes and parasite visitations to find and use host nests, which is known as "hole-nesting" (Evarts 1987).
- **Cloaca**- the opening through which birds pass their excrement; also used directly by both sexes in most bird species to mate
- **Clutch**- group of eggs that a hen lays from one season

- **constraints theory**- "says that when individuals reproduce with nonpreferred partners, they will have offspring of lower viability than when individuals reproduce with preferred partners" (Bluhm and Gowaty 2004).
- **Drake**- male duck
- **Eversion**- the process of being turned outward as with the finger of a glove when the hand is removed
- **Forced copulation**- an act of mating in which one member of the party is unwilling; this may be between pair-bonded individuals and not just extra-pair
- **Good Genes Hypothesis**- choosing mates under sexual selection, in this case for the indirect benefits that they provide, namely genes
- **Hen**- female duck
- **Intromittent organ**- an external organ, usually of males used to deliver sperm. Can be seen in females, where it is used to receive sperm.
- **Mate-choice hypothesis for indirect benefits**- see good genes hypothesis
- **Phylogenetic Evidence**- evidence derived from assumptions about the ancestry of an organism. Based on data drawn from various sources including the fossil record and genetic analysis.
- **Reproductive success**- the relative production of fertile offspring by an individual.
- **Seasonal pair-bond**- a mutualistic bond between two mates, in which both stay near to each other for increased safety and reproductive success. Usually lasting in mallards until the end of the breeding season or when the female lays her clutch.
- **Sexual conflict**- is the result of differing evolutionary interests between the sexes of a species. This conflict is usually due to competition for greater reproductive success amongst members of the same sex but which often involves tactics that reduce the other sex's overall reproductive success.

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2.4.9 About the Author

Figure 2.37

Allen Gu <Goo> is a mentally stable, self-preserving genetic automaton. Born in Birmingham, Alabama, he would go on to spend the majority of his life in Louisiana eating crawfish and frying under the sun. After much preteen angst over his weak kung-fu, he chose to attend Rice University where he would attend BIOS 321. After reading the *Selfish Gene*, he came to realize that everything he had ever done and all the cells of his entire body were being controlled by inanimate objects that are too small to see with the naked-eye. These inanimate objects, he learned were in turn made in the chaotic hell zones of prehistoric Earth completely at random as were all living things. Driven mad by the dark knowledge he had attained of the world and his own existence, he would start on his path to being a *pre-med!!!*

Chapter 3

Parent-offspring interactions

3.1 Adoption and Infanticide in Birds: a Review[1]

Author: Brittany Hodgson

3.1.1 Introduction

Figure 3.1: Male barn swallow about to commit infanticide by throwing the non-related baby bird in his beak out of the nest.
Courtesy of Tico_Bassie and Flickr.

Natural selection causes behaviors that maintain or increase the fitness of an individual to spread in a population and behaviors that decrease fitness to fade away. This idea implies that behaviors now seen in animals must be adaptive. However, behaviors like adopting offspring, which costs energy and time helping them to survive, or like committing infanticide, which wastes energy killing offspring, do not obviously

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[1] This content is available online at <http://cnx.org/content/m34707/1.3/>.

increase the fitness of the actor. Why then would adoptive and infanticidal behaviors be found in so many organisms?

Box 3.1: Siblicide, a type of Infanticide

Birds perform infanticide on their own young, not just on other's young. Although they may not be the actors in the death of their young, they may be passive watchers, allowing another individual to kill their young. One example of this is manifest in siblicide, where adults watch as one of their chicks is repeatedly pecked and abused until it dies. Usually, this occurs in species that live in variable environments. The mothers lay more eggs than she can raise with the resources in the area. Because she cannot support all of these eggs, she allows the biggest and strongest to survive. Sometimes, the mothers may even stack the cards in favor of the oldest. By infusing the first egg with more testosterone and by laying it before laying others, the oldest chick is favored to win because of its big size when the younger chicks hatch. (Hillstron *et al.* 2006 and Fujioka 1985).

In birds, both infanticide and adoption occur in many different species from woodpeckers and hornbills to eagle owls and barn swallows (Hrdy 1979; Stacey and Edwards 1983; Chan *et al.* 2007; Penteriani and Delgado 2008; and Crook and Shields 1985) (see Figure 3.1 and Table 3.1). Moreover, infanticide generally occurs when an adult kills unrelated young (see Box 3.1 (Siblicide, a type of Infanticide)). The circumstances and the reasons behind the adoption and infanticide change with the species studied. In European starlings (*Sturnus vulgaris*), for example, males care for brood by incubating eggs and by feeding the young (Smith *et al.* 1995 and Pinxten and Eens 1994) (see Figure 3.2). Males are facultatively polygynous and will mate with females whose own mates have disappeared (Pinxten *et al.* 1993). However, if these females had already copulated with the males that disappeared, the replacement males will either adopt or kill the brood. Their choice is dependent on the expected paternity in the females' current clutches (if he arrives before it is laid) or how fast the female will mate with him for the next clutch (Smith *et al.* 1996).

Figure 3.2

Infanticide is not so common in other species of birds. In Tree Swallows (*Tachycineta bicolor*), for example, males generally choose to take care of a female's brood, despite low paternity, instead of committing infanticide (Whittingham *et al.* 1993), and in yellow-headed blackbirds (Xanthocephalus xanthocephalus), males actually use their adoption of unrelated broods to attract females for mating (Gori *et al.* 1996).

Males, however, are not the only ones who commit infanticide or adopt unrelated broods. In fact, there are some species of birds where the female commits infanticide. In these cases, like the house sparrow, the replacement mates are females (Veiga 2004). Moreover, infanticide does not always occur when one individual replaces another. In guira cuckoos, members of the communally breeding group may actually kill the hatchlings of the group in order to produce more of the offspring themselves.

3.1.2 Adoption or Infanticide? The European Starlings Dilemma

Table of Species that Adopt or Commit Infanticide			
Common Name	Latin Name	Common Name	Latin Name
Acorn woodpecker	Melanerpes formicivorus	Guira cuckoo	Guira guira
American kestral	Falco sparverius	House sparrow	Passer domesticus
Barn Swallow	Hirundo rustica	Mexican jay	Aphelocoma ultramarina
Eagle owls	Bubo bubo	Oriental pied hornbill	Anthracoceros albirostris
Eastern bluebird	*Sialia sialis*	Tree swallow	Tachycineta bicolor
European starling	Sturnus vulgaris	Yellow-headed blackbird	Xanthocephalus xanthocephalus

Table 3.1: Table of some of the various bird species that will adopt or commit infanticide of unrelated broods

European starlings, like most species of birds, form social pair bonds between mates. Because most avian young require intense parental care, these mating bonds allow the two adults birds to share the burden of feeding, raising and protecting the young (Clutten-Brock 1991; Burley and Johnson 2002). Many bird species engage in this biparental care, even in polygynous species like the European starling (Smith *et al.* 1996). However, these pair bonds are rarely permanent and are broken up as individuals die of predation or starvation or are forced to leave. For example, when a new male wins dominance over a new territory, the previously dominant male has to abandon the territory and any females in the area. These new males then take over and court and copulate with the females. These males are called "replacement males."

Box 3.2: Decision-making in Animals

It is important to note that when we say that animals have decisions and choices to make that we do not mean that the animals consciously rationalize the decision. It is neither logical nor efficient for an animal to think about the problems he faces and decide his course of action when he is in danger of being caught by a predator, dying of starvation or missing out on copulating with a ready female. Instead, animals have built in programs, which allow them to make quick decisions based on the circumstances. These programs are the product of generations of natural selection creating and altering, because natural selection favors those who respond in ways that increase their fitness. Behaviors that allow an animal to escape predation or starvation, or that increase copulations will allow the animal to ultimately pass on more genes. These behaviors will be favored by natural selection and be present in future generations of animals.

When replacement males take over a territory, the females are likely to have already mated with the previously dominant male. In situations where the female is about to produce a clutch or has just produced one, the replacement either adopt the young or kill them. There are many factors that influence what the male does (see Box 3.2 (Decision-making in Animals)). Some of these factors include when the old male leaves, when the new replacement male arrives, and when in relation to the female's egg- laying schedule do these two events occur. In a study by Smith *et al.* (1996), new European starling males quickly replace males that have been experimentally removed, so the day that the old male is males that have been experimentally removed, so the day that the old male is removed corresponds to the same day that the new male joins the territory. This day in its relation to a female's egg laying schedule determines what percentage of the brood the new male can father- his paternity (see Figure 3.2). The greater the number of days before egglaying that a new male dominants a territory and copulates with a female, the greater his expected paternity in the upcoming brood. Furthermore, the greater the paternity that a European starling male expects, the more likely he will be to adopt brood. Males want their own offspring to survive, so they will invest in caring for a brood if most of the young are their direct descendents. Inversely, the lower the expected paternity of a replacement male in a particular brood, the less likely are male European starlings to adopt and the more likely they will be to dispose of the young. This can be seen in the relative number of adoptions and infanticides that replacement males participate in based on when they begin to court female, either before or after her egg laying begins (see Figure 3.3) (Smith *et al.* 1996). A European starling was significantly more likely to adopt a female's brood when he replaced a male before the female's egg laying than after the female's egg laying. Also, there is a higher rate of brood infanticide when replacement males arrive during the female's egg laying. Because a male's expected paternity in a brood is low when he arrives when the female is already laying eggs, there is no advantage for his caring for young that are not his direct descendents- and therefore do not share his genes. It is much easier to kill the brood and court the female. However, in some instances, the male European starlings are better off avoiding infanticide in order to not waste energy (see Box 3.3 (Female Countertactics to Infanticide)). These cases all occur when the replacement male arrives late during the female's egg laying. There are several different hypotheses for this male indifference. First, there may be a cost to laying late in the season. If a male arrives late, this cost may not be worth the energy needed to commit infanticide, copulate with a female and raise a nest of young. There is also a chance that a female may abandon a nest site and abstain from breeding or breed somewhere else (Smith *et al.* 1996). In any case, it is not worth the effort for the male to commit infanticide when the chances of producing another brood with a higher paternity are slim and the effort to produce such a brood is immense.

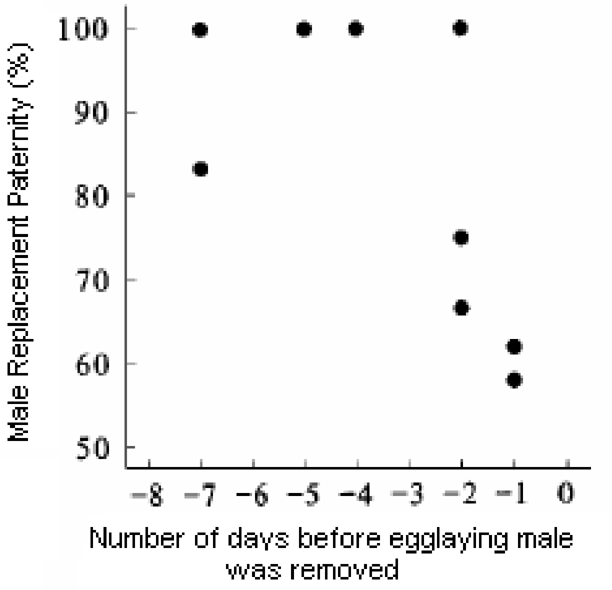

Figure 3.3: The calculated paternity that European starling replacement males have in a brood versus how long before egglaying the new male arrives. 0 is the first day of egglaying.

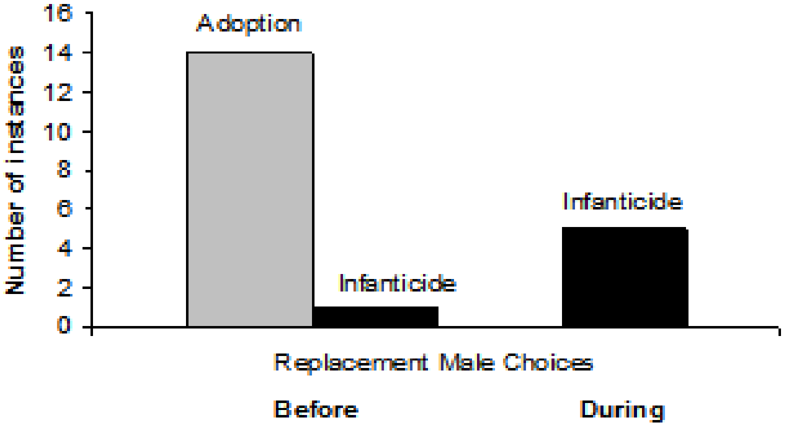

Figure 3.4: The absolute number of adoptions and infanticides by replacement males in an experimental population of European starlings. There is a significant correlation between replacement males's arrival before and during egg laying and their choice of adoption or infanticide. There were no adoptions by replacement males when replacement occurred during egg laying.

3.1.3 Tree Swallows: Low Paternity and High Parental Care

Box 3.3: Female Countertactics to Infanticide

Generally, females do not benefit from infanticide. They have already invested in the young, and the investment is lost with the young during infanticide. The offspring of the old brood and the new brood are still her offspring and share the same relatedness. The fact that females have come up with counter tactics to deter male infanticide is evidence that infanticide does not necessarily increase their fitness. Although they gain the help of the replacement male when raising the new brood, the waste of energy is immense. One cost of infanticide is the female's inability to produce as many offspring in the next clutch as she did in the previous one. This may occur if the area is running low on food due to coming of the end of the season. Typical female counter tactics include delaying egg laying so that males do not bother to kill the brood because of the late season, aggressively defending a previous clutch from replacement males by not letting him into her nesting box, and getting acquainted with the male and soliciting new copulations before he sees the eggs, fooling him into believing that they are his.

Tree Swallows (*Tachycineta bicolor*) are a monogamous bird species that have short breeding seasons and generally live in areas with few nest sites. Because of this, males have little time to find a mate and copulate with her and few resources to even procure this mate. In order to produce any offspring at all, male tree swallows have lower paternity expectations than their European starling counterparts. Male tree swallows are more likely to help females raise young and less likely to commit infanticide. Because of the narrow breeding period window, male tree swallows

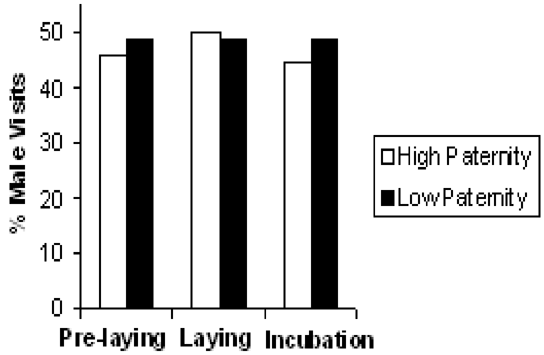

Figure 3.5: The probability of high paternity or low paternity does not impact how often the male visits the female nor when he visits her in the egg laying cycle.

cannot expect females to produce a whole new clutch of eggs where he can have a higher paternity. In fact, males will continue to provide high levels of parental care for young even when their paternity is low (Whittingham e*t al.* 1993) (see Figure 3.4). Since tree swallows do not recognize kin in the nest, adults cannot determine whether a young bird is one of their offspring or an unrelated bird (Beecher 1988). In the experiment that Whittingham *et. al* performed, tree swallow males were held captive and allowed to watch as their mates engaged in extra pair copulations with other males. The number of Figure 3.4. The probability of high paternity or low paternity does not impact how often the male visits the female nor when he visits her in the egg laying cycle. days that the males were held captive and the subsequent decrease in confidence of paternity as the females participated in more extra-pair copulations did not affect the amount of paternal care that the captive males later provided. When it was still probable that the males had some direct offspring, they continued to care for all of the young. The alternatives- to abandon the nest or to commit infanticide- would not lead the males to father more offspring because of the short breeding season and the lack of available nests. In fact, the threshold level of paternity, below which males will actually lower the amount of care they give or even commit infanticide, is close to zero (Whittingham *et al.* 1993). For tree swallow males, it is better to help a few direct offspring and other non-related offspring survive than to have no offspring survive at all.

Figure 3.6: Male Tree Swallow feeding a baby swallow. Courtesy of Steve Byland and Flickr.

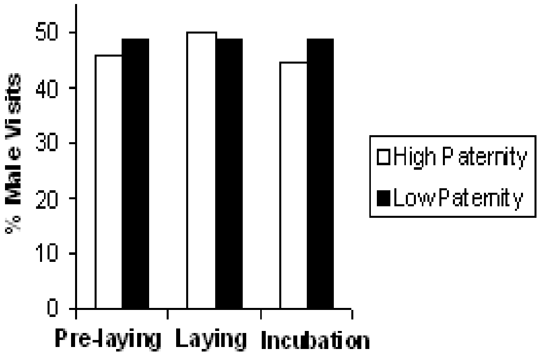

Figure 3.7: The probability of high paternity or low paternity does not impact how often the male visits the female nor when he visits her in the egg laying cycle.

3.1.3.1 How Yellow-headed Blackbirds Attract Mates

In the yellow-headed blackbird (*Xanthocephalus xanthocephalus*), males attract mates by adopting broods of others' offspring. In this species, females choose where to nest based on the number of females living on the territory and the number of active nests. The more females with active nests on a territory, the more resources the territory must have and the safer it must be from predators. These factors will lead females to nest in the same area. Replacement males, thus, may be able to attract new females ready to settle if they accept the presence of unrelated offspring in nests made by previous territorial males. In this case, adoption and not infanticide is the behavior that yellow-headed blackbirds choose as a tool to actually increase eventual fitness (Gori *et al.* 1996).

3.1.3.2 Female Infanticide in the House Sparrow

Due to gamete dimorphism, sperm is cheaper to produce than eggs. Males can, thus, copulate with many more females and father more children than females can produce. Females, however, will devote more resources into the care for the young to compensate for the fewer number (Queller 1997). This allows for males to be more mobile. This, and the fact that because of the internal fertilization of eggs males can never be sure about their expected paternity in a brood, usually leads to males being the sex typically faced with the decision to adopt or kill a brood. However, females are presented with this dilemma too. In the house sparrow (*Passer domesticus*), females have to compete with each other for limited nesting space (Veiga 1990). This competition leads to the selection of behaviors that will increase the chances of a female taking over a nest and her raising her offspring up to fledge. Many times when a new female takes over a previously used nesting site, the other females' young are still there. This new female now has to decide whether she should raise these offspring or if she should kill them. As expected, infanticide is not rare. In one study, female house sparrows committed infanticide over 20% of the time when females replaced other females (Veiga 2004). Moreover, because this nest is visited by the male that was helping to raise the other young, the female will kill off the other young in order to focus more of the male's time and resources on the caring of her own young. She will mate with this male and lay a clutch of eggs where he expects high paternity.

Female infanticide can also occur without a female's taking over a used nest site. In house sparrows, because the females are mated with a polygynous male, they are more likely to kill their rival's offspring in order to get more of the male's energy and time devoted to her and her offspring. When a polygynous male had other nests full of fledglings that needed care, female behavior that would give more, needed attention to her own offspring would be favored. Nearly 90% of these females committed infanticide (Veiga 2004).

Box 3.4: Adoptions: The Misfiring of Adaptive Parental Care

All behaviors do not necessarily have to be directly adaptive. In fact, there are many instances where an animal unknowingly decreases its fitness when performing some action. Some cases of adoption of young birds are examples of this. Kin recognition is not an ability that all bird species possess. Parents cannot tell their own offspring from other young and will resort to certain clues to determine who to feed. For example, if a young bird is hungry and in a nest, the adults in that nest will feed it. It is better for parents to care for all young despite the possibility that some of the young may not be theirs than to risk letting one of their own offspring die by not taking care of it. Generally, the policy of caring for all young in a nest is a safe bet for most two-parent offspring-raising systems because it is not common to find non-related young there, though brood parasitism is a notable exception (Wetzel and Chandler 2008; Krueger and Davies 2002).

3.1.3.3 Infanticide in the Communally Breeding Guira Cuckoo

The South American Guira Cuckoo (*Guira guira*)is one of the few birds that breeds communally, a type of breeding where three or more individuals reproduce together either in a joint nest or nearby nests (Brown 1987; Cariello *et al.* 2002) (see Figure 3.7). Guira cuckoo groups are composed of related and unrelated members, where up to 7 can be reproducing members who share a joint nest (Cariello *et al.* 2002). With a communal clutch of up to 26 eggs, competition occurs between these reproducing individuals, which leads to pushing other eggs out of the nest and to infanticide (Cariello *et al.* 2002; Macedo and Melo 1999). In larger groups where competition between the hatchlings is the most intense, guira cuckoo mothers lay larger, heavier eggs, which hatch into larger, heavier chicks that can better survive (Macedo *et al.* 2004). Smaller chicks are more likely to die due to infanticide than larger ones. Moreover, because older chicks begin to eat and grow before younger chicks hatch, they tend to escape infanticide more often than the younger chicks (Macedo *et al.* 2004). In the guira cuckoo, infanticide is a common occurrence, where nearly half of the young in the communal clutch can be killed. In most cases, an infanticidal adult picks up a few-day old nestling, tosses it out of the nest and pecks it repeatedly (Macedo and Melo 1999). Interestingly, the infanticidal adults are usually accepted members in the guira cuckoo group and not immigrant or replacement individuals. Macedo and Melo (1999) suggest that this could be a reproductive strategy used by the infanticidal adult to force the group to renest, lay more eggs, and possibly allow the adult to produce more offspring.

Figure 3.8: Guira Cuckoo, Guira guira.
Courtesy of Aaron Siirila

Though not typically considered “infanticide,” the guira cuckoo’s pushing other eggs out of the nest is a form of competition and a way to get rid of young that would compete with one’s own offspring for resources and protection. Like adoption and infanticide, the cuckoos have developed this behavior after generations and generations of natural selection. The practice of this behavior increases the fitness of the actor because it allows the actor’s eggs to make up a higher percentage of the total communal clutch. Moreover, cuckoos have developed counter tactics to this practice. By making the eggs heavier and larger, cuckoos have a harder time dumping them out of the nest (Macedo *et al.* 2004). Thus the heavy eggs serve a double purpose: to produce big chicks and to prevent egg-dumping!

3.1.4 Conclusion

Adoption and infanticide are two choices that replacement adults often have when approaching a clutch that may or may not be theirs. The adaptive value of one behavior over the other varies from species to species and depends on the general ability of the replacement adult to actually parent another clutch. When this is a feasible option, infanticide is more likely, but if there are constraints to producing another clutch, adoption becomes the more viable option. The choice between the two has evolved to account for the probabilities of paternity versus the risk of no offspring at all, creating interesting differences between individuals and species.

3.1.5 Discussion Questions

1. The Yellow-Headed Blackbird engages in much more adoption than the species discussed. What factors, beyond the potential to impress new females, might contribute to this different behavior?
2. In a species that always adopts, such as the tree swallow, could infanticide be selected for? Under what conditions?

3.1.6 Glossary

- **Adoption**- An adult's providing parental care for young not their own.
- **Biparental Care**- A system of care where two adults- a male and a female pair- take care of the young.
- **Brood Parasitism**- When another bird, either intraspecific or interspecific, lays an egg in someone else's nest. This is a form of "cheating" because the brood parasite does not have to care for her own egg.
- **Communal Breeding**- Three or more individuals in a group reproduce at the same time, sometimes using the same nest.
- **Direct fitness**- A measure of genes contributed to the next generation by an individual via one's own offspring
- **Egg laying**- The period of time (usually measured in days) during which a female lays eggs using sperm from recent matings.
- **Extra pair (copulations)**- Copulations between 2 individuals who are not in a social pair bond.
- **Indirect fitness** - A measure of genes contributed to the next generation by an individual by helping related individuals except direct offspring.
- **Infanticide**- The killing of a young animal by an adult by preventing it from receiving the resources it needs to develop. In bird species, this most often occurs by adults throwing the young out of the nest, repeatedly pecking it and leaving it to die.
- **Male Investment**- The amount of energy, resources and time that a male puts in to producing and raising young. This includes his preconception effort- his sperm- as well as the care he gives the young and the female bird once the eggs have been laid.
- **Monogamy**- A mating system where males generally mate with one female and help her to raise her brood.
- **Parental care**- The care given by adults to young already hatched in terms of resources and time devoted to the survival of the young.
- **Parental investment**- Activities performed by adults toward the production and survival of young. These activities can will reduce the parent's chances of producing future offspring and include activities before and after the actual production of young.
- **Paternity**- The offspring in a brood that are a male's own offspring.
- **Polygyny**- A mating system where males mate with several females.
- **Replacement male**- The new male that courts a female that has recently lost her old mate by death or a lost fight. If the female has mated with the other male, the replacement male has the option of either adopting a female's clutch or destroying the clutch through infanticide.

- **Social Pair Bond**- A relationship between two birds, one male and one female, that defines a social understanding that they will help each other to raise their offspring. They are not necessarily a sexually monogamous pair.

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3.1.8 About the Author

I was born in Houston, Texas and am a junior at Rice University majoring in Biochemistry and Cell Biology. I love trying and learning new things, so I have enjoyed studying animal behavior. I did not realize how complex the animal world was in terms of behaviors and social relationships until I took this class. Writing this chapter, I got to learn more about certain bird species and their adoptive and infanticidal behaviors and how natural selection allows these behaviors to evolve.

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Chapter 4

Why help someone else breed?

4.1 Cooperative Breeding in Birds[1]

Author: Omar Metwalli

4.1.1 Introduction

Helpers assist in raising nondescendent kin, individuals that are not their progeny, by collecting food, building nests, and warding off predators (Canário et al. 2004). Their presence is consequently expected to increase the survival rate of young hatchlings. The helpers, or alloparents, take on a subordinate altruistic role rather than maximizing their own direct reproduction, so as to increase the native parents' reproductive output. This cost, however, must be outweighed by its benefits if it is to be a positively selected trait.

The benefits of cooperative breeding are more obvious when considered in light of the theory of kin selection formulated by W.D. Hamilton in 1964. Kin selection is a form of natural selection favoring altruistic behavior toward close relatives. Though this behavior does not directly increase an individual's reproductive fitness, as is possible by personal reproduction, it does provide an evolutionary benefit in the form of indirect reproductive fitness. This idea's genetic basis is also explained by W.D. Hamilton's theory, which identifies the ultimate goal of reproduction as the passing on of one's alleles (Hamilton 1963). Helping to raise nondescendent kin as a helper in cooperative breeding systems achieves this goal, albeit indirectly.

Box 4.1: Hamilton's Rule

In accordance with his theory, Hamilton developed a rule by which kin selection could be analyzed quantitatively. The rule, which can be written as an inequality, dictates that genes should exhibit increased frequency when $rB>C$. r represents the genetic relatedness of the recipient to the actor. It is based on the probability a gene picked randomly from each individual will be identical by descent. B stands for the reproductive benefit gained by the recipient, and C denotes the reproductive cost to the altruist. Thus, genes encoding altruistic behavior will gradually become more prevalent if the benefit to the recipient, multiplied by a factor of relatedness, is greater than the cost to the actor. If the cost to the individual performing the action exceeds the product of the beneficiary's fitness gain and the participants' genetic relatedness, evolution will select against the gene and its frequency will decrease.

Though there are numerous examples of kin selection among birds, helpers are not always related to the offspring they rear. In these situations, as among Azure-winged Magpies, there are usually ecological factors that promote cooperative breeding as well as numerous benefits that offset the reproductive costs incurred by helpers (Canário et al. 2004).

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[1] This content is available online at <http://cnx.org/content/m34719/1.3/>.

In most cooperatively breeding birds such as Micronesian kingfishers, helpers are commonly sub-adults, or young individuals that are reproductively mature but choose not to breed (Kesler & Haig. 2007). Other species, such as the brown-headed nuthatch, are conditionally cooperative breeders. Individuals of this type all attempt to breed independently each year and only resort to helping when their nests fail (Cox et al. 2007). In some unique instances, such as in populations of the Seychelles warbler, cooperative breeding is facilitated by not only sub-adults but also post-reproductive grandmothers that have lost their position of breeding dominance (Richardson et al. 2007).

4.1.2 Why Be a Helper?

This section aims to identify the benefits helpers accrue in compensation for their reproductive costs, as well as the external variables that promote cooperative breeding.

The presence of helpers in cooperatively breeding units increases the survival rate of young hatchlings (Canário et al. 2004). This result is obviously beneficial to the new generation but it comes at a price to the helper, who must sacrifice time, energy, and the opportunity of having their own offspring during that breeding season. In light of these costs, there must be an evolutionary reason for birds to still engage in cooperative breeding. An examination of this form of breeding in the azure-winged magpie provides some clues as to why and when it makes evolutionary sense to be a helper.

The azure-winged magpie is a member of the Corvidae, or crow-family, of birds (Figure 4.1). It breeds in small colonies and feeds mainly on insects. Helpers of cooperatively breeding families in this species do not follow a pattern of kin selection in that they are not necessarily directly related to the families they assist (Canário et al. 2004). They contribute to nest building and upkeep, feeding nestlings and brooding females, and warding off predators. In a study of Iberian Azure-winged Magpies in Portugal during two consecutive breeding seasons, researchers found the number of helpers and cooperatively breeding units to be heavily influenced by changes in the weather. The year that experienced significantly more rainfall (~30%) witnessed an increase in the number of helpers and cooperatively breeding units (Canário et al. 2004). This may be attributed to the fact that rainfall has a marked influence on the presence of invertebrates, which are the main component of the Azure-winged Magpie's diet. During rainfall, insects tend to seek cover making it more difficult for Magpies to find them. This reduces the available food supply. As a result, increased numbers of helpers appear because the low probability of successful reproduction caused by limited resources discourages a large proportion of mature adults from breeding and instead encourages them to invest in rearing the offspring of others.

Box 4.2: Do Parents Benefit From Helpers?

In some species, such as the Long-tailed tit and the Arabian babbler, an inverse relationship between the number of helpers and the provisioning rate of the native parents has been documented. This reduction in care by parents of cooperatively breeding units is often correlated with populations exhibiting low rates of nestling starvation and the possibility of having more than one brood per season (Hatchwell et al. 2000). This observation, for example, has not been recorded in Azure-winged Magpie parents, which do not reduce their chick feeding levels when they are aided (Canário et al. 2004). This is due to the fact that these Magpies produce only one brood every season. As a result, the pressure to successfully raise offspring is much higher than in species that have multiple broods per season. Thus, the parents pass on a more significant share of the benefit helpers contribute directly to their offspring.

Figure 4.1: Azure-Winged Magpies
These crow-like communal birds can only be found in the Iberian Peninsula or East Asia.

Though this study demonstrates that cooperative breeding can be caused by ecological factors such as weather and the availability of food, it does not describe why a bird chooses to become a helper rather than a floater, a bird with no territorial or rearing commitments. The natural evolutionary preference towards being a helper can be explained by taking a closer look at cooperative breeding in the Micronesian kingfisher.

4.1.3 The Benefits of Helping

The Micronesian kingfisher (*Todiramphus cinnamominus*) is an endangered native of the Micronesian islands of Guam, Pohnpei, and Palau (Figure 4.2). These small colorful birds live in forest thickets. Both males and females play a major role in caring for young, and offspring often remain with their parents as helpers after they have reached adulthood. This tendency towards cooperative breeding is of particular concern because kingfishers that decide to become helpers at the nest essentially remove themselves from the eligible reproducing population for that breeding season, forfeiting a chance to pass on their genes. Studies using radiotelemetry and remote sensing to record habitat preferences have revealed, however, that despite this disadvantage, Micronesian kingfishers in cooperative breeding families are able to collectively secure better resources and larger territories than those in single pair breeding families (Kesler & Haig 2007).

Figure 4.2: Guam Micronesian Kingfisher
This subspecies is extinct in the wild as a result of the introduction of brown tree snakes to its native island of Guam during WWII.

The presence of additional mature kingfishers in cooperative breeding units allows them to out-compete single breeding pairs for the most beneficial settling sites (Figure 4.4). This prospect of access to ideal territories is just one of the evolutionary motivations for birds to participate in cooperative breeding, and may explain helping behavior beyond a kin selection model.

Kesler and Haig's study also showed that not only did all of the adults in cooperative breeding families enjoy more resources than their single-pair counterparts, all adult members of the cooperative units used equal amounts of resources (2007). Thus, helpers are entitled to the same amount of food and shelter as the native parents, indicating they do not sacrifice their physical well-being to any measurable degree, by participating in a cooperative breeding arrangement. Instead, they are actually given access to exceptional resources they would have not been able to acquire otherwise.

Furthermore, helpers are also eligible to inherit their parents' territory once the parents die. Consequently, any lost reproductive chances they endure while waiting to inherit the territory is offset by the long-term fitness gains of eventually controlling the territory. In an environment with a limited number of ideal territories, such as the Micronesian islands, it is well worth a young kingfisher's time and effort to be a helper in order to attain a premier nesting site (Kesler & Haig 2007). Helpers therefore also benefit from a cooperative breeding arrangement by being provided a breeding territory they do not have to fight or search for.

Box 4.3: Mechanism of Kin Recognition in Long-Tailed Tits

Long-tailed tits respond differently to various broadcast calls (Hatchwell et al. 2001). They are able to differentiate between those of kin and non-kin. This discriminatory behavior could be used in deciding which individuals helper tits will commit to helping. The nature of the calls, however, does not always describe the genetic relatedness of the birds, but rather association with a particular group. This observation is further supported by the fact that parents raising foster chicks do not discriminate between them and their direct progeny because all of the nestlings learn to elicit the

> same vocal cues (Hatchwell et al. 2001). In addition, the helping behavior of cross-fostered siblings shows that they do not differentiate between related and unrelated brood mates, supporting the proposition that the kin recognition mechanism is not innate, but learned through association. Thus, in the case of long-tailed tits, kin selection is based on social relationships rather than actual genetic similarity.

Cooperative breeding thus has many attractive survival benefits to allure prospective helpers. These physical benefits, however, are not the only evolutionary motivation for helpers to assist parents in raising offspring. If the helpers are related to the offspring they are helping to rear, they are actually indirectly benefitting themselves in a genetic sense. By increasing the chance that one of their younger siblings, for example, will survive, helpers are indirectly improving the chance that their own genes will be passed on, since siblings share half of their genes.

4.1.4 Selfish Helping

The motivations, however, for becoming a helper in a cooperative breeding system are not always ultimately based upon improving the chance an individual will pass on their genes. Sometimes, adult birds become helpers for the sole reason of accruing personal benefits. This discrepancy has been observed among Brown-headed nuthatches (*Sitta pusilla*) (Figure 4.3).

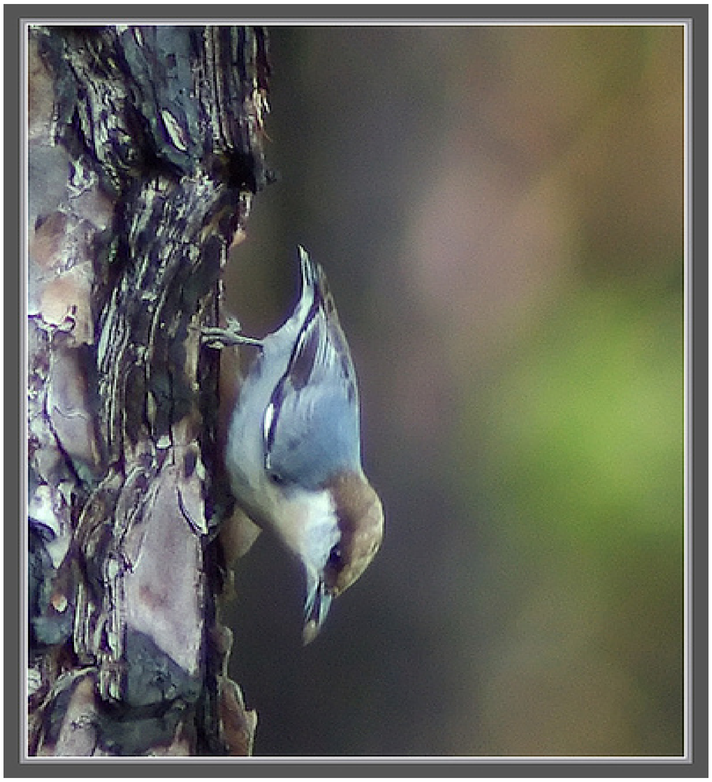

Figure 4.3: Brown-Headed Nuthatch
Nuthatches are small cavity-dwelling passerines (perching song birds). They are usually monogamous, pairing with their partners for life.

In a population of nuthatches studied in north Florida, about 20% of adults were recorded to engage in cooperative breeding, indicating it is a relatively widespread phenomenon (Cox et al. 2007). Surprisingly, a survey of nestling survival rates revealed that the presence of helpers did not actually increase nest productivity. Some nests had up to 5 helpers and yet the average number of nestlings raised by cooperatively breeding and single-pair breeding families was both approximately 4 chicks per season (Cox et al. 2007). This statistic indicates that the majority of benefits resulting in helper activity are enjoyed by the native parents, instead of the offspring; all of the nuthatch nestlings, whether they are raised in a cooperatively breeding unit or not, receive the same amount of total care from their guardians. Additional helpers share in meeting this set quota of care, alleviating the responsibilities of other adults while not ultimately increasing the net care delivered to progeny.

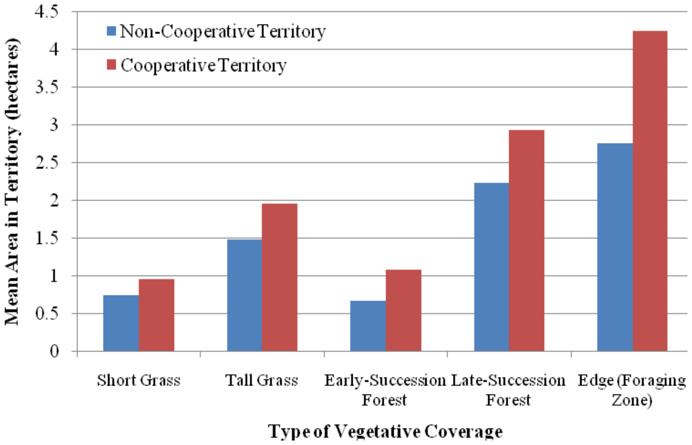

Figure 4.4: Average Area of Types of Habitat in Territories of Non-Cooperative and Cooperative Breeding Families Despite the fact that non-cooperative parents outnumbered cooperative parents, the cooperative families controlled more of every kind of habitat, especially ideal foraging areas (edge zone), due to the assistance of their helpers (Adapted from Kesler & Haig 2007).

Adult nuthatches usually resort to helping behavior following personal nest failure (Cox et al. 2007). The main causes of this failure are often depredation by higher consumers or the destruction of their nest by fire or other natural phenomena. The secondary motivation for helping behavior is the inability of young adults to successfully find a mate and breed. This is often attributed to a shortage in the female nuthatch population or an increased density in local nuthatch nesting sites (Cox et al. 2007). Female nuthatches are more susceptible to predators because they are often taking care of young progeny at the nest, while the males collect food. As a result, they succumb to predation by animals looking for nuthatch eggs or chicks. In reference to the availability of territories, an increased density in nesting sites results in a reduced dispersion of resources among individuals. This decreased supply of resources makes it more difficult for breeding pairs to sufficiently provide their nestlings with food; as a result many pairs will either choose to not produce offspring or become helpers at their parents' nests. Thus, in some bird species the incentives for becoming helpers are solely based on selfish interests, such as securing personal security and food sources, rather than helping indirectly related nestlings survive. In such cases, helping behavior is the cost these individuals pay for access to the benefits of communal living.

4.1.5 Grandparent Helpers

So far, only young helpers capable of reproducing have been examined. Older birds that have become too old to have offspring, however, also sometimes take up the role of helper.

Figure 4.5: Seychelles Warbler
A passerine endemic to the Seychelles Islands, they live in cooperatively breeding units containing up to 3 generations of individuals.

A grandparent as a helping subordinate in a cooperative system is a phenomenon that has been observed in a few exclusive species. The Seychelles warbler (*Acrocephalus sechellensis*) is one of these unique species (Figure 4.5). It is a small song bird found exclusively on the Seychelles islands. Interestingly, the majority of helpers within this species tend to be females (Richardson et al. 2002). Observations gathered over several years suggest that dominant, reproducing females are occasionally displaced by younger, more fertile females (Richardson et al. 2007). These displaced birds either become floaters or choose to join a cooperatively breeding family as a helper.

A population of these Seychelles warblers on Cousin Island in the Indian Ocean has been strictly monitored since 1981. By recording the complete life history and pedigree of the studied warblers Richardson et al. were able to study the phenomenon of grandparent helpers, which make up roughly 10% of the helper population (2002). Between 1981 and 2004 it was observed that about 14% of females in dominant breeding positions lost their status through usurpation by another female, in the remaining cases the females retained their position until they died. 68% of deposed females became subordinates, while the rest became floaters (Richardson et al. 2002). Thus, becoming a helper appears to be a favored outcome among these individuals.

From an evolutionary perspective, as a bird gets older the cost of reproduction increases. At some point in the bird's lifecycle it will no longer be beneficial for it to breed its own offspring. Older females can thus maintain greater reproductive benefits by increasing the reproductive success of their relatives, rather than breeding themselves (Williams 1957; Hamilton 1966). In this manner they are still able to pass their genes on to a limited extent, similar to the sibling helpers in Micronesian kingfishers.

Often the dominant female is deposed by related individuals. In 57% of displacement cases among Seychelles warblers, the new dominant female was identified as being a daughter, sister, or niece of the deposed female (Richardson et al. 2007). Since deposed females tend to help the nest they were originally breeding in, this observation indicates that in most cases the grandparent helper ends up increasing the reproductive success of a closely related warbler. In accordance with Hamilton's theory, this behavior maximizes a grandparent's gene dispersal and as a result, is evolutionarily favorable.

Box 4.4: White Ibis

Non-breeding female White Ibises (*Eudocimus albus*) have been observed tending to multiple nests with which they are not necessarily related (Herring & Gawlik 2007). The females were noted as visiting up to 5 different nests. They would rearrange eggs, weave fresh material into the nest, and shade nestlings. These birds did not brood or feed chicks; this responsibility was fulfilled by the direct parents of each nest. Interestingly, attendant male White Ibises exhibited aggressive behavior to these assisting females, forcing them to abandon their efforts (Herring & Gawlik 2007). This suggests the behavior is concurrently innate and not necessarily based in helping to raise related young. Whether or not this behavior is truly cooperative is thus debatable because these Ibises do not directly assist in nurturing the young and their assistance is not readily accepted by the direct parents.

However, reproductive fitness benefits of helping in these cooperatively breeding warbler communities include more than just the chance to indirectly pass on genes. Subordinate females also have the chance to breed offspring of their own. Unlike other bird communities, such as the Micronesian kingfisher where helpers completely forfeit the opportunity to reproduce, 44% of Seychelles warbler helpers, during every breeding season, are able to directly increase their reproductive fitness by having offspring of their own (Richardson et al. 2002).

In light of these advantages, it is strange that deposed females ever choose to become floaters, a role that provides neither direct nor indirect reproductive fitness. This mystery is accounted for by considering the quality of resources available in different territories. As illustrated by Figure 4.6, it has been observed that the quality of territories on which ousted breeding females become subordinates is consistently higher than the quality of territories where they become floaters (Richardson et al. 2007). Thus, similar to how ecological factors determine the level of cooperative breeding in the Azure-winged Magpie, the probability a displaced warbler will adopt a helping role is dependent upon whether or not the territory holds enough resources to support an additional member.

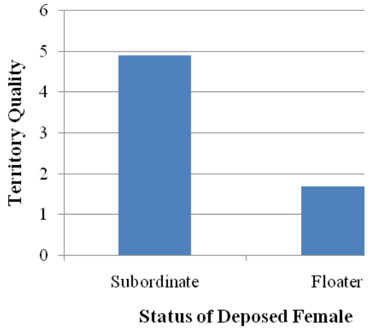

Figure 4.6: Quality of Territory Previously Inhabited by Deposed Female Warblers Values of territory quality were derived from logistic regression analyses and normalized by log transformation. Ousted females that chose to become subordinates usually lived in territories of higher quality than those that chose to become floaters (Adapted from Richardson et al. 2007).

4.1.6 Conclusion

Cooperative breeding is driven by a variety of ecological factors, specific to the circumstances of the species in question. Some adult birds choose to become helpers in an effort to secure food and settling sites when resources are scarce. Others resort to helping behavior because their own personal attempts at reproduction have failed or they have lost their breeding status, and helping is the next best opportunity to pass on their genes, albeit indirectly. In each case, the cooperative breeding phenomenon appears to benefit either the helpers, the parents, or the chicks, creating a beneficial situation for the individuals involved.

Cooperative Breeder	Reason for Helping
Azure-Winged Magpie	Lack of available resources
Micronesian Kingfisher	Access to ideal nesting sites and food
Brown-Headed Nuthatch	Personal breeding failure
Seychelles Warbler (Grandparents)	Best opportunity to pass on genes

Table 4.1: Why Cooperative Breeders Choose to Become Helpers

4.1.7 Discussion Questions

1. Is cooperative breeding actually altruistic behavior? In what situations might it be entirely altruistic, and in what situations does the helper have an “ulterior motive”?
2. While many birds do engage in cooperative breeding, many do not. What are the conditions that likely differentiate these species in terms of environmental factors, predation risks, and breeding patterns?

4.1.8 Glossary

- **Altruism**- helpful behavior that directly increases the fitness of the recipient at the expense of decreasing the fitness of the actor
- **Alloparent**- offspring care-giver that is not a direct parent

- **Cooperative breeding**- social system where individuals that are not the direct parents of the offspring play an active role in nurturing and caring for offspring
- **Direct fitness**- genes are contributed to the next generation through personal reproduction, in the form of descendent offspring
- **Dominant pair**- direct genetic parents of offspring
- **Floater**- bird with no territory or permanent residence
- **Hamilton's Rule**- gene frequency should increase in interactions where $rB > C$, where r is the genetic relatedness of individuals, B is reproductive benefit gained by the recipient, and C represents the reproductive cost to the alloparent
- **Indirect fitness**- genes are indirectly contributed to the next generation by helping non-directly related offspring in the form of relatives that would not have survived otherwise
- **Kin selection**- form of natural selection that occurs when individuals alter their behavior to favorably affect genetically related individuals
- **Nondescendent kin**- young progeny that are not direct offspring

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Chapter 5

Evolution of sterile castes

5.1 A Marine Dwelling Eusocial Organism: Synalpheus Regalis[1]

Author: Esra Deniz Gumuser

5.1.1 Introduction

The major measure of success of an organism's fitness is that the extent to which its genes are propagated through reproduction. Why, then, would an organism forgo the chance to spread copies of their genes by never reproducing? Several answers to this question have been formulated through experiments and observations of eusocial species found in the insect orders Hymenoptera and Isoptera (Wilson et al. 2005, Robinson 1992). One explanation is that **ecological constraints** create situations where eusociality is advantageous for both the reproductive individual and the non-reproducers (Buckle 1980). For instance, nests are difficult and dangerous to come by for most eusocial species, reducing the chances that a solitary individual could find another unoccupied nest, which is necessary for juveniles' survival (Michener et al. 1974). Even if a nest is found, the solitary individuals are unable to defend their nests while foraging for food, resulting in a low survivorship of young due to predation (Batra 1966). In simple social species such as *Liostenogaster flavolineata*, adult worker females have a chance of becoming queen when the current one dies; thus becoming the sole reproductive individual (Bridge et al 2007). By remaining in natal nests to assist the development of juvenile siblings, adults forgo their opportunity to reproduce but still increase their **fitness** (copies of genes in future generations) through **indirect** measures and kin selection (Box 5.1 (Indirect and Direct Fitness)). Overall, in most social species including the sponge-dwelling shrimp *Synalpheus regalis*, eusociality arises due to ecological factors of limited food resources and shelter. These situations can be combated through the creation of castes that chiefly forage, defend, or reproduce—leading to the formation of **eusociality** (Crespi et al. 1995).

Box 5.1: Indirect and Direct Fitness

Several times in the paper, the idea of indirect fitness has been mentioned to replace notions of direct fitness. Fitness is measured in terms of genes contributed to the next generation by an individual; this can be done through indirect or direct measures (Burt 1995). Direct fitness occurs when individuals themselves reproduce, ensuring that their genes are passed onto their own offspring. The sole reproductive female in *S. regalis* propagates its genes through direct fitness, since the offspring owe their existence to her and no one else. On the other hand, indirect fitness entails an individual helping to raise related kin rather than reproducing on their own. By doing so the individual makes certain that the offspring will survive into adulthood, passing on some of their own genes due to relatedness (Burt 1995). The concept of kin selection asserts that indirect fitness can be selected for as long as Hamilton's Rule of C-B(R)$<$ 0 is upheld (Box 3). The male defenders

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[1] This content is available online at <http://cnx.org/content/m34733/1.3/>.

spread their genes to future generations with indirect fitness through caring for juvenile siblings. Therefore, eusocial individuals can only have their genes passed to the next generation through indirect fitness by facilitating the growth of siblings into adulthood—only the sole reproductive individual take part in direct fitness within eusocial species.

5.1.2 The Organism: Synalpheus regalis

The organism used in this chapter, *Synalpheus regalis* (Picture 5.1), is commonly found in sponges within the tropical West Atlantic along with four other eusocial species of shrimp: *Synalpheus filidigitus, Synalpheus chacei, Synalpheus brooksi*, and *Synalpheus "rathbunae A"* (Duffy 1992). These sympatric species of social *Synalpheus* rarely overlap in host sponges used and never co-occur in individual sponges so it looks like the shrimp exclude **heterospecific** competitors (Duffy et al. 2002). The populations in sponges contain a few hundred individuals, each with two generations of kin.For their entire lives, these shrimp live in the internal canals of the host sponge, using it as a food resource and shelter (Box 5.4 (Sponge habitat leading to diversity of *Synalpheus* species)). The shrimp feed on the host tissues as well as on the detritus, which includes bodies of dead organisms or fecal material. Since there is no planktonic stage in this species and no other known mechanism of dispersal, juveniles stay in their natal sponge for the duration of their lives (Duffy et al. 2002). Table 5.3 shows the sampling of 64 sponges from two species that are commonly occupied by sponge dwelling shrimp. Fewer than 5% of the individual sponges used by *Synalpheus regalis* in Carrie Bow Cay, Belize were left unoccupied, implying a strong competition for suitable nest sites that could discourage solitary living. This ecological constraint results colonies with closely related individuals and outside non-related individuals are seen as intruders who are attacked (Duffy et al. 2002). Mature females are easily identified by their ovaries which are visible through their transparent bodies in *S. regalis*. The other shrimp without ovaries are either mature males (large bodied) or juveniles (small bodied). The only morphological caste difference is found in the queen, the sole reproductive individual, who lacks the large snapping claw and instead has a minor claw used for feeding (Duffy et al. 2002). This is feasible since the queen does not need a large claw since she has a caste of defenders, whose primary duty is to ensure her survival.

Picture 5.1: The interaction of two *Synalpheus regalis* facing off in an agonistic interaction (permission obtained: http://web.vims.edu/bio/mobee/index.html?svr=www[2])

5.1.3 The Success of Group Living in Synalpheus Regalis

S. regalis occupies the small internal canals of tropical sponges, with colonies as large as several hundred individuals. The sponge-dwelling shrimp, *Synalpheus regalis*, has increased reproductive success though group living. Experiments show that larger groups out-reproduce smaller groups in this species. In Figure 5.2, it is documented that the larger the colony size, the more eggs produced by the colony, thus greater reproductive success (Duffy 1996b). Through the sampling of unmanipulated colonies, data shows the colonies' reproductive yield increasing by a factor of 177 times in colony sizes ranging from 2-356 individuals (Duffy et al 2002). The colonies of *S. regalis* consist of large kin groups with adults of at least two generations, allowing for the non-reproducing individuals to still pass on their genes through rearing relatives—whether it be through foraging, defending, or any other job that increases juvenile survival—rather than having their own offspring.

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[2] http://web.vims.edu/bio/mobee/index.html?svr=www

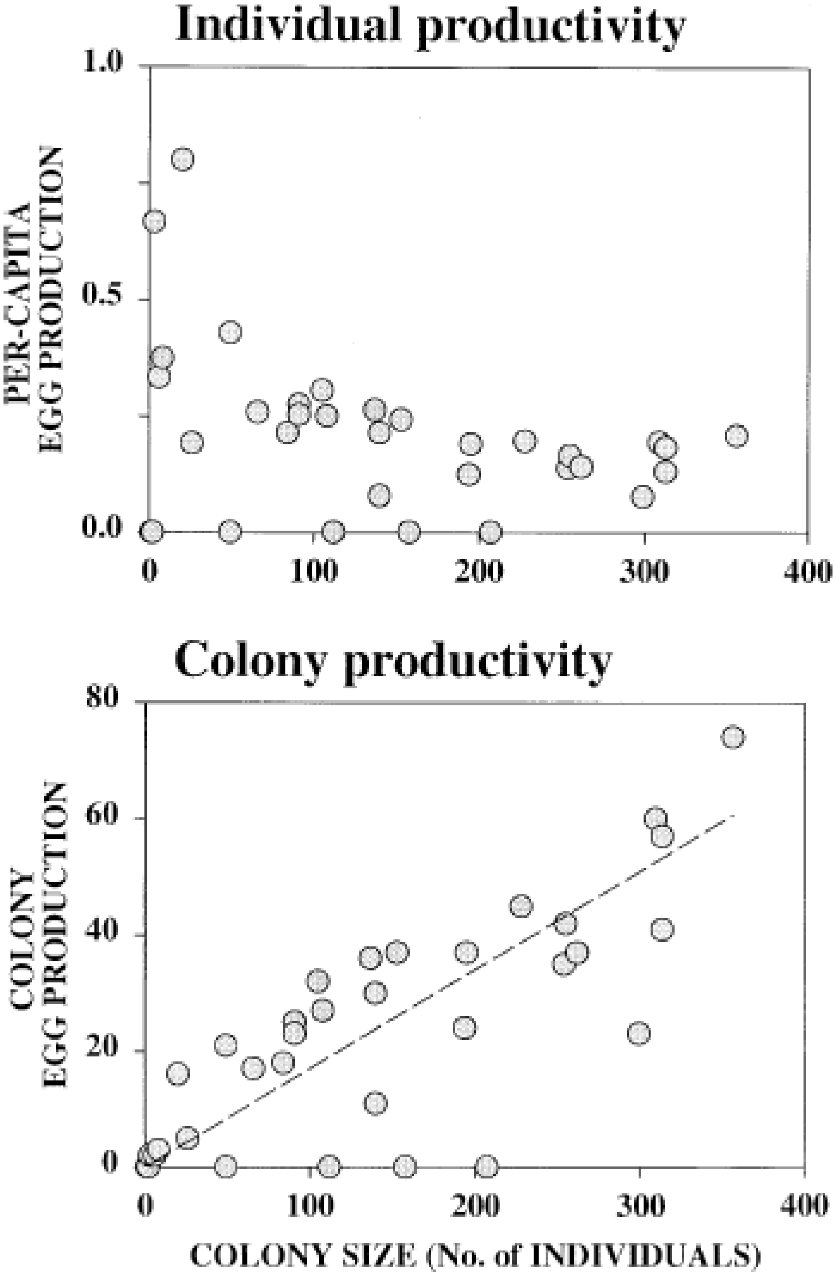

Figure 5.2: Egg production of *Synalpheus regalis* based on total colony egg production and average per capita production, as a function of colony size (number of individuals). Average per capita represents the clutch size divided by the total number of individuals in the colony—the egg number is the size of the clutch. This figure shows that the larger the colony size, the increase in colony egg reproduction (Duffy et al. 2002).

Within the colony there are large males that defend the colony from intruders. Their sole duty is to protect the remaining two castes, the sole reproductive female and the juveniles (Picture 5.3). Experimental data by J. Emmett Duffy show the emergence of castes in the eusocial shrimp—with large males more likely to snap and attack heterospecific intruders than juveniles or female queens (Figure 5.4). Thus the first requirement of eusociality, reproductive division of labor, is satisfied in *S. regalis* (Duffy 1998). This is fulfilled by adults remaining in their natal nests due to the difficulty of colonizing another unoccupied nest. Attempting to join another colony is also difficult since **conspecific** organisms are also seen as intruders to the defenders, causing them to be attacked. Along with the reproductive division of labor, the overlapping of generations and the cooperative care of young are all traits commonly found in eusocial species (Duffy et al. 2002).

Picture 5.3: An adult male defender *Synalpheus regalis* guards an entrance into the host sponge *Lissodendoryx colom biensis*
(permission obtained: http://web.vims.edu/bio/mobee/index.html?svr=www[3])

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[3] http://web.vims.edu/bio/mobee/index.html?svr=www

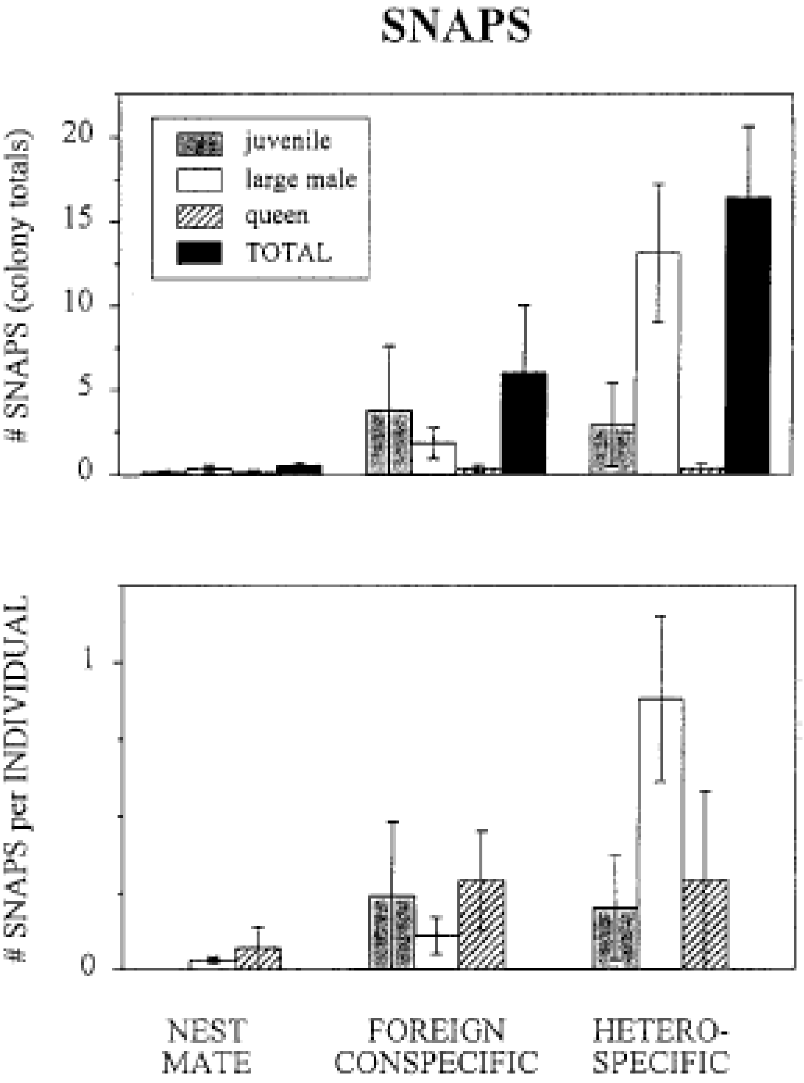


Figure 5.4: The number of snaps per individual and colony in a *Synalpheus regalis* nest, which contains 15 juveniles, 15 adult males, and 1 queen. Both figures show that large males, rather than juveniles or females, are the most likely to attack any intruder, with heterospecific intruders being attack more than conspecificintruders. (Duffy et al. 2002).

5.1.3.1 Kin Selection: Life Insurance and Fortress Defense

How does natural selection favor individuals cooperating to produce a greater, more successful whole, even if it means never reproducing? William D. Hamilton's theory of kin selection helps to answer this question. Kin selection is rooted in genes producing copies in two manners: **direct** fitness by rearing offspring or indirect fitness by helping to care for relatives who also share these genes (Box 5.1 (Indirect and Direct Fitness)). Therefore helping your relatives will always be advantageous. Natural selection favors this altruistic behavior when the cost of helping kin is less than the reproductive benefit achieved for the beneficiary of the altruism. This reproductive benefit can be evaluated by examining not only the benefit to the other individual, but also the degree of relatedness between the altruistic individual and the beneficiary (Box 5.2 (Calculating Hamilton's Rule)) (Hamilton 1964). Thus kin selection explains how eusocial behavior could arise in sponge-dwelling shrimp. The benefit in this ratio is very large, since juveniles (the sole means to pass your copy of genes) are incapable of fighting for themselves due to the lack of claws. The non-reproductive defenders ensure that these juveniles would survive, exalting a cost for not reproducing that is greatly overshadowed with the ascent of the juveniles into adulthood. Since juveniles never leave their natal nest, there is a high coefficient of relatedness in the sponges. By living with relatives, members of the colony can alter their behavior within the colony as a juvenile, breeding female, or a large male (Agrawal 2001). For example, even though some juveniles are not offspring of the large male sponge-dwelling shrimp, they share some of the same genes, resulting in an indirect fitness benefit for the large males when they ensure the survival of the juveniles. Allozyme data collected by Duffy et al. prove that the majority of colony members are full siblings—allowing for kin selection and indirect fitness to take place due to a high degree of relatedness.

Box 5.2: Calculating Hamilton's Rule

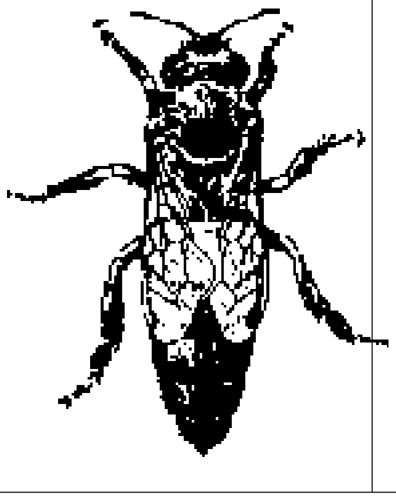
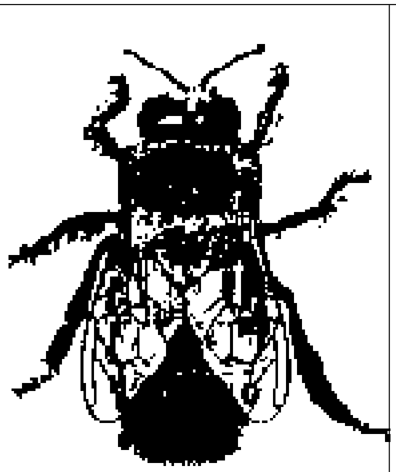
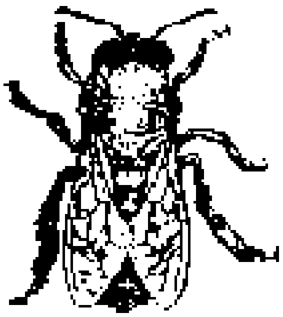
Hamilton's rule is a mathematical formula in determining if altruistic indirect fitness can be selected for by kin selection. The formula is C-B(R)<0, with C as the cost of the action for the actor, B as the benefits the recipient obtains from the action, and R is the relatedness between the recipient and the actor. For instance, suppose that a diploid female forgoes the opportunity to reproduce, instead remaining on her parents' nest to assist in the development in her siblings. The juveniles of this species require tremendous parental care in terms of feeding, thus would greatly benefit from the assistance of a sibling. This species is monogamous resulting in siblings having the same parents, a genetic relatedness (R) of $\frac{1}{2}$. The cost of not reproducing would be forgoing the chance to produce two offspring. However the benefits the parents receive through the helper daughter would be increasing the clutch size to five offspring. Therefore (2)-(1/2)(5)= - $\frac{1}{2}$ which is less than 0. Since the value is less than zero, the presence of a helper daughter, that forgoes the opportunity to mate, will be selected for under kin selection.

Fortress defense is one of the two factors that influences organisms to help their relatives rather than reproduce on their own. Fortress defenders nest and feed in protected enclosures that can accommodate many individuals, especially a class specialized as soldiers for territorial defense. The main advantage of grouping for these social insects is to defend the valuable resource of the nest since it provides protection and a source of food for the juveniles—the idea that two or more snaps, a defense mechanism of *S. regalis*, is better than one against intruders. Since food is already present in the nests, the focus of grouping in this case is not for foraging, but rather for protection against predators. Examples of other fortress defenders include mole rats (Sherman et al. 1991; Jarvis et al. 1998), social shrimp (Duffy 1996a), thrips (Chapman et al. 2000), aphids (Benton et al. 1992), beetles (Schuster et al. 1985), and termites (Thorne 1997; Bartz 1979).

The second factor is life insurance which arises in social insects that forage for food outside of the nest, which exposes them to predators (Box 5.3 (Life insurers: *Apis andreniformis*)). These insects must obtain nourishment outside of nest, unlike fortress defenders, since the young can not feed themselves and require food for development which the nest does not provide (Strassmann et al. 2007). The parent must undertake dangerous foraging for young in order for them to reach adulthood, but if the parent dies all of the offspring also die due to starvation—wasting the investment the parent had placed in the brood. However, an adult daughter can prevent this from occurring by staying in her natal nest to help protect and feed the dependent young. Therefore, if the parent dies while foraging the adult daughter will be able to take her place and raise the dependent brood, taking the role of reproduction as well. The different characteristics of Fortress Defenders and Life Insurers are portrayed in Table 5.2 (Queller and Strassmann 1998).

Box 5.3: Life insurers: *Apis andreniformis*

In the black dwarf honey bee, *Apis andreniformis*[4] , the daughters of the queen care for the larvae, maintain and defend the hive, and forage for food outside of the nest (Picture 3). This species is a eusocial species of life insurers since they forage for food outside of the nest in order to feed the dependent juveniles (Arias et al. 2005; Keller et al. 1994). The queen bee smells each egg ensuring that all of the eggs are produced by the queen; if an egg smells foreign then it will be immediately removed from the nest by the queen (Pirk et al. 2004; Visscher et al. 1995). There can only be one queen and the chance of individual survival is very low making direct fitness unlikely for a solitary individual. The worker bee has a better chance of increasing its fitness through indirect fitness, rather than direct fitness, by helping the queen mother rear offspring.

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[4] http://en.wikipedia.org/wiki/Apis_andreniformis

A Queen Bee	**A Drone Bee**	**A Worker Bee**

Table 5.1: The three castes of Honey Bee
Apis andreniformis[5] (permission obtained: NDSU)

Characteristics	Fortress Defense	Life Insurers
Taxa	Thrips, aphids, beetle, termites	Ants, bees, wasps
Main advantage of grouping	Valuable, defensible resource	Overlap of adult gen
Food	Inside nest or protected site	Outside nest
Juveniles	Active, feed selves and may work	Helpless; need to feed
Nonsocial ancestors	Not necessarily parental	Highly parental
First specialized caste to evolve	Soldiers	Foragers
Colony Size	Usually small	Often large
Ecological Success	Usually limited	extensive

Table 5.2: Table 2: Differences of two types of social insects, fortress defenders and life insurers (Queller and Strassmann 1998)

5.1.4 Synalpheus regalis: Fortress Defenders

Sponge-dwelling shrimp are fortress defenders (Table 5.2). The risk of predation is not most severe outside of the nest, but rather inside of it from intruders. Thus larger colony members, most of who do not breed, defend the sponge against any intruder impinging on the sponge. The defenders of the colony are large and overtly aggressive, possessing snapping claws to use against intruders, and tend to be older than the rest of the colony. This age related polytheism is a common trait in labor specializing social insects that also express eusociality (Wilson 1971; Oster and Wilson 1978). These large shrimp allocate their energy to protecting the nest, rather than parenting (Table 5.2). The attacks of predators against shrimp can lead to wounds and even death. By allocating the fighting to just the male defenders, it is ensured that the reproductive individual will be protected and will survive to reproduce (Robinson 1992). These fortress defenders are also protecting the most valuable resource of the nest, the sponge itself that provides food and nourishment for the juveniles. Since most of the defenders do not breed, the only way to secure their genes in future generations is to protect their juvenile siblings, allowing them to grow to adulthood free from predation.

5.1.4.1 Examples of Eusocial Fortress Defenders

Synalpheus regalis has been accepted as a eusocial species due to the vast importance division of labor has provided for populations. For all populations, the juvenile is a precious commodity that must be brought to adulthood to ensure the spread of gene copies. With a caste system, *S. regalis* is capable of doing just this, having a defender caste that ensures the safety of the nest's juvenile as well as the queen. Other eusocial species have also classified as either fortress defenders or life insurers; with the primary distinction being the importance of the nest as a food source seen in fortress defenders. The eusocial termites also classify as fortress defenders (Thorne 1997). Similar to sponge-dwelling shrimp, nests of termites provide nourishment for juveniles and adults, reducing the need for foraging. Termites are similar to *S. regalis* due to the presence of a soldier caste to defend the colony against intruders—in both organisms the nest is very important since it provides nourishment, houses juveniles and reproductive individuals, and serves as protection. However unlike *S. regalis*, in the termite species *Zootermopsis angusticollis* female soldiers

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[5] http://en.wikipedia.org/wiki/Apis_andreniformis

are also present. Normal female pre-soldiers (callow soldiers that will molt into soldiers) have oviducts, a seminal receptacle, and eggs, thus is capable of reproduction. Once the pre-soldier molts into a mature female soldier, the reproductive organs ceases development, making the female infertile (Thorne 1997). Using molecular analysis, all species of termites have been found to differentiate into castes not genetically, but via developmental instructions that allow them to become any one of the castes depending on hormonal stimuli (Figure 5.5). The first developmental pathway is the sexual line recognized by the presence of wing buds; the second pathway, apterous, leads individuals to become workers (Watson et al. 1985). Further research is necessary in *Synalpheus regalis* to determine what developmental pathways, or any other mechanism of differentiation, is used in the formation of soldiers versus the reproductive individual.

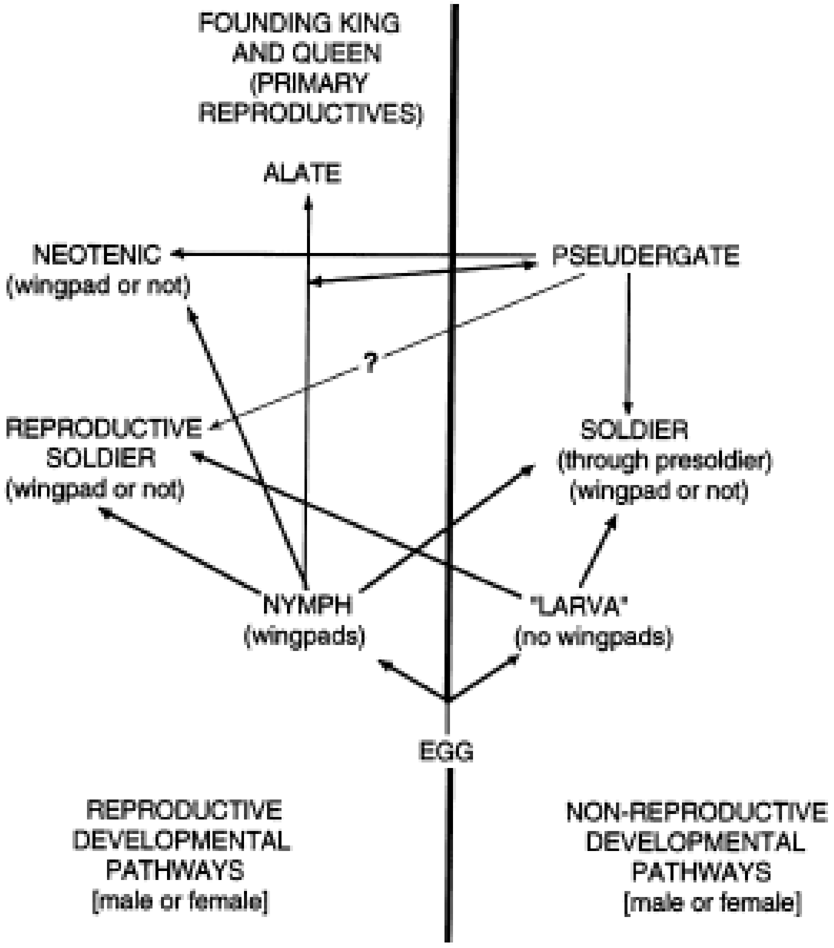

Figure 5.5: Developmental pathways present in the all species of termites that contain flexible developmental options—transitions can occur at any of the instars. For instance, the larva, nymphs, and pseudergate are all workers of the colony but can differentiate into fertile alates or neotenic reproductives (soldiers). (Thorne 1997).

Aphids are another fortress defender eusocial species, sharing several similarities with sponge-dwelling shrimp and termites. The gall-forming *Pemphigus spyrothecae*, along with all other aphid species, contain a caste of soldiers common to *Synalpheus regalis* and termite species (Benton et al. 1992). These soldiers cluster around the entrance to the gall, actively attacking predators with their sylets and hind legs. This act is very altruistic since it is common to die while defending their relatives. During summertime of peak reproduction, three hundred aphids could be found in a gall of which 50% are soldiers (Foster 1990). However, the soldiers also perform another function of housekeeping by removing any honeydew, exuviae (shed skins), and any other waste including dead aphids from the gall. This cleaning of the nest allows for growth of the juvenile aphids —yet is still a dangerous act due to the chance of falling from the gall entrance (Benton et al. 1992). Further research is necessary to determine alternative functions of the soldiers of *Synalpheus regalis*. The acts of soldiers, whether defense as in *S. regalis* or non-defensive as in gall-forming aphids, are seen as forms of altruism. By sacrificing their safety to house-keep or attack intruders, these fortress-defenders protect the important commodities of the nest, the reproductive individual, and of course the related juveniles that will ensure copies of their genes will pass to future generations.

5.1.5 Conclusion

The species of *Synalpheus* has been discovered to be eusocial species due to its adherence to the three contingencies of eusociality: cooperative care of young, reproductive division of labor, and overlapping of generations. As fortress defenders, a caste is present in all five *Synalpheus* species that constantly defend the precious commodity of the sponge. The sponge is important since it provides nourishment for the growing juveniles, while providing shelter for the colony. Ecological constraints limit individuals from dispersing due to the scarcity of unoccupied sponges (Table 5.3). Also, conspecific species are still regarded as intruders, resulting in an attack from the sponge's defenders—making the joining of a new sponge colony very difficult. Further research is necessary to determine what developmental pathways produce reproductive females and the soldiers. Perhaps even the soldiers of *Synalpheus* posses another function, similar to the eusocial aphids.

	Xestospongia cf. *subtriangularis*	*Hyattella intestinalis*
Number of Sponges Sampled	34	30
% occupied exclusively by *S. regalis*	82	17
% occupied exclusively by other species of shrimps	9	77
% occupied by both *S. regalis* and other species of shrimps	9	7
% unoccupied	0	0

Table 5.3: Table 1: Distribution of *Synalpheus regalis* on two host species of sponges—since zero sponges are unoccupied, there is a high competition amongst the shrimp for a sponge habitat, making solitary life very difficult and group living a better alternative. (Duffy 1996b)

Box 5.4: Sponge habitat leading to diversity of *Synalpheus* species

Sponges are commonly used among *Synalpheus* species as well as other sessile organisms as shelters. This is largely due to the aqua-porous canals that saturate the tissues of many sponge species allowing an exchange of water with the environment, which also serve as living spaces for *Synalpheus* species. The mean size and size range of canal spaces differ in four commonly used sponges *Agelas clathrodes, Niphates amorpha, Xestospongia rosariensis,* and *Spheciospongia vesparium* (Duffy 1992). These canal size differences were reflected in the various body sizes of the shrimp species associated with each of the sponge. This change in body size increases the variations among sponge colonies. Furthermore, dispersal from the natal sponge is very uncommon, leading to the restriction of gene flow among sponge colonies. With the added affect of body size variations due to sponge's canal spaces and the halting of gene flow because of lack of dispersal, speciation events are common among sponge-dwelling shrimp. Perhaps the use of the sponge as a habitat has resulted in sponge-dwelling shrimp being very diverse with 24 species living sympatric—species residing together without any physical barrier—lifestyles in the San Blas Islands (Duffy 1992).

5.1.6 GLOSSARY

- **Altruism**- This is any behavior that benefits the receiver of the action while being detrimental to the actor. An example would be a male *S. regalis* defender being injured in combat against an intruder—the juveniles benefit (receivers) from this action because their lives are saved, while the action is detrimental to the male defenders (actors).
- **Caste**- Forms of polymorphic animals that perform a specific function in the colony. Castes are a common characteristic of eusocial species. In the case of *S. regalis* there are three castes: large males who are defenders, a female who reproduces, and juveniles.
- **Conspecifics**- Organisms belonging to the same species. In Figure 5.4 male defenders are seen to be less aggressive towards intruders of the same species than those organisms of different species.
- **Direct Fitness**- The genes contributed by an individual to future generations through producing offspring. Direct fitness is any gene transmission directly in the bodies of an organism's offspring that completely owe their existence to their parent's action of reproduction.
- **Division of Labor**- Individuals in the colony have different tasks depending on various variables such as size and gender.
- **Eusociality**- A group in which a specialized, non-reproductive caste works for the reproductive members of the colony, forgoing their chance of reproduction. Most common eusocial organisms are found in the orders *Hymenoptera* (bees, wasps, ants)and *Isoptera* (termites), as well as in naked mole rats, sponge-dwelling shrimp, aphids, and thrips. The three requirements of eusocialityare: cooperative care of young, reproductive division of labor, and overlapping of generations.
- **Fitness**- The measure of genes that an individual in a colony contributes to the next generation, usually stated in terms of the number of surviving offspring of the individual.
- **Gene Flow**- This is the transfer of genes (in the form of alleles) from one population to another through means of dispersal (movement of individuals). The presence of gene flow decreases the genetic diversity among populations, but increases diversity within a population depending on the presence of the gene. In sponge-dwelling shrimp, dispersal is very low which halts the presence of gene flow between sponge colonies, inducing a speciation event.
- **Heterospecific**- Organisms that belong to different species. In Figure 5.4, the male defenders attacked intruders of different species at a higher level than against conspecific intruders.
- **Indirect fitness**- The genes contributed by an individual by helping to rear descendant kin into adulthood that would not have survived without their assistance. The non-reproducers of eusocial organisms depend on indirect fitness since it is the primary method of propagating their genes without reproducing.

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[6] http://www.jstor.org/stable/4221852?&Search=yes&term=mole&term=rats&term=eusociality&list=hide&searchUri=%2Faction%2FdoBasic

5.2 Evolution of Eusociality in Mole-Rats[7]

Author: Sheena Shah-Simpson

5.2.1 Introduction

Mole-rats (family Bathyergidae) are a type of rodent found in Africa. They live underground in burrows made up of different chambers for their nests, latrines, food storage areas, alongside chambers for foraging, in which they dig with their incisors and foreclaws. They eat roots, tubers, and bulbs. Most species of mole-rat are solitary, coming together only for mating. A few species, though, form colonies where many mole-rats live together in large complex burrows they have dug because it makes it easier to gather food and reduces predation risks.

Of the species that live in colonies, eusociality has evolved independently at least twice, in *Heterocephalus glaber*, the naked mole-rat (), and separately in *Cryptomys damarensis*, the Damaraland mole-rat (Allard and Honeycutt 1992, Jarvis and Bennett 1993, Walton et al. 2000, Faulkes et al. 2004). Colonies in both species have three morphologically distinct castes. The first caste is made up of the breeders, usually one female "queen" and her one to three mates, who breed and encourage the workers in their daily tasks. The second caste is formed by the workers, usually mole-rats who are highly related to the queen. These workers are reproductively suppressed by their own hormones that are secreted due to social cues from the queen, keeping them working instead of reproducing. They take care of the offspring, forage for food, and patrol the burrows. The final caste is the dispersal caste, made up of mole-rats of a slightly larger build who act as workers until they leave the colony to either found or join another. The dispersal caste is virtually the only form of gene flow in these mole-rat populations since the colonies are usually separated by a large distance that is dangerous for mole-rats to cross above ground.

As a result of the limited gene flow and environmentally-necessitated **inbreeding**, colony members are often highly related, allowing the emergence of castes and **reproductive skew** where only a few members have all of the breeding rights. This evolution of eusociality falls in line with the inclusive fitness (or kin selection) theory, which states that by forming large colonies and giving up reproductive rights, workers gain more **inclusive fitness** when the colony is led by a related female queen than if they dispersed and tried to navigate the risks of founding a new colony (Hughes et al. 2008).

5.2.2 Parallel Evolutions of Eusociality

The family Bathyergidae has five genera of mole-rats. The members of three of those genera always live solitarily in wet regions and are larger than the other genera (Table 5.4). Members of the other two genera, *Cryptomys* and *Heterocephalus*, are social and have varying degrees of cooperative breeding, including two cases of eusociality (Faulkes et al. 2004). *H. glaber*, the naked mole-rat, and *C. damarensis*, the Damaraland mole-rat, the two eusocial species, occur in two different genera and are therefore not as closely related as two species from the same genus (Figure 5.6).

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[7] This content is available online at <http://cnx.org/content/m34734/1.3/>.

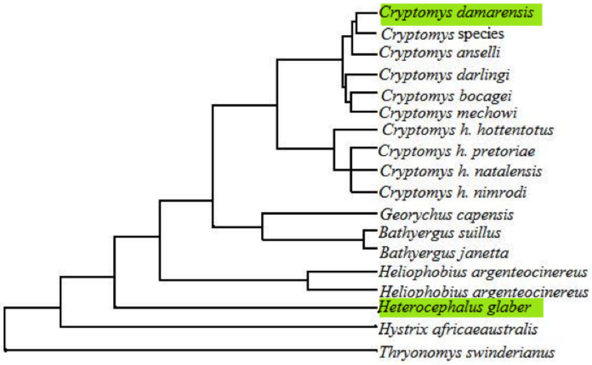

Figure 5.6: In this phylogeny of Bathyergidae, *H. glaber* and *C. damarensis* are marked as eusocial species of mole-rat. *H. africaeaustralis* and *T. swinderianus* are not in the family Bathyergidae.

Multiple phylogenies constructed from analysis of mitochondrial DNA and nuclear DNA from different species of mole-rats agree that eusociality in mole-rats either evolved multiple times or evolved once earlier and was lost multiple times (Allard and Honeycutt 1992, Walton et al. 2000, Faulkes et al. 2004). These phylogenies also agree that *H. glaber* is the most **basal**, or the first to diverge from the rest of the species, and it is separated from *Cryptomys*, and therefore *C. damarensis*, by the three solitary genera (Walton et al. 2000, Faulkes et al. 2004). It is more likely, then, that social behavior evolved twice in mole-rats rather than evolving once and being lost multiple times. Allard and Honeycutt (1992) see this parallel evolution in two species that both live in a harsh, **arid** environment as support of the theory that sociality is influenced by environmental factors.

Genera	Social?	Habitat
Heterocephalus	Yes	Dry
Heliophobius	No	Wet
Bathyergus	No	Wet
Georychus	No	Wet
Cryptomys	Yes	Dry and Wet

Table 5.4: Summary of sociality and habitat for the five different mole-rat genera.

5.2.3 Extrinsic and Intrinsic Factors

Evolution of eusociality	

continued on next page

Costs:	Some reproductive rights, inbreeding
Benefits:	Steady food source, protection from predation, some reproduction
Maintenance of eusociality	
Costs:	All direct reproduction
Benefits:	Indirect fitness through kin selection, steady food source, protection from predation

Table 5.5: The costs and benefits of staying in the natal nest for mole-rats as eusociality evolved and as it is maintained.

Reeve et al. (1990) point out that a combination of both **extrinsic**, meaning ecological, and **intrinsic**, or genetic, factors contributed to the rise of cooperative breeding and eusociality. Specifically, the extrinsic factors in naked mole-rats and Damaraland mole-rats include predation pressures, a patchy food source, and hard soils which make forming a new colony difficult. The intrinsic factor is a high relatedness between colony members. Combined, these factors maintain eusociality in mole-rats since the organisms remain in their natal colonies despite the cost of not being able to reproduce. They do, however, gain greater **fitness** on average than if they disperse.

Originally mole-rats were likely the offspring of unrelated, monogamous parents (Hughes et al. 2008) and stayed in their natal nests because of ecological pressures. The benefit was a greater overall fitness because they did not have to face the dangers outside the nest, and the original cost was marginal, as reproductive rights had not yet been lost (Table 5.5). Staying in the natal colony, however, reduced access to unrelated mates, which led to inbreeding. Reeve et al. (1990) found that today in naked mole-rat colonies more than 80% of matings that occur are either between siblings or between parents and offspring. Overall, these mole-rats have an average relatedness of 81% to their other colony members (Reeve et al. 1990) while average relatedness between full siblings is 50%.

As relatedness increased due to inbreeding and more individuals remained in the nest, a dominance hierarchy likely formed. The more dominant individuals held more reproductive rights. Gradually, the costs and benefits of staying changed slightly for non-breeders because of the inbreeding. The non-breeders gave up reproductive rights (the cost), thereby diminishing their **direct fitness**. However, they still had the benefit of avoiding outside dangers. More importantly, they gained greater **indirect fitness** because they were raising young highly related to them. In this manner they helped pass on their genes indirectly through the offspring of their relative, an act that added to their inclusive fitness. This inclusive fitness was greater on average than if they left to have their own young after the costs for leaving, such as predation and food risks, were taken into account.

5.2.4 Fortress Defense and the Aridity Food Distribution Hypothesis

Fortress defense and the Aridity Food Distribution Hypothesis are two different hypotheses that use extrinsic factors to explain part of the cause of the rise of eusociality. The fortress defense theory holds that eusociality evolved in order to avoid predation (Queller and Strassmann 1998). Fortress defenders are unique from other social organisms in that they nest and feed within an area protected from predators. In addition, the food they eat is not well distributed. These combined factors favor staying in a safe location with access to food over the risks of leaving and reproducing (Alexander et al. 1991, Queller and Strassmann 1998).

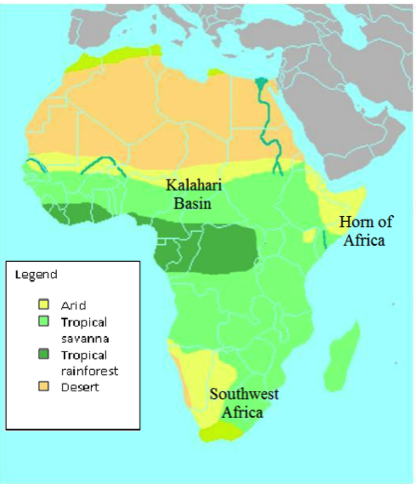

Figure 5.7: This is a simplified climate map. *Heterocephalus glaber* and *Cryptomys damarensis* are found in the arid regions of the Kalahari Basin, the Horn of Africa, and southwestern Africa.

The Aridity Food Distribution Hypothesis, the second theory based on extrinsic factors, states that eusociality in *H. glaber* and *C. damarensis* evolved due to selective pressure from the arid environment that they both inhabit (Faulkes et al. 1997b, Figure 5.7). According to Jarvis et al. (1998), mole-rats find the dry soil of their habitats hard to dig, a constraint that increases their energetic expenses in efforts to obtain resources. These habitats have sporadic rainfall and high evaporation rates (Figure 5.8), so there is a limited time period in which to work after the rain has stopped before the ground is too hard again (Jarvis et al. 1998). Mole-rat colonies maximize the number of members for cooperative foraging and group living so that after a rainfall they can better exploit the short time they have and reduce the risks of failure in foraging (Box 5.5 (Testing the Aridity Food Distribution Hypothesis)). The two hypotheses examine the ecological factors involved in the evolution of eusociality. Intrinsic factors, such as hormone regulation, however, are also involved.

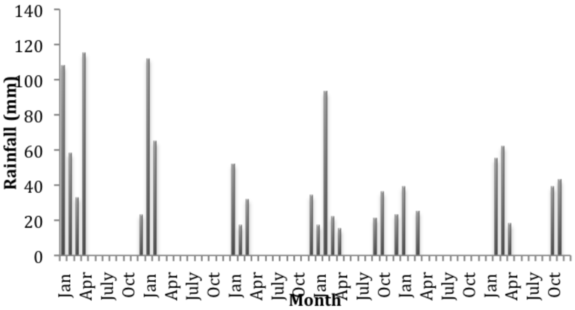

Figure 5.8: Mole-rats burrow only after a rainfall of at least 15 mm over seven days when the moisture has reached burrow depth. Rainfall meeting these conditions at Dordabis, located in southern Africa, where Damaraland mole-rats are found, is shown here from January of 1988 through December of 1993, demonstrating the limited occasions for burrowing (Jarvis et al. 1998).

5.2.5 Reproductive Suppression and Incest Avoidance

Both H. glaber and C. damarensis experience a great **reproductive skew**, meaning only a few members of each species ever achieve reproductive success. This is part of the definition of eusociality. For naked mole-rats, less than 1% of the population ever reproduces, and for Damaraland mole-rats less than 8% ever reproduce (Jarvis et al. 1994). This begs the question of how these two mole-rat species suppress reproduction. The current belief is that naked mole-rats and Damaraland mole-rats suppress their workers through different mechanisms.

Box 5.5: Testing the Aridity Food Distribution Hypothesis

Using **fractal dimension**, which measures to what extent the burrow fills the area (Le Comber et al. 2002), Sichilima et al. (2008) investigated assumptions of the Aridity Food Distribution Hypothesis in *Fukomys mechowii,* a cooperatively breeding species of mole-rats. They examined burrow fractal dimension differences between the rainy season and the dry season, the relationship between fractal dimension and the number of colony members, and the relationship between fractal dimension and food mass in the burrow. They found that burrow fractal dimension increased with the number of colony members and during the rainy season, and that burrows with higher fractal dimensions had more food. This gives substantial support to the Aridity Food Distribution Hypothesis because it indicates that digging and burrowing is limited by energy demands during the arid season, one of the assumptions of the hypothesis. In addition, the risks of failing to find the patchily distributed food sources are reduced by greater numbers of foraging colony members (Sichilima et al. 2008). Similarly, Lovegrove and Wissel (1988) found foraging risks for solitary individuals in an environment with widely dispersed resources are high. Lovegrove also found, using math-based models, that the shift from solitary to group living is expected when there is a depression in the food density, which occurs when shifting from a **mesic**, or moderately moist, environment to an arid one (Lovegrove 1991), which falls in with the Aridity Food Distribution Hypothesis.

Naked mole-rats have no incest avoidance mechanism, unlike Damaraland mole-rats. Without those mechanisms there is no reason why workers should not breed with each other, yet they do not, suggesting that something must be preventing them. One possibility is that the queen **shoves** her workers (see Box 5.6 (Why shove your colony mates?)), especially the larger ones who are more likely to breed eventually, to suppress reproduction (Jacobs and Jarvis 1996). Another is that some chemical or other social signal is given to suppress reproduction. Despite not knowing how exactly it is accomplished, it is known that when reproductively suppressed female mole-rats are removed from their colony and kept singularly their reproductive suppression is reversed (Faulkes and Abbott 1993, Clarke and Faulkes 1999). Since H. glaber do not avoid incest on their own, reproductive suppression is the sole method for maintaining the reproductive skew.

Box 5.6: Why shove your colony mates?

Jacobs and Jarvis (1996) looked at **shoving** in *H. glaber*, the naked mole-rat, testing a hypothesis that it occurs because of a conflict between a queen and her non-breeding colony members. The work-conflict hypothesis supposes that non-breeders withhold aid because they may become breeders or because it gives them more inclusive fitness, so the queen shoves them to encourage work. The effect of shoving, then, would be an increase in work. The actual results, however, were quite different. They found no relationship between relatedness and shove rate, so the queen shows no kin bias in her shoving. She is however, more likely to shove her larger workers than smaller ones. More importantly, shoving does not increase work rates. In addition, larger colony members work less than smaller members even though they are shoved more often, and non-breeders occasionally shove other non-breeders (Jacobs and Jarvis 1996). The fact that non-breeders shove each other suggests that shoving can be used to assert dominance. The larger workers are likely members of the dispersal caste found by O'Riain et al. (1996) and Braude (2000). The queen shoves them more often because they pose more of a threat to her dominance, and possibly, shoving helps ensure their reproductive suppression.

Naked mole-rats are **facultative inbreeders**, meaning they will inbreed since they have no aversion to it. Given the option, however, they choose to outbreed (Clarke and Faulkes 1999, Ciszek 2000). Both Clarke and Faulkes (1999) and Ciszek (2000) found experimentally that reproductively active females generally preferred unfamiliar mates to familiar ones. In order to distinguish familiar from unfamiliar mole-rats, comparable to distinguishing kin from non-kin, they likely use scent (Box 5.7 (Kin Recognition)). In naked mole-rats, kin recognition does not help with reproductive suppression, but does allow for incest avoidance given the opportunity to outbreed. **Outbreeding** encourages gene flow, which lessens the impact of deleterious alleles on offspring fitness. Breeding with non-related mole-rats helps lower the **inbreeding depression**, which is the decrease in overall fitness of offspring and their reproductive capabilities caused by inbreeding.

Box 5.7: Kin Recognition

In order to maximize inclusive fitness, mole-rats must ensure that their aid is given only to relatives and not to outsiders who exploit them. As a result, they must have some way to identify relatives. As O'Riain and Jarvis (1997) point out, direct determination of relatedness in mole-rats will not work too well since relatedness in colonies is high. It is not surprising, then, that mole-rats identify colony members instead of kin. Colony members are generally highly related, and mole-rats are unlikely to encounter many foreigners inside their burrows. The probable mechanism used by mole-rats to identify foreigners and colony members is odor familiarity (O'Riain and Jarvis 1997). However, in common mole-rats and naked mole-rats, odor familiarity must be continually reinforced. If a mole-rat is removed from its colony for long enough (at least twelve hours), upon reintroduction it is viewed as foreign since it has lost the distinctive scent of the burrow (Burda 1995, O'Riain and Jarvis 1997).

Another result of kin recognition, in naked mole-rats at least, is that patrollers can identify intruders and start an alarm to get rid of them. Colony members want to keep foreign naked mole-rats out of the colony because the intruder reduces their chance at eventually gaining breeding rights (O'Riain and Jarvis 1997), especially given that breeders prefer outbreeding to inbreeding.

Damaraland mole-rats, however, are **obligate outbreeders**, meaning they will only breed with foreign mole-rats (Burland et al. 2002, Burland et al. 2004). Rickard and Bennett (1997) examined *C. damarensis* colonies, both in the lab and the wild, from which the dominant female was removed, either due to experimental removal or a natural death. They found that the colony remained reproductively quiescent, or stopped reproduction, until an unrelated male was introduced, then a former female worker would become the new breeder (Rickard and Bennett 1997). Their work provides a strong example of the incest avoidance Damaraland mole-rats have.

For a while, it was thought that incest avoidance in Damaraland mole-rats, unlike in naked mole-rats, was sufficient to maintain the reproductive skew. Reproductive suppression was therefore unnecessary. A recent study by Burland et al. (2004) has called these ideas into question, however. They found from samples taken from wild colonies that unrelated non-breeders of the opposite sex coexisted within colonies, providing opportunities for non-breeders to mate. In addition, they found offspring of queens with different fathers than the male breeders. They suggest that either males pass through the colonies or females can briefly leave (Burland et al. 2004). Either way, non-breeders come into contact with unrelated, potential mates, yet they do not mate. Due to this, Burland et al. (2004) believe some reproductive suppression occurs in *C. damarensis* as well which contributes to the reproductive skew. They do not know yet at what stage suppression is achieved, ovulation, copulation, or implantation (Burland et al. 2004). In order for any outbreeding to occur, however, some mole-rats must be willing to leave their natal nest and disperse.

5.2.6 Dispersal and Morphologically Separate Castes

So far this paper has examined mainly one strategy for workers, the one in which they stay in the natal colony to maximize their indirect fitness, and how that strategy impacts reproductive suppression and incest avoidance. There is however, a second strategy in which the workers leave their natal colony and disperse, either to form a new colony or invade another, in the hopes of becoming a breeder and gaining direct reproduction (O'Riain et al. 1996). Dispersal for the naked mole-rat and the Damaraland mole-rat has high ecological constraints, though, because digging a new burrow for a new colony in the hard ground is difficult. In addition, a small starting colony experiences a greater risk of not finding food when foraging, and the risk of predation is high when leaving the colony. Spinks et al. (2000) performed a within-species comparison in *Cryptomys hottentotus hottentotus*, or the common mole-rat, between mole-rats in an arid environment and those in a mesic environment (Figure 5.9). They found that the inclusive fitness for individuals is no longer maximized after reaching a certain colony size and there are greater fitness benefits in dispersing due to increased competition for resources like food. They also found, however, that the higher ecological constraints at the arid sites forced the individuals to remain in the colony longer due to the higher costs of dispersal (Spinks et al. 2000). These findings suggest that group living for *H. glaber* and *C. damarensis* was further encouraged by the large environmental constraints on dispersal.

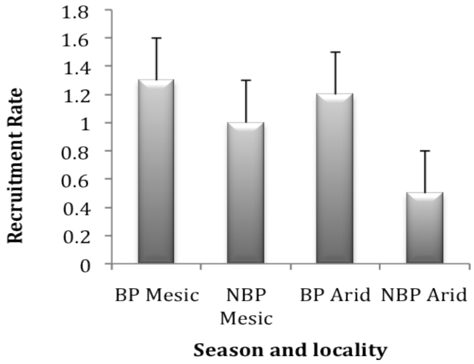

Figure 5.9: The average annual recruitment rates among common mole-rat colonies at arid and mesic sites during the breeding period (BP) and non-breeding period (NBP). The only significant difference in recruitment rates at the 5% level occurs between the BP and NBP arid sites (Spinks et al. 2000).This suggests that common mole-rats find it much harder to disperse in arid sites during the non-breeding period.

Box 5.8: What is the queen's morphology in naked mole-rats?

O'Riain et al. (2000) have discovered that queens in naked mole-rats have a morph of their own, like that found in eusocial insects. Queens, it seems, have a longer vertebrae than female workers that is dependent on successful reproduction, not just attempted reproduction. This is probably due to hormones released during the later stages of pregnancy or during lactation. The extension provides some benefits, like allowing for a larger reproductive tract and more pups in a litter at a time. This phenomenon helps explain why pup litter size increases from one birth to the next. New queens have a smaller vertebra than do older queens (O'Riain et al. 2000).

The evolution of eusociality in such varied organisms as insects and mole-rats shows a surprising convergence. The fact that queens have a morph of their own, like that found in some eusocial insects, shows an even greater degree of convergence. This natural convergence of traits leads to the belief that similar selective conditions must be present for the evolution of the traits in such varied organisms. More importantly, it seems to point out that the selective factors are more likely to be extrinsic than intrinsic because the organisms are so different genetically (O'Riain et al. 2000).

Despite the risks, though, certain members of both the naked mole-rat and the Damaraland mole-rat attempt to leave each year, generally directly after the rainy season (O'Riain et al. 1996, Braude 2000, Hazell et al. 2000, Scantlebury et al. 2006). These mole-rats form their own caste within the colony and have morphological differences that separate them from the other workers and from the queen (Box 5.8 (What is the queen's morphology in naked mole-rats?)). O'Riain et al. (1996) and Braude (2000) found both in the lab and in the wild that naked mole-rats have a separate dispersive morph. This caste of mole-rats has significantly more body fat than normal workers. They act as workers, albeit lazy ones, until after the rains, when they attempt to disperse (O'Riain et al. 1996, Braude 2000). According to Braude's field findings, most of the dispersers attempt to found new colonies, with only a few attempting to join established ones. O'Riain et al. (1996) found that within the established colonies, the newcomers are treated aggressively by the workers, but not the breeders, showing the conflict of interest between workers and breeders. The workers see the newcomer as a threat to their chance at becoming a breeder while the reproductive sees the newcomer as a possible mate. Often, the newcomer was forced out by the workers (O'Riain 1996).

Similarly, Damaraland mole-rats have a dispersive morph made up of bigger mole-rats who do less work (Hazell et al. 2000, Scantlebury et al. 2006). Scantlebury et al. (2006) found that these mole-rats work little until after rains, when they substantially increase their work in comparison to normal workers. The disperser mole-rats are also significantly bigger than the queen, who is significantly larger than the workers (Scantlebury et al. 2006). The disperser morph in both species has an advantage that allows it to attempt the second strategy, dispersing and gaining direct reproduction. Its larger fat stores allow it to travel longer distances without starving and provide a good reserve of energy when beginning reproduction (Scantlebury et al. 2006). Overall, the disperser morph, while costly to its natal colony in terms of energy consumed and not used (O'Riain et al. 1996, Scantlebury et al. 2006), benefits itself through the potential for direct reproduction and provides gene flow for these highly unusual and fascinating mammalian species (Faulkes et al. 1997a).

5.2.7 Conclusion

The evolution of eusociality in mole-rats can be explained primarily by the Aridity Food Distribution Hypothesis which uses the environmental factors of aridity and unequal food distribution to explain why certain species of mole rats evolved to be eusocial. This also accounts for the separate evolution of eusociality in two different species. As a eusocial species, the mole-rat has tiers of breeders, workers, and dispersers. The situations in which mole-rats will and will not breed is not entirely understood, but appears to be more socially or hormonally driven, as even mole-rats who are not mole-rats do preserve their ability to reproduce, even if they do not use it. The dispersal tier of the mole-rat eusocial hierarchy is essential to allowing for enough outbreeding to sustain healthy offspring, and allows large, successful colonies to spread their genes even further. The entire hierarchy of eusociality in mole-rats is certainly intricately evolved, from intrinsic differences to social cues that allow the mole-rat to survive in harsh conditions.

5.2.8 Discussion Questions

1. In mole-rats, non-breeders do not lose reproductive capabilities. If non-breeder tiers of the mole rat did engage in reproductive behavior, how might this interfere with the eusocial structure of the colony? Would this behavior increase that individual's fitness, why or why not?
2. Eusociality appears to have evolved twice separately in the mole-rat. What conditions would likely allow for eusocial evolution in other mole-rat species, or even in other organisms that are typically solitary?

5.2.9 Glossary

- **Arid climate**- characterized by severe lack of available water
- **Basal clade**- the first to diverge from the lineage in a cladogram
- **Dimorphism**- two distinct body forms of an individual within a species
- **Eusocial**- applies to a society with reproductive division of labor, overlapping generations, and cooperative care of young
- **Fractal dimension**- the extent that the burrow fills the area it inhabits
- **Fitness**- ability of an individual to stay alive and pass on genes
- **Inbreeding**- breeding with relatives, leads to less genetic variation
- **Inbreeding depression**- a decrease in offspring size, fertility, and fitness due to inbreeding as recessive deleterious traits are more likely to manifest themselves in homozygous individuals
- **Inclusive fitness**- the combination of direct fitness and indirect fitness gained
- **Indirect fitness**- the fitness gained by helping a relative and impacted by the degree of relatedness
- **Kin Selection**- altruistic acts directed towards kin that lead to greater overall inclusive fitness because of an increase in indirect fitness
- **Mesic**- having a moderate supply of moisture.
- **Shoving**- nose-to-nose pushing for protracted periods of time
- **Outbreeding**- reproduction between two different populations , leading to more genetic variation

- **Reproductive skew**- distribution of breeding between members of a population where some members hold more breeding rights than others

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5.2.11 About the Author

Figure 5.10

Sheena Shah-Simpson is an undergraduate from Arlington, Texas, majoring in Biochemistry and Cell Biology. In her free time she likes to play, or attempt to play, musical instruments, read, hang out with her friends, listen to good music, and dance. While studying animal behavior she learned fascinating things about conflicts of interest, between species, within species, within individual families (parent-offspring conflict is particularly interesting), etcetera. Writing this chapter, Sheena also learned many extraordinary things about such varied topics as incest and different morphologies within just one family of animals, the ever-fascinating mole-rats.

Chapter 6

Communicating, eavesdropping, and deception

6.1 Costs and benefits of non-predator eavesdropping in mammal-bird alarm call interactions[1]

Author: Emily Prehn

6.1.1 Introduction

Nearly all animals communicate in some way or another, be it through visual cues, noises or sounds, smells, touch, or even taste or chemical interactions. Communication includes at least two individuals: the sender and the receiver. The sender is the animal that sent the signal in the first place; the receiver is the intended audience of the signal. But in many cases, a third party is introduced to the communication: an eavesdropper. An eavesdropper is an animal that receives a signal meant for someone else. Within interceptive eavesdropping, the eavesdropper gains information from signals; within social eavesdropping, the eavesdropper gains information from signal interactions (Box 6.1 (Social Eavesdropping in Great Tits)) (Peake 2005). In this chapter, we will focus primarily on interceptive eavesdropping found in mammal-bird interactions.

The specific type of animal communication we will be considering here is alarm calls. Many social animals, from titmice to mongooses, make use of alarm calls. When an individual, either an assigned sentry or otherwise, notices a predator, it communicates the presence of that predator to the rest of the community by using one of the earlier mentioned types of signal. For instance, many types of birds employ loud, shrill sounds to alert others to the danger; this behavior is assumed to have evolved to aid close relatives. Many animals other than the birds' conspecifics, however, listen (eavesdrop) to the alarm calls.

Picture an eastern chipmunk foraging under a tree. Suddenly a hawk swoops overhead. The chipmunk, concentrating on its eating, does not notice it; a tufted titmouse sitting above it in the tree does (Figure 6.1). The titmouse calls out, warning its own family, and at the same time inadvertently warning the chipmunk. The chipmunk looks around, realizes its danger, and scampers to safety. We will call this kind of interaction "increased vigilance following another's call," and will examine other examples of it and the costs/benefits of this type of behavior later in the chapter.

Other animals that recognize and respond to one another's alarm calls include hornbills and Diana monkeys, dwarf mongooses, and many more. What benefits does an eavesdropper receive, and are there any costs to its behavior? We will explore this question within the context of several sets of organisms (Table 6.1).

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[1] This content is available online at <http://cnx.org/content/m34711/1.3/>.

(a) (b)

Figure 6.1: When the tufted titmouse (Baeolophus bicolor) (left) gives its alarm call, the eastern chipmunk (Tamias striatus) (right) responds with heightened anti-predator behavior. Titmouse from Badger 2006; chipmunk from "eastern chipmunk."

6.1.2 Overview of alarm calls (conspecific)

Alarm calls within a species can be given for a number of reasons (Table 6.2, adapted from Wheeler 2008). One of the foremost reasons to alarm one's community is to warn one's kin. By helping kin to survive, an animal is ensuring that more of its genes will be passed on to the next generation. Studies have shown that kin warning is the primary reason chipmunks give alarm calls (da Silva et al 2002); studies have also shown that the long-distance calls of Diana monkeys function as kin-warning systems (Zuberbuhler et al 1997). These studies examined what types of stimuli triggered the animals to alarm, as well as studied which animals alarmed. The assumed cost of this behavior is that the predator will be more likely to find and eat the animal that makes a loud alarm noise; the assumed benefit is the probability that more of the alarming animal's genes will continue on to the next generation, whether through children or close relatives. Parental care and mate protection are also forms of kin selection.

Another key hypothesis for why animals alarm call is the "perception advertisement hypothesis" (Bergstrom & Lachmann 2001; Zuberbuhler et al 1997). This theory states that prey animals will often sound the alarm after they've spotted ambush predators – that is, predators that rely on the element of surprise to get their prey. If the predator is spotted, it will likely have less success in hunting and will have to expend more energy to kill the prey that is forewarned. If the prey spots the predator, then, the prey can alarm to tell the predator that it has been spotted and will have to work harder than it had anticipated. This knowledge is sometimes enough to encourage the predator to leave and attempt to sneak up on another meal. The cost here is the same as before: the predator is more likely to spot the caller. But the benefit is that the predator might attack at all: since through alarming the caller is able to save both itself and its kin, the benefits clearly outweigh the cost.

Sender Referenced	Eavesdropper	Description	Study
Tufted titmouse 2008	Eastern chipmunk	Chipmunks increase vigilance	Schmidt et al.
Diana Monkey 2004	Hornbill	Hornbills distinguish between different alarm calls	Rainey et al.
Hornbill	Mongoose	Work as a team; mongoose relies on hornbill's sentry duty	Anne et al. 1983

Table 6.1: Organism examples offered in the text, along with a brief description of interaction and the study referenced

Hypothesis in	Prediction	Previous support
Kin selection	Individuals related to more conspecifics more likely to call	rodents
Parental care	Individuals with more offspring more likely to call	Primates. Rodents, Birds
Male protection	Mating males more likely to call	Birds
Selfish herd	Animals group following call	Birds
Predator confusion birds	Conspecifics engage in sudden movement/sounds following call	Rodents
Group maintenance	Dominant individuals in group more likely to call	Primates
Mobbing recruitment	Conspecifics mob predator following alarm	Birds
Pursuit deterrence	Conspecifics don't respond/are not present	Primates, rodents, birds

Table 6.2: Table listing several hypotheses supporting individuals' alarm calling despite risk to self and the behaviors that would be expected in each case. Also examples of animals in which said hypotheses have been given support.
*Table modified from Wheeler 2008.

There are also hypotheses that in many species alarm calling is even more selfish; these hypotheses include mobbing recruitment, selfish herd, and predator confusion (Wheeler 2008). In the mobbing recruitment hypothesis, the alarm call attracts the caller's conspecifics, and together they "mob" the predator, attacking it and driving it away. In the selfish herd hypothesis, the alarm call causes the group to "bunch up," packing together more densely and thus making it harder for the predator to pick off any one animal. In the predator confusion hypothesis, all the conspecifics respond to the call with flurries of movement or a cacophony of sound, confusing the predator and hopefully driving it off. In all of these examples, it is clear to see how the individual benefits.

No matter what the conspecific reason is for alarming, eavesdroppers can still benefit. Any of these calls, no matter what their intent is, signifies the presence of a predator. In some mixed-species flocks of birds, heterospecifics together mob a predator following an alarm call (Johnson et al 2003); most of the time, however, there is no interaction between the signaler and eavesdropper. The other exception to this rule is in heterospecific partnerships, but we will discuss that later.

Animals that use alarm calls often use variation within the types of calls to demonstrate different things. For instance, in yellow-bellied marmots, the type of call given changes depending on how much danger the threat presents (Blumstein & Armitage 1997). In great gerbils, the type of call given varies according to how close the predator is to the caller, or the nearness of the danger (Randall & Rogovin 2002). Some animals, such as the Diana monkey, even have different alarm calls for different predators (Rainey et al 2004a). Animals can also distinguish about when to listen to alarm calls. Squirrels discriminate between callers, paying more attention to neighbors and paying less attention to squirrels who alarm multiple times without cause (Hare 1998). Goshawks respond to goshawk alarm calls more often during certain times, such as nesting, than at others (Kennedy & Stahlecker 1993).

6.1.3 Increased vigilance following a heterospecific's alarm call

Remember our chipmunk-titmouse example from our introduction? Studies have proven that chipmunks do, in fact, show heightened anti-predator behavior when they hear a tufted titmouse's alarm call (Figure 6.1) (Schmidt, et al. 2008). In their study, Schmidt, et al. quantified the effect that birds' alarm calls have on eavesdropping mammals (2008). To do this, they set up several different foraging areas, including food for the chipmunks, and played different sound samples. The samples included wood thrush song, a common sound in the area; the call of a broad-winged hawk, a predator of chipmunks; and three different titmouse calls: a "contact call" that they give under low-threat situations; a mobbing call that they give when an avian predator is perched nearby; and a "seet" call that they give when a predator is flying low or otherwise posing a major threat. They then observed and recorded how many seeds were left at each site, and determined that the more seeds there were left, the less the chipmunks in that area foraged, presumably because of their evaluation of the risk. If there were more seeds left, then the chipmunk spent more of its time watching for predators or fleeing than it did actually foraging. (Schmidt, et al. 2008)

Figure 6.2 shows the results of their experiment, with the comparative amount of seed left in the areas with each type of call played. Sure enough, the chipmunks responded to titmouse alarm calls by foraging less and engaging in anti-predator behavior more. The chipmunks responded to the "mobbing" call and the "seet" call, each of which signified the presence of a predator. The chipmunks did not respond substantially to the control call, with the songs of the wood thrush, nor did they respond to the non-alarm calls of the titmouse. (Schmidt, et al. 2008)

Interestingly, the researchers' hypothesis regarding the hawk call was proven incorrect. They had assumed that the chipmunk would respond to this clear evidence of a predator's presence with anti-predator measures, but instead the chipmunk had no clear response. Schmidt, et al. hypothesized that an attacking predator would not call, betraying its position, so a chipmunk hearing a hawk call could assume that the hawk presented no immediate danger for them. (Schmidt, et al. 2008)

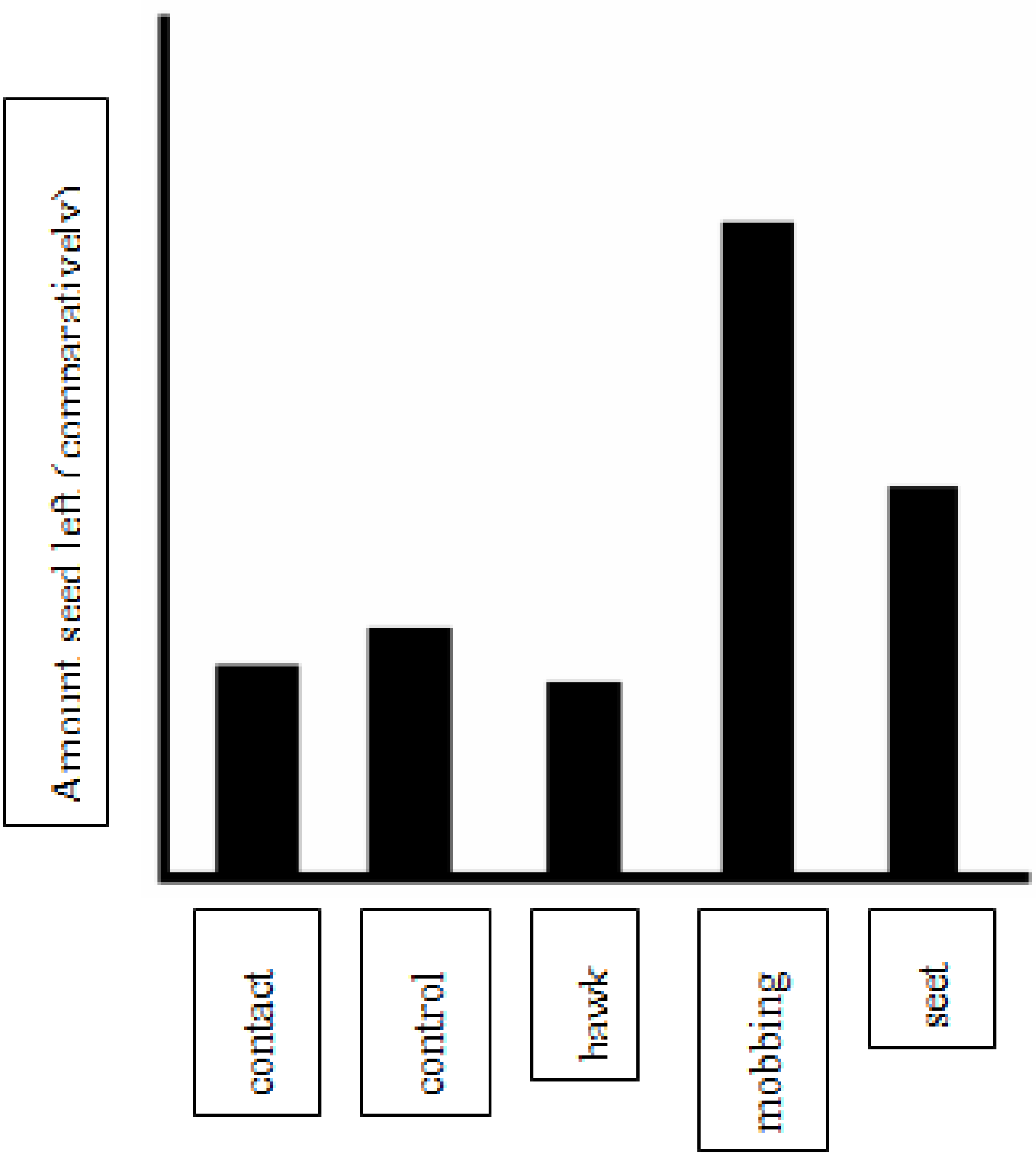


Figure 6.2: Amount of food remaining in each area following certain call presentations. The most food was left (least amount was eaten = least time was spent foraging) following the mobbing call; the next least amount of food was eaten following the seet call; there was practically no change between the food amounts left following the contact, control, and hawk treatments.
*figure adapted from Schmidt et al. 2008

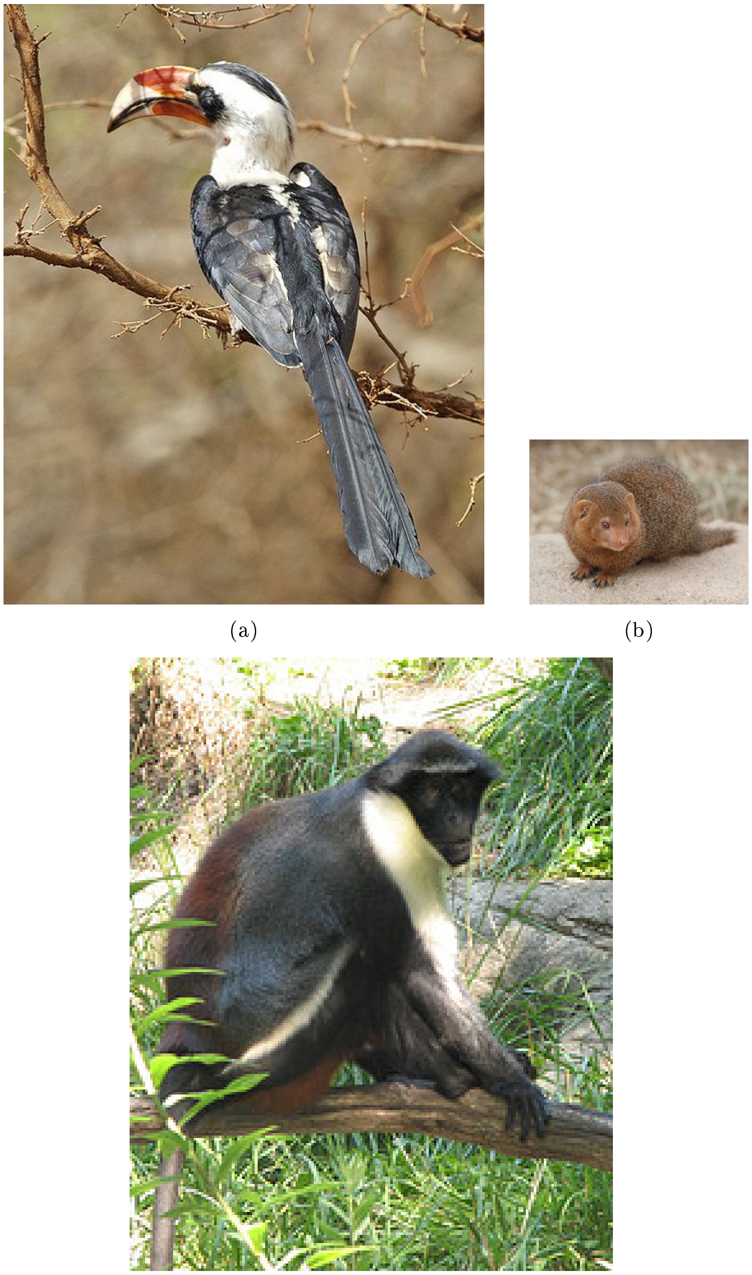
6.1.4 Distinguishing between different types of alarm calls in eavesdropping

The last study included data about how the chipmunk has to respond to all of the titmouse's alarm calls, since the titmouse does not have specific calls for specific predators. But this does not mean that no animal gives specific information about a predator. The Diana monkey, for example, gives a different type of alarm call depending on what predator is attacking (Figure 6.3) (Rainey, et al. 2004). The Diana monkeys then respond with different behaviors depending on what type of predator is attacking. For example, in Hauser and Wrangham's study, it was reported that when an alarm call for a viper is given, primates look towards the ground; when an alarm call for an aerial predator is given, the primates look up (1990). The yellow casqued hornbill takes advantage of the differences in calls for specific predators in its eavesdropping, since it only shares one common predator with the Diana monkey. (Rainey, et al. 2004)

Crowned eagles attack both hornbills and Diana monkeys, but leopards attack the Diana monkey and not the hornbill. Rainey, et al. conducted their experiment to determine if hornbills, and by extension other eavesdroppers, can distinguish between different types of alarm calls. By using experimentation similar to that described in Schmidt's study, they discovered that hornbills can indeed tell the difference between the different alarm calls; they respond with increased anti-predator behavior only when the alarm call identifying their common predator is given (Rainey, et al. 2004).

6.1.5 Partnership in eavesdropping: giving alarms for another's predator

The hornbill also shares a communication relationship with the dwarf mongoose, with an important difference that sets it apart from the previously-mentioned relationships (Figure 6.3) (Anne, et al. 1983). The hornbill and the dwarf mongoose share a mutualistic relationship, hunting together in their home region of Kenya. It is one of the closest heterospecific partnerships found in free-living vertebrates (Anne, et al. 1983). Hornbills will often congregate around the termite mounds where the dwarf mongooses sleep, waiting for them to wake up so the group can begin hunting. Likewise, if mongooses wake up and go outside and there are not many hornbills waiting, the mongooses will wait for more to arrive. The hornbills also sometimes wake up the mongooses, so they can begin hunting earlier.



(a) (b)

(c)

Figure 6.3: The dwarf mongoose (Helogale undulata rufula) (center) eavesdrops on the hornbill (left), which in turn eavesdrops on the Diana monkey (Cercopithecus diana) (right).
Diana monkey image from Shears 2007; shown is Von der Decken's hornbill (Tockus deckeni) from Yap 2008; mongoose from Silfverburg 2006.

The two species share the same types of prey and many of the same predators. They use these similarities to form a valuable partnership. Hornbills stand sentry duty, to warn the mongooses of approaching predators, while the mongooses hunt, flushing prey out in the open where the hornbills can also dine on them. Anne, et al. (1983) used observation to determine that dwarf mongooses use fewer of their own sentries when hornbills are present in the hunting groups, meaning that the dwarf mongooses trust their partners to warn them of danger. Likewise, the hornbills call out a warning even for raptor species that do not prey on them, but that do prey on the mongooses. This information implies that the heterospecific alarm calls between hornbills and dwarf mongooses are unusually deliberate; the hornbills seem to be warning the mongooses, implying a direct communication rather then eavesdropping.

Figure 6.4 displays the results of Anne et al.'s study, with the numbers of times that mongooses flee when different calls are given, depending upon the presence of hornbills. When an alarm call was given, the mongooses fled more when there were no birds, implying that the mongooses were more skittish, devoting less time to foraging when their hornbill partners were not present. Both in the presence of alarm calls and not, the majority of mongooses only fled the area following the fleeing of the hornbills; clearly, the mongoose cues its defensive strategy off of the hornbill's.

What are the costs and benefits of this partnership? The hornbill suffers the usual cost of being more visible to predators, as well as sacrificing time and effort alarming for something that doesn't threaten them or their conspecifics.

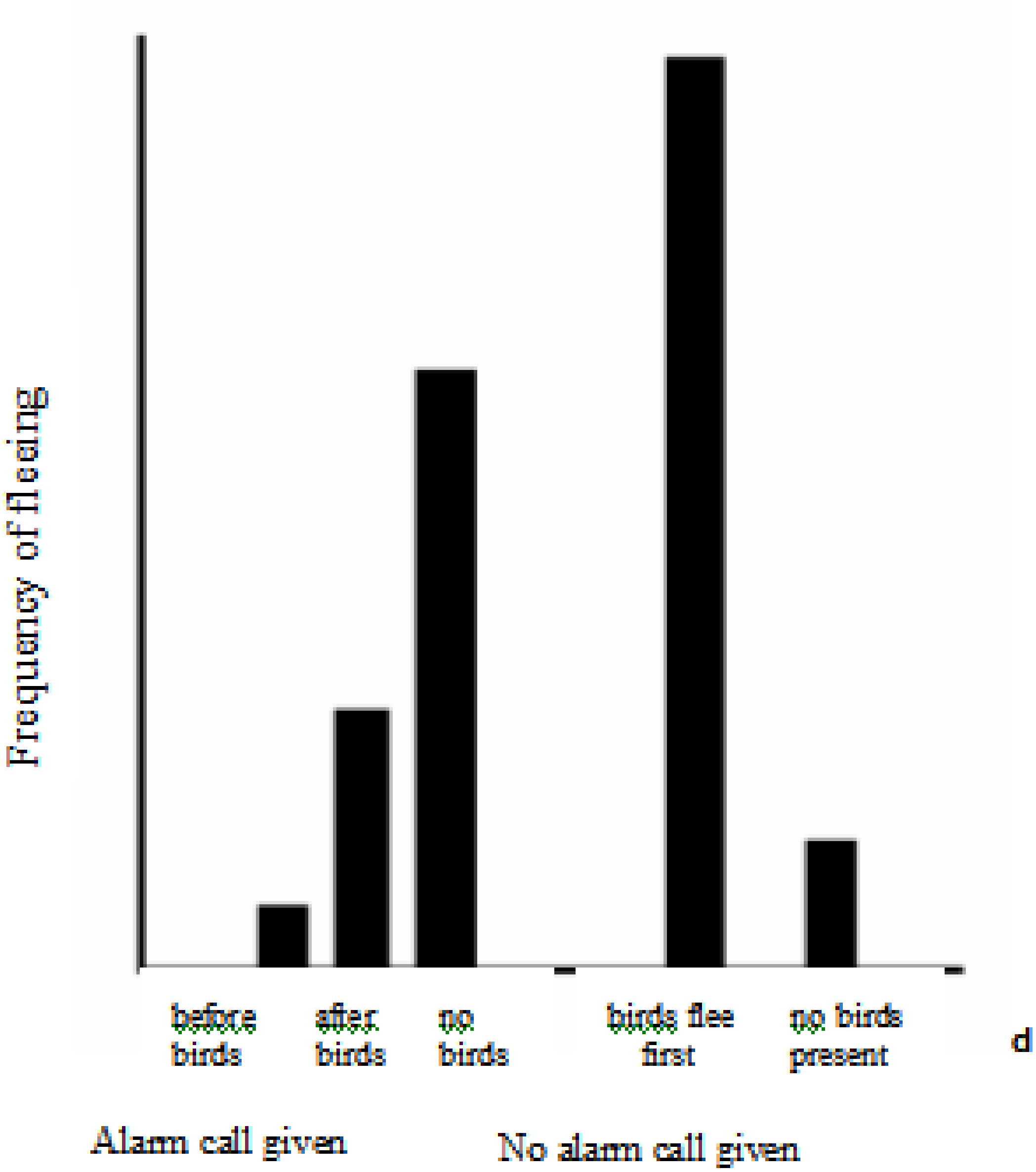


Figure 6.4: Frequency of fleeing in mongooses related to who's standing sentry duty.

6.1.6 Benefits and Opportunity Costs

Let us now examine the costs and benefits to the players in these interactions. The cost to the titmouses, the Diana monkeys, and the hornbills for alarming at the presence of predators is an increased chance of being spotted, the same cost it would have without the chipmunks' eavesdropping. Their benefit is also not affected by the presence of the chipmunks, the hornbills, or the mongooses; namely, increased survival for themselves and their relatives and conspecifics, making the impact on the senders of the signal negligible. The cost to the receivers in all this interaction is that they had to learn to develop this behavior, as well as to recognize which of the calls are alarm calls, which are not, and sometimes which are relevant to mutual predators. Since all the eavesdroppers haven't a limited mental capacity, the effort of learning these skills takes the place of some other behavior that it would be able to learn (Schmidt et al. 2008). While this cost may not seem like very much, the benefit of knowing when a certain predator is approaching must outweigh the opportunity cost of potentially using that learning ability to better understand how to acquire mates or feed offspring and therefore is certainly not trivial. The benefit, however, is the ability to forage more safely and more efficiently and being able to rely on others' alarm calls rather than spending great amounts of time looking around for threats. Instead, the eavesdroppers can concentrate on their foraging, so long as they keeps an ear out for alarm calls. Because the eavesdroppers benefit in the first two examples while the senders of the signals incur no harm, these interactions could be characterized as commensalism.

Only in the case of the hornbills and mongooses is the relationship more mutualistic. The hornbills, which send the signals, have the added benefits of easier access to their prey as the mongooses flush the prey into the open. The mongooses have to give up some of their food that they find; they also have to trust that the hornbills will in fact alarm for their predators, as well. The mongooses gain a better warning system: hornbills, from their stations in the sky or trees, can see more terrain and therefore more predators. This system of sentry duty allows the mongooses more time to forage while the hornbills exert less energy in foraging, benefitting both while both contribute to the association.

Box 6.1: Social Eavesdropping in Great Tits

The two types of eavesdropping are interceptive, which we have discussed in this paper, and social. Social eavesdropping occurs when animals are paying attention not only to the signals one animal gives, but instead to the interplay of at least two different signal systems (Peake 2005). An interesting example of a social eavesdropper is the great tit.

Male great tits are territorial, defending their areas of forest from intruders, including other male great tits. They are very intelligent in their guarding, however, making use of information other than that they gain from their own confrontations. By judging from a series of interactions whether or not a male poses a threat, the great tit is able to save energy that does not need to be spent on defense.

Let's say male great tit B trespasses into male great tit A's territory. Male A is able to quickly defeat tit B, chasing him out of his territory and into his neighbor's, tit C. If tit C is then defeated by tit B (who tit A beat with ease), then tit A realizes that tit C is not actually a dangerous threat. The next time tit C intrudes, tit A will expend less energy in his attempts to drive him out. (Peake et al 2002)

6.1.7 Glossary

- **Animal communication**– the method animals use to transfer information between one another. The method may include a visual cue, a sound, a smell, a touch, or a chemical release. For animal communication to evolve, the sender of a signal must always benefit; the receiver, not necessarily.
- **Alarm call** – in many species of animals, an individual or individuals will keep a lookout for predators while the others go about the usual tasks of the species. If a predator approaches, the lookout(s) communicates their presence to the rest of the community via one of the methods listed above.
- **Eavesdropping**– eavesdropping occurs when an individual other than the sender or the intended receiver receives a communication. The two types of eavesdropping can generally be categorized as being interceptive or social (Peake 2005).
- **Interceptive Eavesdropping** – occurs when an individual receives a call directed at another animal(s), thereby keeping the message from reaching the intended audience. This type of eavesdropping is rare with regards to visual and auditory communications.

- **Social eavesdropping** – occurs when an animal overhears a signal directed at another animal(s), but does not prevent the signal from reaching the intended recipient. This type of eavesdropping often occurs with regards to visual or auditory signals.
- **Conspecific**– if two animals are conspecific, they belong to the same species. If a type of communication or eavesdropping is conspecific, it occurs between two animals of the same species.
- **Heterospecific**– if two animals are heterospecific, they belong to different species. If a type of communication or eavesdropping is heterospecific, it occurs between two animals belonging to different species.
- **Sympatric**– if two groups of animals are sympatric, they share the same living area or territory. For example, red squirrels are sympatric with Eurasian jays.
- **Allopatric**– if two groups of animals are allopatric, they do not share the same living area or territory. For example, the polar bear, found within the northern Arctic Circle, is allopatric with the penguin, found in Antarctica.
- **Fitness**– if an animal has increased fitness, it has an increased ability to pass on its genetic material, usually by producing more offspring. Most traits, including eavesdropping, develop because the ancestors who developed the gene for that trait had increased fitness over other animals of the same species, leading to more of their genes in the species' gene pool. The fitness of members of a species over one another is known as relative fitness.
- **Mobbing**– a defensive response in social animals. After one animal gives an alarm call, alerting the group to the presence of a predator, other members of the group join him or her, then together attack ("mob") the predator.

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6.2 Primate Alarm Calls[19]

Author: Samantha Berkey

6.2.1 Introduction

Primates live in complex social structures and have developed extensive and highly varied communication systems. A distinctive type of communication found across primate species is loud, attention drawing calls. These are **alarm calls**, which are adaptive as anti-predation measures. The specific alarm calls' structure and function vary from species to species, as each type of primate faces different ecological challenges and lives in different kinds of groups.

Alarm calls can function to alert group members which specific predator is approaching (Seyfarth et al, 1980). Primates such as the vervet monkey or white-faced capuchin have evolved very distinct calls that

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they only use in response to certain predators (Digweed et al, 2005; Seyfarth et al, 1980). This system allows the primate to recognize the difference in calls and to pick the anti-predator response that is most adaptive. For example, a predator that hunts from the air should elicit a different alarm call than one that hunts from the ground, and the primates should respond appropriately by moving lower or higher in the trees (Seyfarth et al, 1980).

Box 6.2: Primate Phylogeny

The primates used to illustrate the functions of alarm calls have varying degrees of relatedness. They can be classified as Old World (residing in Africa and Asia) or New World (residing in the Americas) monkeys, and exhibit a few distinct differences. The Old World monkeys, or Platyrrhines, have flatter, outward-pointing noses, larger canines, and are generally larger in body size. The New World monkeys, or Catarrhines, are hook-nosed and tend to be more terrestrial. We can evaluate species' relatedness by examining a phylogenetic tree (see Figure 6.5).

The capuchins and tamarins are both New World monkeys related by two past divergence events. Their common ancestor split once, and then each of these two species diverged again to give four new species, two of which were the capuchins and tamarins.

The vervet monkeys and Diana monkeys (guenons) and baboons are Old World monkeys that also share a common ancestor. After diverging at this ancestor, the vervet monkey and Diana monkey ancestral line underwent three more speciation events, while the baboons stayed a distinct lineage.

By this phylogenetic tree, it appears the vervet monkeys and Diana monkeys are the closest relatives, and are about equally related to baboons as capuchins and tamarins are to each other. The types of alarm calls observed in each species match this tree. The Diana monkeys and vervet monkeys both use three referential alarm calls (see Table 6.3). The tamarins and capuchins each have an aerial alarm call and a terrestrial alarm call. In addition, both species use their terrestrial alarm call as a general warning (see Table 6.3).

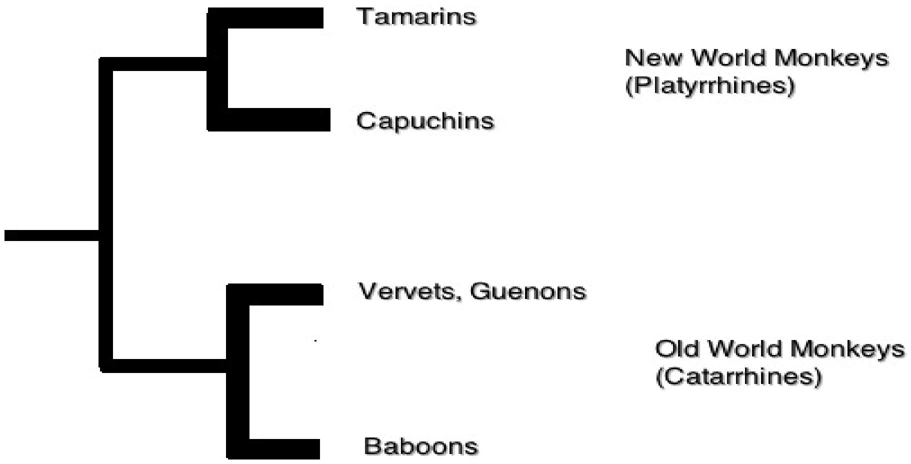

Figure 6.5: The phylogenetic tree of primates shows the varying degrees of relatedness. The three main sub groups are the Hominidae, Platyrrhines, and Catarrhines

Other alarm call systems convey the degree of risk (Fischer et al, 2001). A system based on urgency has evolved in primates with only one escape strategy. These alarm calls differ in their frequency and duration, but don't refer to any specific threat (Fischer et al, 2001). The South African chacma baboon has evolved a graded urgency system that allows it to respond with a quick escape from a high-risk situation, or perhaps ignore the warning when the risk is very small (Fischer et al, 2001).

Primate species that use specific alarm calls have also evolved calls that communicate directly with the predator (Zuberbühler 1999). These systems appear in species that face attack from predators that rely on surprise tactics. Alarm calls for ambushing predators are much louder and more conspicuous than those given in response to other types of predators, as if the primate is letting the predator know it's been spotted and is now out of luck (Zuberbühler 1999).

6.2.2 Communication among Primates

Primate Species	Type of call	Sounds like	Suggested Meaning	Observable Response

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Diana Monkeys (*Cercopithecus Diana*)	clear call	symmetric tonal call	Signals the area is free of threats	The monkeys responded with their own clear calls and continued their daily activities.
(Boxes A2-E4: Zuberbühler et al, 1997; Zuberbühler 2000)	crowned-hawk eagle alarm call	loud, shrill	A crowned-hawk eagle has been spotted	The monkeys descend from the treetops.
	leopard alarm call	loud, shrill, with many changes in frequency	A leopard has been spotted	The monkeys run into the treetops.
White-faced Capuchin (*Cebus capucinus*)	aerial alarm call	harsh, given in single bursts	Signals that an aerial predator has been spotted	The monkeys scanned the sky then retreated down the tree
(Boxes A5-E6: Digweed et al, 2005)	alerting call	bark-like, given in long bouts	A more general signal for terrestrial predators; sometimes may also draw attention to non-predators that are causing a disturbance (better safe than sorry)	The monkeys scanned the sky and then usually ran into the treetops; occasionally they would mob the predator
Chacma Baboons (*Papio cynocephalus ursinus*)	contact bark	tonal, clear bark	These are the two extremes of the range of barks Chacma baboons possess. The contact barks signify there is no risk, while the alarm barks indicate a very threatening situation. There are intermediate barks that allow the baboons to express varying degrees of risk.	The baboons ignore contact barks but investigate intermediate ones

continued on next page

(Boxes A7-E8: Fischer et al, 2001)	alarm bark	harsh, shrill bark	Signify a high degree of risk	The baboons fled to the trees
Vervet Monkeys (*Cercopithecus aethiops*)	leopard alarm	short tonal call	A leopard has been spotted	The monkeys ran up into the treetops
(Boxes A9-11E: Seyfarth et al, 1980; Seyfarth et al, 1986)	eagle alarm	low-pitched staccato grunts	An eagle, or other aerial predator, has been spotted	The monkeys scanned the sky and ran into dense brush
	snake alarm	high-pitched chutters	A snake has been spotted	The monkeys examined the ground around them
Moustachedand Saddle-backTamarins (*Saguinus mystax and Saguinus fuscicollis*)	aerial alarm call	high frequency, staccato	An aerial predator has been spotted	The tamarins scanned the sky for the potential danger
(Boxes A12-E13: Kirchhof et al., 2006; Fichtel 2007)	terrestrial alarm call	low frequent, more drawn out	A terrestrial predator has been spotted; this call is also sometimes used as an all purpose alert	The tamarins scanned the ground for the potential danger and retreated into the treetops

Table 6.3: Comparison of Primate Communication Systems

6.2.2.1 Calling Frequency Increases with Risk of Predation

Many primate species use alarm calls to mitigate the threat of predation. Close range **clear calls** are observed in multiple primate species (Gautier & Gautier 1977; Zuberb*ü*hler et al, 1997). The clear calls could be used to avoid predation, as a form of vigilance, in which case the frequency of calls should increase with heightened risk of predation (Uster et al, 2001). Multiple predators threaten Diana monkeys as they forage throughout the day, and individuals often find themselves out of sight of other group members (Uster et al, 2001). The clear calls that males produce may function to confirm that a particular area is safe. Fitting with this idea, the monkeys produce calls most often when they are widely dispersed, when they are about to move to a new area, in areas of low visibility, and when they are foraging separately to find food (Uster et al, 2001). In other words, the Diana monkeys call more often when there is an increased risk of predation. All of this corroborates the hypothesis that Diana monkeys use clear calls as a form of **mutualistic vigilance** to communicate about the presence of danger, and this communication increases when the monkeys face an increased chance of predation.

6.2.2.2 Predator Specific Alarm calls are Adaptive

Besides calling to give a reassuring "all clear" signal, primates use alarm calls to indicate danger, sometimes in very specific ways. Primate alarm systems can often consist of distinct alarm calls for different predators. These **functionally referential** signals should be adaptive because certain responses are beneficial in one instance but harmful in another; a species with predators that attack in different ways should develop distinct alarm calls to allow the primate to choose the beneficial strategy. Vervet monkeys (see Figure 6.6), which face attack from both the air and the ground, have evolved three calls: a short tonal call for leopards, a series of staccato grunts for eagles, and a high pitched **chutter** for snakes (Evans 1997; Seyfarth et al, 1986). Vervet monkeys will run into the trees, safe from ambush, in response to a short tonal leopard call, but will hide in dense brush, closer to the ground, in response to grunts for eagles (Seyfarth et al, 1980). If Vervet monkeys could not identify different predators by different calls, they would have to simply guess which evasion strategy to use, and may end up choosing a strategy that makes them easier prey.

Figure 6.6: A Vervet monkey forages in the treetops while listening for alarm calls from other group members.
(Picture obtained with permission from http://flickr.com/photos/stignygaard/2434572058/).

The semi-arboreal and semi-terrestrial white-faced capuchin (see Figure 6.7), which also faces predators from the ground and the air, has an aerial predator alarm and a terrestrial predator alarm (Digweed et al, 2005). The aerial alarm always results in a rapid descent from the treetops, while the terrestrial alarm has a more diverse response. It will sometimes lead to retreat into the trees, but may also lead to closer inspection or mobbing of the threat. Capuchins have more than one escape option open to them based on the predator, which makes it especially advantageous to have different alarm calls that allow the capuchin to pick the "best" strategy (Digweed et al, 2005).

Box 6.3: Comparative Studies on Functionally Referential Alarm Systems

Predator specific alarm systems are proposed to be beneficial in primates that face multiple predator types and that can respond with different survival strategies (Macedonia & Evans 1993). Other

> species that face similar ecological conditions should have similar alarm systems. Small songbirds have two different anti-predator strategies, either mobbing a perched predator or hiding from one in flight, and have developed two distinct alarm calls for each type of behavior (Marler 1955). These birds give a high frequency "seet" or a short "chink" in response to an airborne or perched predator respectively; this is similar to the system used by the white-faced capuchins. Another bird species, chickens (*Gallus gallus)*, also gives distinct aerial and terrestrial alarm calls (Evans 1993). Chickens will crouch down or run for cover in response to the aerial call, but stand up tall in a vigilant stance when responding to a terrestrial call (Evans 1993). All of these species can respond to different types of predators in distinct ways; consequently, they have evolved functionally referential alarm systems. Cooperatively breeding meerkats have developed three distinct alarm calls, in a system similar to that of vervet monkeys. The meerkats always respond to an aerial call by running to a bolthole, but scan the area and then move to a different burrow system in response to a terrestrial alarm call (Manser 2001). In response to their "recruitment" call, which seems to be used for snakes, meerkats approach the source of the call cautiously and inspect the area (Manser 2001). As with the vervet monkeys, the meerkats have evolved a specific alarm system because certain anti-predator responses are more beneficial in a specific case (Manser 2001).

Other semi-arboreal and semi-terrestrial primates, such as tamarins and the red-tailed sportive lemurs, seem to have developed predator-specific alarm systems for the same reason (Kirchhof et al, 2006; Fichtel 2007). Kirchhof observed that mustached and saddleback tamarins' alarm calls do correspond with certain predators by measuring the time spent searching in a certain direction by the listening tamarins. He found tamarins spent a significantly longer amount of time looking up in response to the aerial alarm call but a much longer time looking down in response to the terrestrial alarm call (Kirchhof et al, 2006). Putty-nosed monkeys are another species that uses two distinct calls, pyows and hacks (Arnold et al, 2006). The monkeys combine these two calls in various ways; however, eagles always elicit hacks first and more often. The Putty-nosed monkeys use the different sequences of the distinct calls to determine whether an aerial or terrestrial predator is attacking (Arnold et al, 2008). These alarm calls are predator specific which is advantageous to species with multiple escape strategies.

6.2.2.3 Alarm calls that Indicate Urgency are also Adaptive

In species with only one escape strategy, identifying the predator has less value. Instead, it might be more helpful to evolve a communication system that conveys the degree of risk. A primate that can only escape to the trees for safety would prefer to know whether the predator is fifty feet away or in the bush next to him, but not necessarily which type of monkey-eater he must avoid. Chacma baboons face a wide range of predators but do not have multiple escape strategies. The baboons use the same calls, which range from tonal clear barks to harsher alarm barks for all types of predators, but vary the calls to convey the degree of risk (Fischer et al, 2001; Cheney et al, 2003). The baboons respond differently based on the duration and frequency of the calls, simply ignoring any intermediate calls that are not urgent alarm calls (Fischer et al, 2001). One of the first clues that this system may be based on risk determination is the increase in alarm calls when the group is more widely dispersed (Rendall et al, 2000). This is expected; a greater area of dispersal increases the danger to each individual, representing heightened danger. In addition, chacma baboons may give a few scattered alarm barks when confronted with relatively low risk predators such as hyenas or wild dogs (Cheney et al, 2003). Lions, however, always elicit frequent harsh alarm barks from more than one baboon because they pose a greater risk (Cheney et al, 2003). The most frequent alarm calling occurs when baboons cross water infested with crocodiles. This is a high risk situation for the chacma baboons, thus it makes sense that a call system based on the degree of the threat would cause the baboons to bark most frequently in response to their riskiest predator (Cheney et al, 2003). The baboons even barked in response to harmless objects that could potentially be crocodiles, such as floating elephant dung or submerged hippos (Cheney et al, 2003). The heightened sensitivity and increase in call frequency in response to a more threatening predator confirms that their system is meant to demonstrate the relative urgency of the threat, not the particular predator (Fischer et al, 2001).

Box 6.4: Comparative Studies on Urgency Gradient Alarm Systems

Alarm systems that convey urgency should be beneficial in primates if the species has only one anti-predation response. If this system has evolved because the primates can only respond in one way, but do not always need to waste their energy in responding to a non-urgent threat, then a similar system should have developed in other species with limited strategies. The California ground squirrel has two distinct alarm calls, a whistle and a chatter, that were originally believed to signal either large raptors or terrestrial predators (Owings & Virginia 1978; Owings & Leger 1980). However, the California ground squirrel does not have multiple anti-predator strategies, and its alarm calls were eventually found to denote the degree of urgency, instead of the specific type of predator (Owings & Hennessy 1984). Belding's ground squirrels are another species that use alarm calls; again, these squirrels have only one way of dealing with predators, and thus their alarm calls vary in frequency and duration depending on the risk a predator presents (Robinson 1981; Robinson 1980). Even though only one response is possible, it is advantageous to know how quickly to respond to a predator. If the risk is not great, perhaps the squirrel should continue using its energy to forage or find mates. These ground squirrels have developed alarm systems similar to those of the chacma baboon, which affirms the idea that limited anti-predator responses will result in the evolution of a risk based alarm system.

6.2.2.4 Alarm calls can discourage predation

An additional hypothesis for the evolution of alarm calls asserts that primates may actually communicate to the predator (Zuberbühler 1999). An alarm call directed at a predator would let the predator know he had been spotted; this strategy could be adaptive if the predator relied on surprise for successful hunting and could be expected to give up once spotted. A predator that relies on ambush might "realize" that to catch this monkey would take more time and energy than attacking a group of unsuspecting monkeys. Six different monkey species in the Tai forest on the Ivory Coast are subject to predation by leopards, which hunt by surprise (Hoppe-Dominik 1984), and all give different alarm calls in response to a leopard versus a chimpanzee predator (Zuberbühler 1999). The alarm calls given in response to leopards are much more conspicuous than those given to chimpanzees, who are not as dependent on surprise and hunt using the acoustic cues of their prey (Boesch & Boesch 1989; Zuberbühler 1999). This **conspicuous signal** seemed to be directed at the leopard, as it was repeated often and affected the leopards' hunting behavior – the leopard gave up the hunt after the alarm calls more often than can be attributed to chance (Zuberbühler 1999).

Figure 6.7: A White-faced Capuchin monkey keeps an eye out for any potential predators. (Picture obtained with permission from http://flickr.com/photos/atbaker/395960391/[20])

Box 6.5: Interspecies Understanding

Recent studies suggest that primates may understand and respond to the alarm calls used by other species. Diana monkeys are often observed to form mixed species groups, notably with the red colobus monkey and the campbell's monkey (H*ö*ner et al, 1997; Zuberbuhler 2000). Originally, these associations were thought to be due to improved foraging efficiency, but this hypothesis does not stand as the primates have different diets (Noë et al., 1997). Instead, its been proposed that group intermingling provides increased protection from predation; this view is supported by the red colobus monkeys' increase in association with Diana monkeys during their main predator's, the chimpanzee, hunting season (Noë et al., 1997). These two primate species also decrease their vigilance and increase their exposure when associated with another group, further supporting the idea that the pressure from predation is mitigated (Bshary et al., 1997). The decreased risk is most likely due to the Diana monkeys' skill as ground sentinels accompanied by the red colobus monkeys much better effectiveness for aerial predators. In fact, red colobus monkeys were significantly more exposed from below and descended to the ground more often when associated with Diana monkeys (Bshary et al., 1997). However, this hypothesis requires proof that the monkeys are actually communicating between each other about the presence of predators using alarm calls. A study on Diana monkeys and Campbell's monkeys, who also form associations, has suggested that this is the case. Campbell's monkeys produce two distinct alarm calls in reference to crowned eagles

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and leopards, and Diana monkeys respond by producing their own distinct alarm call (Zuberbuhler 2000). The Diana monkeys always give their leopard call in response to the Campbell monkey's leopard call, and their eagle call in response to the Campbell monkey's eagle call (Zuberbuhler 2000). Additional species need to be studied, but it appears that primates may have evolved to understand the meanings in other species alarm calls.

If using a conspicuous signal is adaptive, then other primate species in the same situation should show the same patterns; those species with referential alarm calls should give the more conspicuous one to the predator type using surprise and a less conspicuous, warning signal in response to the predator type not dependent on surprise. This is found in Diana monkeys, which give two different calls in response to their terrestrial predators, chimpanzees and leopards, or eagles (Zuberbühler 1999; Zuberbühler 2000). However, the Diana monkeys give much more conspicuous signals in response to eagles and especially leopards, which are the most dependent on ambush attacks (Zuberbühler et al, 1997).

Alarm calls can vary to a wide degree among primate species, but have evolved to be advantageous. Each type of system, whether it refers to a specific predator or the degree of urgency, is the most adaptive type available in the precise ecological conditions.

6.2.3 Discussion Questions

1. Why are there variations in the types of alarm calls (predator specific, risk specific, etc) that different predators use?
2. What might be some risks of alarm calling?

6.2.4 Glossary

- **Alarm calls**- These are loud, attention getting calls that indicate the presence of a predator or other threat. They are made by one or more individuals and benefit others, and so have been extensively studied as examples of kin selection and reciprocal altruism.
- **Apes**- The apes are in the family Hominidae, which includes the gorillas, chimpanzees, orangutans, and humans. They are omnivorous, agile tree climbers native to Africa and Asia.
- **Chutter**- A rapid, staccato series of notes that sound like "chit."
- **Clear calls**- These are tonal calls audible over about fifty meters. Diana monkeys use clear calls to signal that an area is currently threat free.
- **Conspicuous signal**- This is a behavior that seems to communicate directly to a predator to draw its attention but results in a higher survival rate. For example, skylarks sing when chased by predatory merlins.
- **Comparative study**- A study in which the characteristics of distinct species facing related ecological situations are compared for similarities and differences. These studies are used to support claims that specific ecological conditions are the reason for the evolution of certain behaviors. For example, multiple species that can employ different anti-predator responses have evolved alarm calls that specify predators by type.
- **Ecological Conditions**- The ecological conditions are the sum of the organism's habitat; these include climate, geology, predators, prey, and any other factors that influence an organism's fitness.
- **Fitness**- An organism's fitness is its chance that its genes will be successfully passed down to future generations. Relative fitness is usually used because that determines whether an individual's genes will increase in frequency in the population in future generations. Fitness depends on a variety of factors, including reproductive success and predator avoidance.
- **Functionally referential alarm system**- An alarm system where acoustically distinct calls refer to specific predators and lead to specific responses.
- **Monkeys**- The monkeys are a very diverse group that may be classified into New (Platyrrhini) or Old (Catarrhini) World monkeys. Monkeys exhibit a great range of characteristics; they may be herbivores or omnivores, and some are arboreal while others live on the savannah.

- **Mutualistic vigilance**- Diana monkeys exhibit mutualistic vigilance when foraging out of sight of one another; each watches a different area for predators and lets the others know that the area is safe. All the monkeys benefit because with a smaller area to watch they can use more energy for tasks such as foraging instead of vigilance.

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6.2.6 Biography

My name is Samantha Berkey and I am from Sarasota, Florida. I am a sophomore biology major at Rice University and hope to eventually go to graduate school. I'm very interested in doing research, though I haven't quite decided whether to go into microbiology and medical research or study animal behavior and evolution.

6.3 Intra-Species Communication & Foraging in Social Insects[23]

Author: Leo B. Carter

6.3.1 Abstract

Some social insects communicate when collecting food or looking for new nest sites in variety of different ways. Recruitment tactics are crucial for scouts to communicate the location of new potential resources and nest sites to their nest mates. The forms of communication necessary depend on distance from the nest to the resource, the type of resource, and the recognizable landmarks along the trajectory. Stingless

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[22] http://whozoo.org/mammals/Primates/primatephylogeny.htm

[23] This content is available online at <http://cnx.org/content/m34739/1.4/>.

bees employ a method of pilot flights in which they guide recruits to the newly found resources and use pheromones to either discourage or encourage exploitation of a certain site based on its profitability. In certain ant species, tandem runs and pheromone signals are employed to show recruits directly how to arrive at resources. The most complex communication system is employed by *Apis mellifera* (the honeybee), which employs a combination of a waggle dance on the comb surface to indicate distance and direction of a new site, a piping signal, a tremble dance, pheromones, and carried scent that are all used in recruitment and to communicating the quality and type of resource and its location. Path integration is used for greater accuracy in communication. The quorum rule is employed by both ants and bees in order to end recruitment and to ensure division of labor as well as the efficient exploitation of food resources. When communication methods are imprecise or insufficient, individuals in many insect species ignore nest mate signals and defer to previously acquired field knowledge and personal information on resource profitability and location to decide a course of action. Complex social communication has made eusocial insects some of the best exploiters of natural resources in the animal kingdom.

6.3.2 Introduction

Eusocial colony-dwelling insects have been dubbed super-organisms because of how intricate and advanced the communication and labor division is in these populations, often functioning more like a collection of cells rather than a group of individuals. They are so successful evolutionarily that although they amount to only 2% of insect species, eusocial insects account for more than half of the biomass of land-dwelling arthropods (Hölldobler & Wilson 2009). The complex hierarchies and social structures of insect colonies would be completely impossible without advanced forms of communication. A social insect colony must be able to explore and harvest resources over a much broader area than a solitary organism might. In order to do this, very sophisticated intra-colony communication strategies on the whereabouts of potential resources and a flexible system of division of labor are essential. Terrain, colony size, and nesting environment all have enormous impact on the forms and precision of intra-species communication. Social insects such as ants and bees have been discovered to use various modalities (scent, sound, and chemical signals) and highly tuned behaviors to communicate resource location and profitability. The incredible variety of strategies is also crucial in regulating the division of labor, which changes in response to the shifting needs of the colony. It is important to understand how honeybees compile and decide on variable data observed during waggle-runs, and which modalities (or sense types) of signals stingless bees and bumblebees follow towards food resources. Carried scent, various pheromone indicators produced by the insects themselves, vibrations and dance behavior all interact in complex ways to formulate language.

In foraging, it is supposed that through the use of previously acquired landmark information and path integration, insects are able to measure and assimilate environmental and personal information that allow them to travel between food source and nest and communicate with recruits with increased precision. Path integration involves an insect keeping accurate track of the distance and terrain it covers upon leaving the colony (Collett & Collett 2000), which provides it with accurate information for the return journey. Bees and ants can remember both landmarks and the distance and direction traveled, allowing them to take direct routes back to their nests without having previously traveled the shortcut (2006). This suggests they possess the ability for problem solving and independent decision-making. This ability is crucial for communicating the whereabouts of the new site to its colony mates.

What is certain is that, even in communication, benefits to senders of a signal must outweigh the costs of the process of communication. The waggle-dance is intended to recruit workers to forage at a specified resource location, but how? When and how do bees transition from one role to another? The piping signal of honeybees, once believed to be a begging signal for a sucrose reward (Michelsen et al. 1985), has been studied thoroughly and is now understood to signal a stop to the honeybee waggle dance (Pastor & Seeley 2005). This piping behavior is often coupled with a distinct 'tremble dance' which ends foraging recruitment and initiates a stage of reception. A returning forager unable to find a receiver for the nectar it has gathered will engage in this behavior (Seeley 1992). We will explore how insects transition from role to role. Once it is no longer beneficial for a worker or forager to engage in the costly activity of communication, it will abandon this role for another. Both ant and bee scouts shift from their role of guide to transporter with the aid of the Quorum Rule, which Pratt tells us occurs when they observe enough of their nest mates at the intended resource site (Pratt 2008).

Furthermore, when it is insufficient, social insects can't rely exclusively on the information they receive from their nest mates and must employ certain techniques to account for discrepancies. The receivers of communication must also know when to disregard signals or compare multiple sources or sometimes the received information with their own personal knowledge. Different species of insects, based on prior experience at food sources, can choose to disregard certain sensory signals and even interpret them differently when the quality of resource changes. For example, stingless bees will mark food sources with either attractant or repellent chemical signals that can be disregarded if the profitability at a particular resource location changes (Sánchez et al. 2007). Ants cannot rely solely on the tandem run, where they carefully guide a worker to a food source or nest site, and even the highly specialized honeybee waggle dance is not perfectly precise. These methods of communication must be supplemented by additional information such as the carried scent of a particular food resource and forager's prior experience at a resource location. We will look into exactly how different species of social insects communicate locations of resources, change particular roles, and how they are able to deal with the issues of incomplete or imprecise information when recruiting and foraging.

6.3.3 Reinterpreting Multimodal Signals by Stingless Bees & Bumblebees

Stingless bees, which have a simpler communication system than honeybees, use methods of pheromone or scent trails, pilot flights and vibration cues to guide recruits to new resources. Olfaction and the used of attractant and repellent chemicals on food sources is the principle means of forager recruitment (Nieh 2003). Boogert et al. (2005) showed that the stingless bee Trigona corvina was even able to interpret the attractant and repellent signals of different bee species. However, they must be at the resource for these signals to be of any use. To lead them towards the resource from the hive, the guides make quick flights, or pilot runs, through the group of recruits to keep them together and show them the way towards the new resource (Aguilar et al. 2005). When they become lost in transit or they receive incomplete information, they can cope with this by incorporating multimodal signals in decision-making (Kulahci et al. 2008). Kulahci et al. (2008) performed experiments that showed that bumblebees trained on food sources having both visual and olfactory cues were more accurate in their selection of profitable food sources. Stingless bees use pheromone trails close to the food source to aid in final orientation of the new recruit, and it is speculated that spatial information can be communicated within the hive through antennal contact and vibrations (Nieh 2003). Hrncir et al. (2005) also found that specific thoracic vibrations of the stingless bee *Melipona seminigra* may be a method by which to communicate resource location. They found the intensity of the signal was directly related to the energy output during a foraging run, meaning the weaker the vibration the longer the distance traveled.

A bee recruit must therefore decide which signals to follow in a particular situation, and the more the better. However, the more sensory input processed by the bee, the longer it takes to make a decision. This is called the speed-accuracy trade-off (Kulahci et al. 2008). A bee may therefore prefer to use a quicker single mode when foraging near a nest site, whereas when a food source is farther and more difficult to find, olfactory and visual signals can be used together, especially if the resource is highly profitable. This is called the efficacy trade-off hypothesis (Hebets & Rapaj 2005). Once learned, if the quality and benefit of the resource is high enough, it will outweigh the cost of increased sensory input (Kulahci et al. 2008). In Cameron's study, even bumblebees were shown to mark profitable food sources with sucrose rewards to entice and recruit fellow foragers. What is interesting is that they were capable of interpreting these positive signals as negative once the food source had become unprofitable (1981). *Scaptotrigona mexicana*, a stingless bee species, can also associate the same pheromone marker as both a negative or positive signal depending on food source quality (Sánchez et al. 2008). They are thus able to interpret the same signal in different ways, suggesting the ability for individual decision-making and the capacity for experienced-based learning.

6.3.4 The Honeybee's (Apis mellifera) Waggle-dance

Bumblebees and stingless bees implement various modalities of communication but none are as advanced as the unique dance strategies of honeybees. Honeybees have evolved separate forms of communication that are influenced by their foraging and nesting environment and their brood size. A returning honeybee scout must communicate to the rest of the hive the location of a newly found food source or a potential nest site. They execute a 'Waggle Dance' where the scout performs quick forward moving abdominal vibrations as it crawls in straight line across the surface of the comb. It returns in semicircles of alternating directions to its starting place and then begins again a variable number of times (De Marco & Menzel 2005). It is an advertisement for the distance and direction of a new resource completed in a cyclical figure-eight pattern. Dance observers group closely together around the dancer, often coming in contact with her, thereby registering the source's odor and often receiving samples of food that the forager has returned with (Hölldobler & Wilson 2009).

The length of the waggle phase depends directly on the distance to the resource. The longer the waggle face, the farther the resource is from the colony. The direction is also encoded in the angle of the dance (Von Frisch 1974)(De Marco & Menzel 2005). The returning foragers situate themselves on the 'dance floor' and begin a waggle phase in the direction of the food source with the sun as their azimuth. The length of the run is directly linked to the distance to the source (Beekman et al. 2008): the longer the tail-wagging period in the forward-moving part of the dance, the greater the advertised distance (Von Frisch 1974).

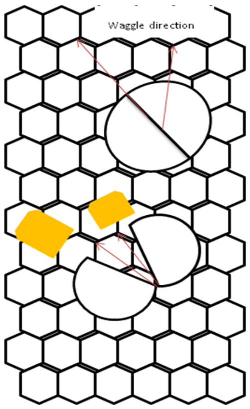

Figure 6.8

Figure 1 Redrawn fromTanner & Visscher (2008)

As far as direction is concerned, Von Frisch was able to prove that, because bee dancers advertising for the same location would change orientation throughout the day, they use the Sun as their 'North Star,' so to speak. If the food source is in the direction of the Sun, the dancers move directly upwards along the surface of the hive, shifting away from the vertical orientation depending on its angle and direction from the Sun (Von Frisch 1974). Also, the honeybee's ability to see polarized light permits them to forage and communicate even when the Sun is obscured and during nighttime (1974). Honeybees can map mentally the paths they travel, meaning they are capable of path integration. This influences the locations they communicate. When a waggle dance indicates a particularly remote distance, the spatial and directional information communicated may be insufficient on difficult terrain. Chittka et al. preformed a set of experiments with trained honeybees in which they proved that foragers are able to memorize and sequence even multiple landmarks along a path to a resource. Foragers can respond to them contextually even if they are not in direct proximity to a food source, allowing them to follow specific memorized trajectories from one landmark to the next (1995). De Marco and Menzel found that because of path integration, when forced to follow a detour, a honeybee scout is actually capable of communicating a theoretical untraveled route with the use of visual references and odometric mapping of the terrain (2005). Therefore, honeybees communicate both distance and direction in their dance (Gardner et al. 2007), that are both actual and hypothetical, taking into account a variety of environmental references (see figure 1).

Seely et al. have also shown in their experiments that waggle dancers communicate even the quality of the food source. They noticed that, while the waggle phase remained constant, the length of the return phase was directly related to the quality of the food source—the longer the return, the higher sucrose content of the resource (2000). This unique and highly variable dance is crucial for the colony to keep track of changing resource conditions and successfully and efficiently exploit specific sources (Seeley & Visscher 1988, cited in Beekman et al. 2008).

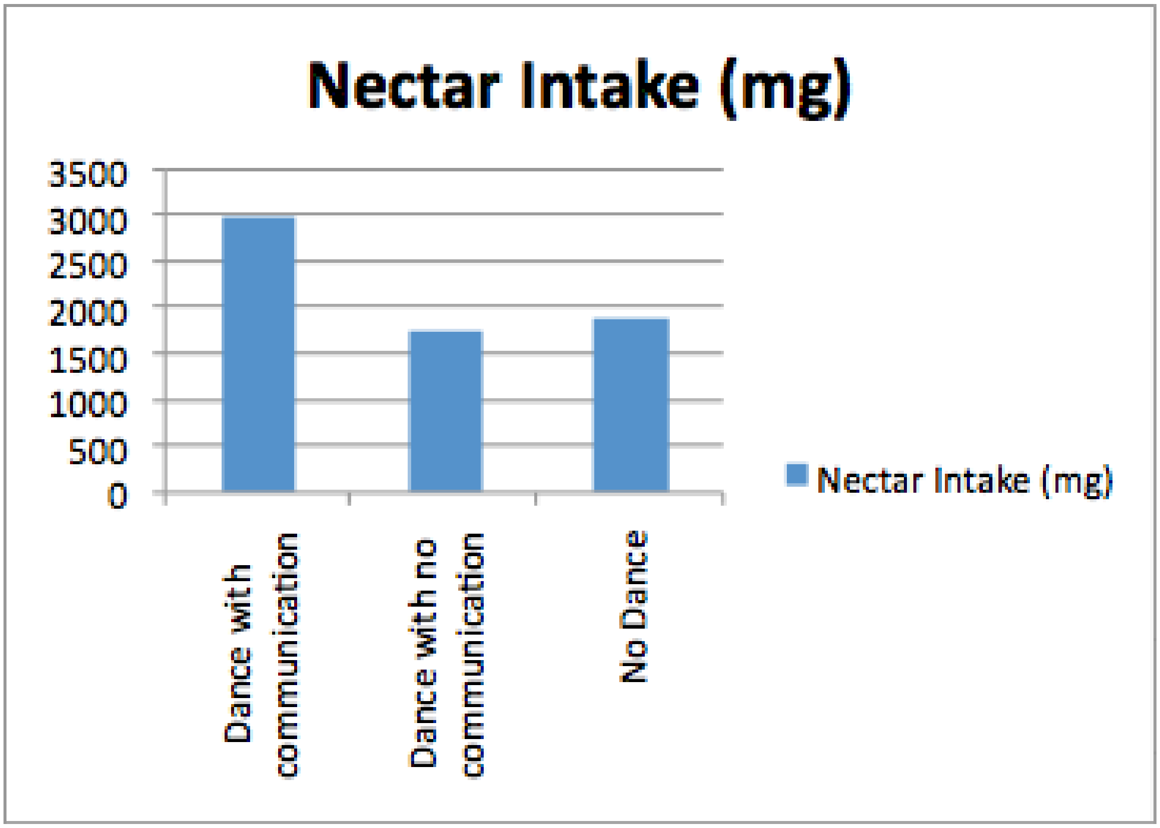

Figure 6.9

Graph 1, Increased nectar intake due to waggle-dance recruiting. Redrawn from Beekman and Lew (2006)

In the absence of waggle dancing, bee colonies search for resources in a more spread out and random area encountering resources of variable quality (Beekman & Lew 2006), as opposed to focusing the recruitment on a patch of high profitability. Foragers will not advertise a site with low profitability nor will they return with a sugar reward, which would be used to excite nest mates (Von Frisch 1967). But searching large areas with various workers allows them to localize a particularly profitable resource that foragers will then advertise to the rest of the workers. Graph 1 above shows how observation of the waggle-dance increases the nectar-intake of the foragers, but without communication (recruitment) is as ineffective as not dancing at all.

6.3.5 Box 1: Bite Recruitment in Polybia Wasps

Colonies of the paper wasp *Polybia* are much smaller than most honeybee colonies. They also have a distinctly unique method of forager recruiting completely dissimilar to the honeybee waggle dance. The paper wasp's approach to recruiting foragers to food sources is much more aggressive. As Sean O'Donnell shows in his study, the wasp recruiters bite one another, a signal that was used by scouts to recruit other wasps to begin foraging. He found that bitten wasps have an increased likelihood to initiate foraging. In order to test his hypothesis, he removed active foragers from nest sites and found that in relation to the control sites, foraging greatly decreased throughout the following days. This, he noted caused a marked decrease in food gathering and as he had predicted a drastic increase in the rate at which non-foraging worker wasps were bitten. Those that were bitten often began a foraging role soon after. It is important to note that just as the honeybees cope with inaccuracy of waggle dances by deferring to prior knowledge on food sources, some paper wasps initiated foraging even without being bitten (O'Donnell 2006).

Olfactory communication proves to be even more advanced in honeybees and also plays an important role in the recruitment process. In addition to scents gathered from the environment, Thom et al. in their experiments proved that the returning recruiters secrete as many as four complex pheromones while engaging in the waggle dance. They showed, by injecting one such chemical into a test population, that it increased the number of recruits that left the hive after the waggle-dance. As many as four distinct chemical signals, produced only by waggle-dancers during their runs have been shown to increase the number of recruits that begin foraging (Thom et al. 2007). Von Frisch's experiments also showed that a nectar scent carried by a forager can be traced by a dance-observer to a particular flower, thereby increasing the accuracy of the recruitment process (Von Frisch 1974).

6.3.6 The Variability of Waggle-dance Communication

The effectiveness of the waggle-dance is highly variable within individual honeybee colonies. Colonies with eggs fertilized by multiple males (multiple-patriline) have been shown to increase foraging rates, larger stores of food and higher individual health compared to single-patriline colonies (Mattila et al. 2008). That is to say, queens that breed with more than one male increase the productivity of their nest. It is strange that decreased relatedness within the brood would in fact increase productivity, but the reasons are clear. What Mattila and her colleagues discovered was that in a genetically diverse population, worker efficiency was improved by the genetic variability of communicational behaviors. They showed that multiple-patriline colonies had an increase in foraging rates of 27-78% and engaged in 36% percent more waggle dances daily than genetically uniform colonies (Matilla et al. 2008). Not only does genetic diversity increase resistance to diseases in the hive, but it also allows for varying degrees of specificity in waggle dances. Decreased relatedness creates an increased need for more highly specific communication, as well as an increased variability in the waggle-dance. This increased variety of dance, according to the Tuned Error Hypothesis, may also lead to a larger search area. This is not necessarily a negative outcome. It occurs also when workers witness only a limited number of incomplete waggle runs and perhaps could allow bees, even at a short range, to find unexplored food resources next to the one being indicated by the dancer. Since the dances that indicate more remote locations are more precise and last longer, the search area at both close and far distances should theoretically be comparable (Tanner et al. 2008).

Between honeybee species, hive location preference has directly influenced differentiation of dancing techniques through evolution. Beekman et al., found that *Apis florea* does not increase the relative precision of its dance based on context, whereas *A. mellifera* does (2008) as more and more bees begin and sustain a waggle-run advertising a highly specific site (Oldroyd et al. 2008). *A. florea* has no need for dance consensus or the high levels of accuracy because recruiters do not need to express exact locations. Their potential nest sites, such as exposed branches on trees, are easily identifiable even from a distance. The complication of A. *mellifera's* dance is believed to have arisen when the species changed nesting habits from open-dwellings to cavity nest sites (Beekman et al. 2008)(See Table 1 for dance summary). Because it is difficult to pinpoint a possible nest site that is within a cavity as opposed to in an open area, the bees needed to evolve a more precise system of communication. This was made possible through relative consensus on the profitability of a possible nest site (Oldroyd et al. 2008). In the *mellifera* species, ‘piping’, which is achieved by vibrating the thorax against the surface of the hive, is performed by dance-watchers in order to elicit a stop in the waggle-dance (Pastor and Seeley 2005). Once a nest site has been agreed upon and the quorum reached, workers will engage in ‘piping’ and ‘buzz-running’ to signal that it is time to evacuate the old nest (Oldroyd et al. 2008).

Piping is sometimes supplemented by a unique ‘tremble dance’ in which the forager will rotate its body around an axis, vibrating in place (Seeley 1992). Seeley informs us that this behavior occurs when there is a surplus influx of nectar, and that it signals both that bees should stop recruiting and that more workers should begin receiving nectar for storage (1992). Conversely, if there are not enough foragers, sometimes what is called the

‘shaking’ dance, executed by quick up and down vibrations of the thorax, will signal recruits to go to the ‘dance floor’ (or comb surface) to receive information on the newly found resource (Hölldobler & Wilson 2009). But how does *A. mellifera* reach a consensus between large numbers of individuals on a particular nest site?

Table 1. The Dances of *A. mellifera*

Name of Dance	Characteristics of Dance	Purpose of Dance
Waggle Dance	A waggle and return performed cyclically and alternatively	To signal the direction and distance of food sources (De Marco & Menzel 2005)
Tremble Dance	Vibrating quickly and rotating while moving across hive surface	To signal the end of forager recruitment and beginning of nectar harvest (Seeley 1992)
Shaking Dance	Quick up and down vibrations of the thorax	To tell recruits to go receive information about new forage site (Hölldobler & Wilson 2009)
Piping	Vibrating thorax against surface of hive	To signal the end of the waggle dance (Pastor and Seeley 2005)
Buzz Running	Moving in a zigzag pattern across surface while buzzing their wings	To signal when to evacuate the old nest (Oldroyd et al. 2008)

Table 6.4

6.3.7 How Honeybees Cope with Waggle Dance Informational Conflicts

There is a notable conflict between personal and communicated information. This conflict is present within the waggle dance itself. Marco and Menzel show that, because of path integration, a scout’s dance may encode both the actual distance traveled as well as the shortest theoretical distance to a desired destination (2005). Gould also noticed the discrepancy between the actual location of the food source and where the foragers following the waggle-dances arrived (1974). Actual and theoretical directions and distances to locations are obscured because of this, and can therefore vary widely from scout to scout. How will an inexperienced worker interpret these highly variable signals? Tanner and Visscher’s study shows that, surprisingly that the range of possible locations expressed in the dances is more variable then the flights of newly recruited bees (2008). It is by averaging the observed waggle-runs that the recruits are able to fine-tune their trajectory. This is precisely how *A. mellifera* reaches its colony ‘consensus.’ Tanner and Visscher’s data show that those bees that observe the waggle-runs the longest will have a more accurate path trajectory. Also, those bees that advertise longer will be more likely to be observed and followed (2008). Furthermore, the most profitable locations are advertised more vigorously, more at length and by more individual recruiters than those that are less so (Oldroyd et al. 2008), and are therefore more likely to be observed. This is conflict and competition at its most productive and beneficial to the colony.

There are clearly certain disparities between personal and communicated information. Therefore, for these complex informational systems to succeed, a certain amount of individual decision-making is also needed. For example, if the odor of a certain flower brought by a scout-dancer is familiar to a dance observer but the demonstrated location is unknown, a bee will use preexisting private information to forage locations of known food sources and will disregard the new information conveyed in the waggle dance (Grüter et al. 2008). In one study, Grüter et al. found that 82% of tested bees returned to previously visited food patches when they received unknown spatial and scent information (2008). Workers on the surface of the hive will swarm recruiters that return often with the scent of a certain flower on them. Grüter et al. informs us that often times that, depending on the specific pollen detected on the nest mate, the worker may have sufficient knowledge to begin foraging at previously visited sites. They show that this reactivation would lead 93% of experienced foragers with divergent private data to return to an old foraging location (2008).

6.3.8 Box 2: Quorum & Tandem Runs in the ant Temnothorax curvispinosis

Ants communicate predominantly through olfactory cues, but one particular behavior called Tandem Running is used to recruit foragers to a new location. It involves slowly guiding a worker along the path to the resource or nest site. The follower maintains contact with the guide with its antennae (see image below). Tandem running increases the number of recruited ants as well as informing them on location of a resource or possible nest, whether or not the run is finished to completion. Ants may supplement this information by laying down pheromone trails on the return to nest from a food source (Chu et al. 2003). Pratt (2008) notes that this process is slow and costly to the ants so they must know when to disengage from this behavior and began gathering or ‘transporting,’ where they literally carry their nest mates to the newly discovered site. The ants are able to decide, by monitoring the group of nest mates at the new site for when it has enough workers already established there, when it will be most profitable to stop tandem runs and begin transports (Pratt 2008). This is an example of the quorum rule in use. There is a close analog to this behavior in honeybees. Once a new nest site has been decided on, certain scouts will fly quickly through the moving swarm in order to ‘point’ the new recruits in the correct direction (Beekman et al. 2006). Ants are typically members of large-sized colonies that can number in the millions. This means that often they rely more on group foraging and chemical signals and less individual and learned knowledge (Beckers et al. 1989).

Figure 6.10

The guide and recruit maintain close contact during a tandem run using their antennae.

6.3.9 Conclusions

Although some of the findings exposed in research on bee language are still hypothetical, much has been discovered on the forms and modalities of communication, as well as an insect's individual ability to defer to knowledge gathered in their environment on profitable resources and an internal mapping system with which it compiles information on its paths. Within the field, many discoveries are still being made and old theories revised. For example, for decades it was believed that *A. mellifera* had two distinct dances to communicate distance and direction to recruited dance-observers (Von Frisch et al. 1967). Recently however, these two dances have been shown to be the same, varying only in the length of their waggle phases, which depend on how distant the advertised resource is—the closer, the shorter the waggle-phase (Gardner et al. 2007). Honeybee dancing, piping and pheromone cues can truly be described as an interrelated form of language capable of transmitting many different meanings. The tremble dance is one example in that it can be interpreted in two distinct ways by forager recruits and dancers (Seeley 1992). We have seen that because of the variable specificity and accuracy of honeybee waggle-dancing, recruits often receive incomplete information. Averaging observed dance information allows for a theoretical consensus in *A. mellifera* on the ideal potential nest site. In bees and ants, using various types of olfactory, visual, auditory, and sensory signaling allows for the development of complex systems of networking, multi-modal evaluations of resources, and labor distribution within these finely tuned super-organisms. These communication strategies are crucial to the complex division of labor and the efficiency of resource foraging in all species of eusocial insects.

6.3.10 Discussion Questions

- Why are the dances that bees use considered to be "languages"? Is this assessment a legitimate one?
- Why is the flexibility of the dances and their interpretation important?

6.3.11 Glossary

- **Eusociality**- Indicative of a high level of social stratification including reproductive division of labor, overlapping generations and cooperative care of the young
- **Landmark-based Information**- Information gathered by insects in the environment that allow them to orient themselves with regards to a food source or the nest.
- **Multiple-patriline Colony**- A colony with one queen who has mated with multiple males. In the case of honeybees, this is often indicative of a successful and active colony with respect to a single-patriline colony. All natural colonies are founded by queens that have mated many with many males, all in a short space of time.
- **Odor/Olfactory Communication**- Communication by insects using either the pollen and odor of familiar or unfamiliar flowers to help describe a food sites location, or scent attractants and repellents in the form of pheromones produced in their own bodies.
- **Path Integration**- The ability of an animal to return to an initial location using cues such as landmarks as well as memory-based notions of distance and direction.
- **Pheromone**- A chemical substance secreted by one individual intended to elicit a specific response from another member of the same species. They can be attractants or repellents and are often interpretable in a variety of ways based on context.
- **Private Information**- Information gathered by individual insects that allows them to disregard an unknown location that is communicated by one of their kin in favor of prior knowledge on food resources.

- **Shaking Dance**- A dance executed by forager usually in a time of low nectar yield, but immediately following a resource discovery. It signals to recruits to go to the hive surface and observe waggle-dance runs. The dancer executes quick up and down movements of the abdomen sometimes with its front legs on the recruit. (Hőlldobler & Wilson 2009).
- **Single-patriline Colony**- A colony with one queen who has fertilized all of her brood with the sperm from only a single male. In the case of honeybees, it is often unfavorable in terms of overall colony efficiency and health, and is only found in experimental situations since in nature queens always mate multiply.
- **Tuned Error Hypothesis**- Predicts that built in inaccuracies and the brevity of short-run waggle dances allows for equal distribution of scouting recruits at close ranges and at a more precisely indicated distant ranges (Tanner et al. 2008).
- **Tandem Run**- A technique employed by ants in which a guide leads a recruit along a path towards a potential food site. During the run, the follower and guide often maintain contact with their antennae.

- **Tremble Dance**- A honeybee forager executes this dance by vibrating quickly and turning about an axis as much as 50 degrees per second while slowly moving across the hive surface. It signals an end to forager recruiting and the initiation of nectar reception (Seeley 1992).
- **Waggle Dance**- Two phases, the waggle phase and the return phase performed alternately and cyclically characterize this method of honeybee communication. Direction and duration of the waggle phase is directly linked to the direction and the distance to the site communicated (whether it be a food source or a potential nesting site).

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Chapter 7

Deception between predators and their prey

7.1 Why Copy? The Evolution of Mimicry[1]

Author: Michael Schiff

7.1.1 Introduction

Biological studies today are done under a lens of the theory of evolution by natural selection. This means that populations change over time because the ratios of specific **genes** within individuals change through time as the environment around that population changes, and that these changes make the individuals in the population better able, in some way, to pass their genes on to the next generation. This leads to the understanding that most genes that are actually expressed in a given individual should generally be adaptive to that individual's environment because the maladaptive genes would have been outperformed by the adaptive ones through time. Traits can be adaptive in two general ways: either by A) directly increasing the organism's **reproductive success** or B) increasing its survivability, which generally leads to an increase in reproductive success. Mimicry is most often adaptive in the latter sense, i.e. that it increases the individual's chance to survive long enough to reproduce one or more times. For example, a bull snake looking like a rattlesnake increases its survivability because predators are less likely to eat something that looks like a venomous rattlesnake. There is seemingly a contradiction here though, as many forms of mimicry make the organism more susceptible to predation via loud colors or conspicuous displays, such as a king snake mimicking a coral snake. So why should mimicry have evolved in the first place?

Box 7.1: Coral Snake Mimicry

The System: There are many species of coral snakes and similarly colored/patterned snakes throughout the tropical and temperate parts of North and South America. Several are extremely venomous, some mildly venomous, and many are non-venomous.

The Story: When Batesian mimicry was first described, coral snakes and their supposed mimics were often used as seemingly obvious examples. Many non-venomous species seem to suffer less predation due to having similarly colored bands along their bodies as do true coral snakes. However, as more research was performed, the system showed itself to be more complex. In 1878, Fritz Muller suggested another type of mimicry system, Mullerian mimicry (Wickler 1968). This mimicry is basically the same idea as Batesian mimicry except that it extends to mutual mimicry of different venomous species. In short, multiple dangerous species mutually benefit by mimicking each other because it gives each individual less chance of being a "mistake" a predator attacks before learning

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[1] This content is available online at <http://cnx.org/content/m34757/1.3/>.

> not to attack species with that pattern because they are venomous. This seemed to apply readily to coral snakes because several of their mimics are also venomous. But then herpetologist Robert Mertens came along and suggested that this is still partly incorrect because the true coral snakes have such potent venom that would-be predators would not survive a defensive bite. Therefore he suggested that it is actually the mildly venomous snakes that are being mimicked by both the true coral snakes and the non-venomous species. This was later labeled as Mertensian mimicry It should however also be noted that many newer studies suggest the similar patterns and coloration of these species to be due to similar environmental factors, not mimicry at all (Herrera, Smith, & Chiszar 1981), and that predators may not avoid true coral snakes at all (Beckers , Leenders & Strijbosch 1996a).

There are several hypotheses around as possible answers to this question. In general they come down to the benefit of mimicking outweighing the cost of being more conspicuous. Also, many mimics (like the bull snake example) are not especially conspicuous compared to non-mimetic relatives, meaning that the cost of mimicking another organism is even lower. There are many different forms of mimicry, but the main categories discussed here will be Batesian mimicry, death feigning, a form of aggressive mimicry called **caudal luring**, and sexual mimicry. The most common technique for the study of mimetic systems is the comparative method, since most systems involve two or more separate species and the same basic system is found in many groups of animals. However, within species observation and experimental studies are also performed when applicable. Snakes make a great model group for learning about this subject because all of these broad categories can be found within the suborder serpentes. There are a few especially interesting cases of snake mimicry as well.

7.1.2 Batesian mimicry

Figure 7.1: Eastern Coral Snake, *Micrurus fulvius*, compared to King snake, *Lampropeltis sp.* Photos by Snakecollector on Flickr and *∼DAWN∼* on flickr respectively.
*See end of reference section for intellectual property

The most well known and extensively studied form of mimicry is a type of defensive mimicry known as **Batesian mimicry**. It was first described by, and later named for, Henry Bates who proposed mimicry as the reason for unrelated species of butterflies often having very similar patterns. Batesian mimicry is where a member of a palatable species has the same color patterns and/or body size and shape as a non-palatable species. That is to say that a species that predators would have no problem eating mimics a species that is dangerous or distasteful to eat in either looks or behavior, often both. The benefits to the mimic here are relatively obvious. It gains a greatly decreased chance of being preyed upon since predators will associate it with the dangerous or distasteful nature of the mimicked species. The cost-benefit hypothesis therefore asserts that this benefit outweighs whatever cost the mimicry has on the individual.

Figure 7.2: Bull Snake, Pituophis catenifer sayi. Note that the dorsal markings are similar to those of many rattlesnakes. Photo by Lady Shmee on flickr.

The most well known suggested example of this type of mimicry in snakes is the coral snake and its mimics. However, this system is far more complex than originally thought and is discussed at length in Box 7.1 (Coral Snake Mimicry). Another common, and far less complex, system of Batesian mimicry in snakes are the cobras and their mimics. Several species of non-venomous snakes copy the shape of a cobra's hood and strike posture. A further and really excellent example is that of the bull snake, *Pituophis catenifer sayi*, mimicking rattlesnakes in both looks and behavior (Herrera, Smith, & Chiszar 1981). Not only are the two species patterned very similarly, but the rattlesnake covers all of the bull snake's **native range**, and the bull snake also vigorously shakes its tail when threatened, even though it lacks the rattlesnake's rattle. These traits all added together strongly suggest that bull snakes are true Batesian mimics of rattlesnakes. However, there is some concern expressed by a few scientists that rattlesnakes are too venomous to allow predators to learn from "mistakes" (see Box 7.1 (Coral Snake Mimicry)). It has been strongly suggested though, that a rattlesnake does have control over how much venom it injects with any given strike (see figure 3) and often delivers a "sub-lethal" amount when defending itself (Hayes, LavÆn-Murcio, & Kardong 1995). Recently, it has also been shown using model snakes with distinctively viper-like markings that Batesian mimicry definitely does not need bright warning colors to be effective (see Figure 7.4) (W*ü*ster et al. 2004).

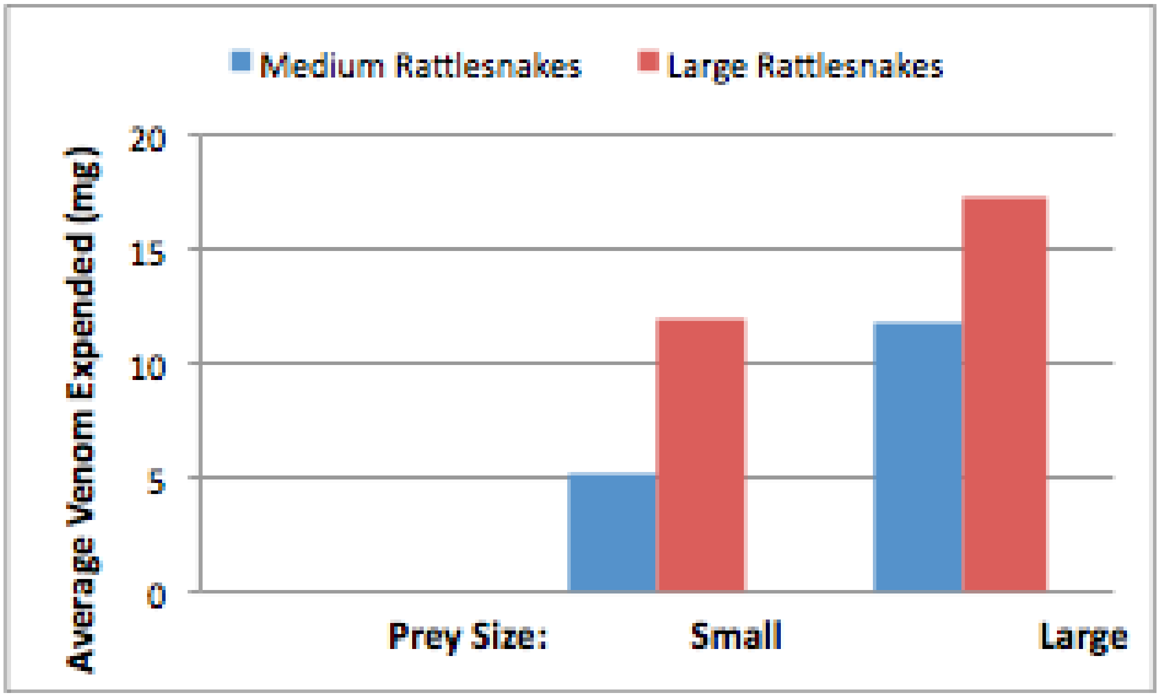

Figure 7.3: Amount of venom expended per hit by large and medium rattlesnakes on large and small prey. This figure shows that rattlesnakes inject different amounts of venom depending on prey size. It supports the idea that rattlesnakes have control of some sort on the lethality of a bite. (Recreated from Hayes, Lavin-Murcio & Kardong 1995)

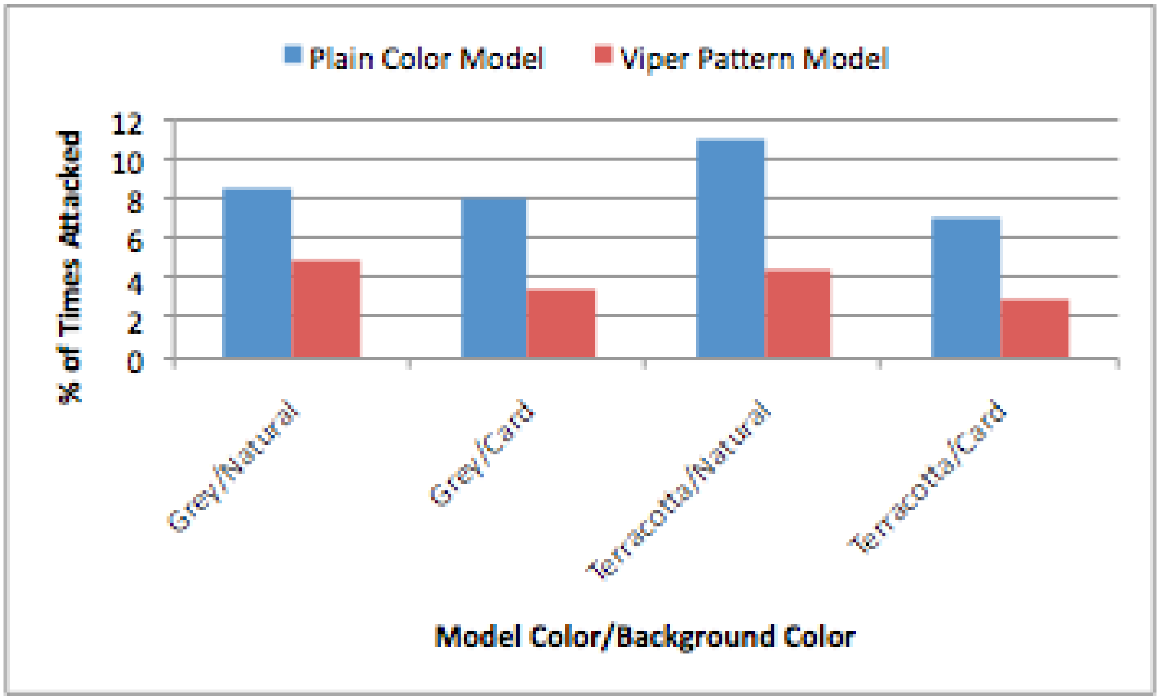

Figure 7.4: Percent of time solid colored model snakes were attacked compared to models of the same base color with viper patterns. This shows that predators learn to avoid venomous snakes without bright warning colors, in support of the hypothesis that bright colors are not necessary for a Batesian mimicry system (Recreated from Wüster et al. 2004).

In both these cases, the non venomous snake increases its survivability by mimicking the venomous snake to the point that predators think they are the same species (and therefore themselves venomous). They are very good examples because the mimic does not gain any conspicuous colors that would hinder it from catching prey or make it more likely to be spotted by would be predators. There are two other forms of defensive mimicry that are subtypes of Batesian mimicry called **Mullerian mimicry** and **Mertensian mimicry**, which are forms of defensive mimicry between multiple venomous species and are explained with the coral snake mimics in Box 7.1 (Coral Snake Mimicry).

Box 7.2: Olfactory Mimicry

Another possible type of defensive mimicry is **olfactory mimicry**. It has been shown in the past that a few plants mimic the smell of dead meat or female insects to attract pollinators into the flowers. However, many scientists were skeptical of the possibility for defensive mimicry based solely on olfactory cues without any visual ones. In 1975, James A. Czalpicki and his colleagues performed an experiment that showed olfactory mimicry could theoretically serve as a form of defense (Czalpicki, Porter, & Wilcoxon 1975). During the experiment, several garter snakes were divided into two groups. Members of both groups were mostly fed minnows, but they were also fed night crawler worms on occasion. The experimental group was given a small dose of lithium chloride, which would make them mildly ill, while the control group was injected with saline solution. The results showed that the experimental group later rejected minnows that were dipped in “night crawler surface extract” so they smelled like the worms, but didn’t reject regular minnows. The control group did not reject the minnows that smelled like worms. Also, as a further experiment, they ran the same test but included some minnows made to smell like salamanders, without injection of LiCl, which neither group rejected. This showed that the experimental group rejected the earlier minnows because they smelled specifically like night crawlers and not because they smelled different from their normal meals for the previous several weeks. It seems though, that there have not been any cases found in the wild were olfactory mimicry is used by a species specifically for defensive purposes to date.

7.1.3 Death Feigning

Another interesting defensive mimicry behavior in snakes is the well known death feigning of American hognose snakes, *Heterodon spp.* When threatened, a hognose snake flips onto its back and starts writhing around as if it is about to die from serious illness. This is followed by bloating and excretion (Munyer 1967). The snakes perform this display in water as well as on land, but tend to move more quickly to bloating and stillness when in water. When flipped back upright, the snake immediately flips onto its back again and continues the bluff. But what evolutionary purpose does death feigning really have? One possible explanation, and the most likely for hognose snakes, is that feigning death in such a dramatic and disturbing way will make the predator think that the snake has a disease or parasites and will not eat it for that reason (Milius 2006). It has also been discussed with insect and fish species that feigning death can provide defense by way of the bad odor emitted by many species displaying this behavior or can even be a form of aggressive mimicry that lures unsuspecting scavengers near the organism, which then 'comes back to life' and eats them. Some cases of similar behavior have been misinterpreted as death feigning, but are actually a form of defense where the bloating of the individual just makes it hard to swallow.

Figure 7.5: Hognose snake, Heterodon sp, feigning death by rolling over and regurgitating its last meal. Photo by Benimoto on Flickr.

General Type of Mimicry	Specific type of Mimicry	Species

continued on next page

Defensive Mimicry	Batesian Mimicry	Bull Snake, False Cobra
	Death Feigning	Eastern Hognose Snake
	Mullerian Mimicry	Certain Asiatic Pitvipers
	Mertensian Mimicry	Coral Snake*
Aggressive Mimicry	Caudal luring	Pygmy Rattlesnake, Green Tree Python, Puerto Rican Racer
	Lingual luring	Garter Snakes
Sexual Mimicry	Female Mimicry	Garter Snakes

Table 7.1: lists the six most common categories of mimicry among snakes (in order of when discussed in the paper) and species that are examples of that mimicry.
*Similar color patterns in coral snakes and would-be mimics may be a result of other shared environmental factors besides warning colors.

7.1.4 Caudal Luring

One of the types of mimicry that is increasingly being studied within the past two decades is caudal luring. This is a form of aggressive mimicry where an individual uses its tail to mimic the shape and movements of a species eaten by their prey, most often worms or insect larvae, in order to attract a meal. This is done by the strategically moving its tail back and forth in a specific way meant to look like the mimicked species, often with their body hidden. Caudal luring is most well known among pit-vipers but has also been shown to happen in pythons and boas (Murphy, Carpenter, & Gillingham 1978) and colubrids (Tiebout 1997 and Barun, Perry, Henderson, & Powell 2007). In his paper, Tiebout explains that the occurrence of caudal luring in colubrid snakes that share ranges with rattlesnakes opposes the hypothesis that rattle snake rattles evolved from small nubs on snake tails used in caudal luring. He states that given this evidence, the other hypothesis for rattles: that they evolved from a hard tail nub used to rub against grass and leaves to ward off danger, is much more likely. A few interesting studies on the subject have shown that younger snakes are much more likely to caudal lure than adults (Rabatsky & Farrell 1996b and Rabatsky & Waterman 2005). However, the reasons for this are still somewhat unclear. It has been suggested that the type of prey has a significance caudal luring, where younger snakes generally eat lizards, frogs, and large insects that would likely prey on worms and larvae, but it was shown that pygmy rattlesnakes, *Sistrurus miliarius*, which still eat these prey items even as adults, also generally stop caudal luring upon reaching adulthood. In their 2005 paper, Rabatsky and Waterman also tested a hypothesis made by Neill that males of sexually dimorphic species that perform caudal luring, such as pygmy rattlesnakes, will have better success rates than females. The theory is that a longer tail segment in males compared to females will be better able to mimic movements of different types of organisms, and therefore will seem more desirable or more realistic to the intended prey. In support of the hypothesis, they found that it took juvenile males less than half the time it took juvenile females, on average, to lure prey within striking distance while caudal luring, as shown in Figure 7.6 (although only one individual prey was attacked within a 30 minute trial period).

Box 7.3: Lingual Luring

While garter snakes, *Thamnophis spp*, are much better known in terms of mimicry for often being sexual mimics, some have been found to perform an unusual form of aggressive mimicry known as lingual luring (Welsh & Lind 2000b). Lingual luring is very similar to caudal luring except an individual flicks its tongue against the water instead of waving its tail in the air or along the ground. Most other characteristics of the two are generally the same, and they are both used to mimic the snake's prey's prey. However, while caudal luring has been observed in some lizards, lingual luring has not to date. Lingual luring is distinguishable from normal tongue flicking by the position of the tongue and duration of flicking. Also the authors show that like caudal luring, lingual luring is almost exclusively done by juvenile snakes, not adults. Lingual luring is best known in a slightly different form used by alligator snapping turtles, *Macrochelys temminckii*, where the shape of the tongue mimics prey much like in caudal luring by snakes and lizards.

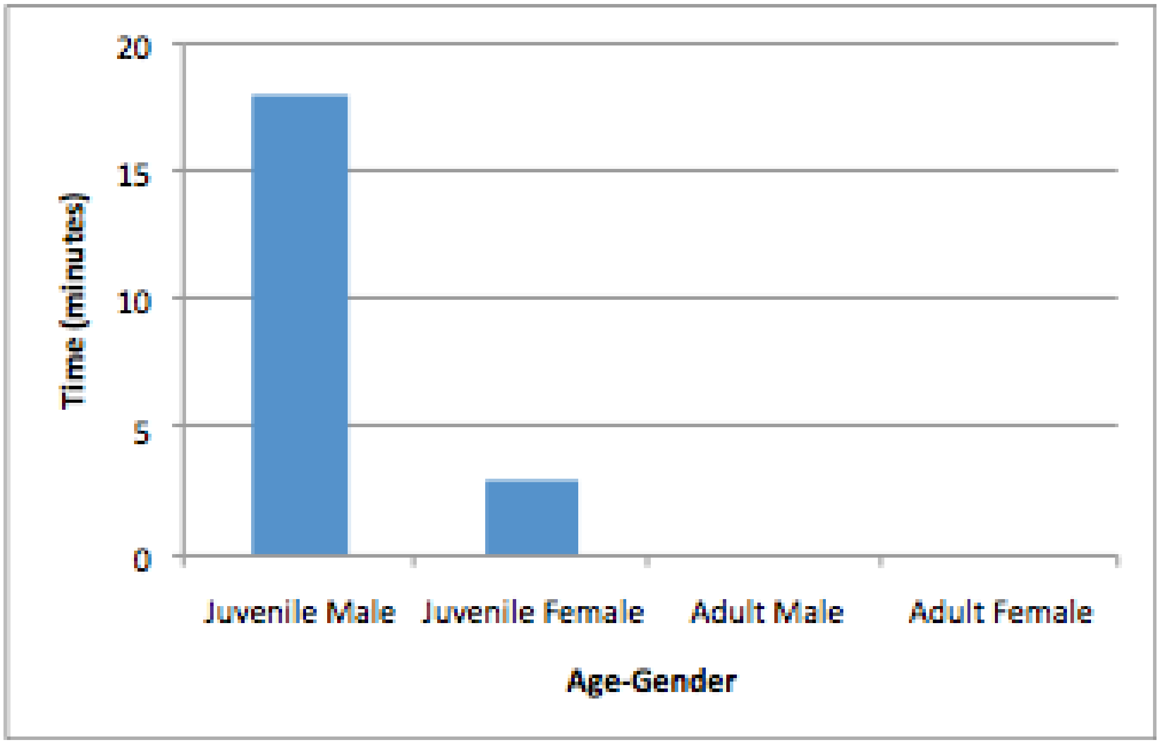

Figure 7.6: Approximate median amount of time spent caudal luring by each age-gender group of pygmy rattlesnakes to lure prey into striking range. No caudal luring behavior was displayed by any adult snakes, male or female (Recreated from Rabatsky & Waterman 2005).

Box 7.4: Competitive Mimicry

In a 2007 paper, Meredith Rainey and Gregory Grether explained another possible classification of mimicry that is often left out of other mimicry classifications and research. They argued that competitive mimicry, or mimicking another species to gain access to resources over a competitor, should be included in these lists. According to the paper, there are three types of **competitive mimicry**: mimicking a non-competitor, mimicking the competitor itself, and mimicking a competitor's predator (Rainey & Grether 2007b). Mimicking a non-competitor is said to be beneficial because a competitor will not see you as a threat and will either share the resource or can be surprise attacked for it. An example given is some surgeonfish mimic angelfish in order to not be attacked by damselfish when invading the damselfish's territory. A possible reason to mimic a competitor is if the competitor uses display against its own species during disputes, but fights against other species. This would allow the mimic, win or lose, to avoid costly battles with the mimicked species. Due to the complex nature of this form of mimicry, natural examples are not perfectly clear. The reasons for mimicking a competitor's predator are obvious in that the mimic can scare

> off the competitor without costly displays or battles. Burrowing owls can make a hissing sound that sounds very similar to rattlesnakes and has been shown to scare away rodents from burrows that were too large for the owls to easily kill themselves.

Most of the species that have been found to use caudal luring are terrestrial species, but some arboreal species have been shown to use this as well (Murphy, Carpenter, & Gillingham 1978). It has also been shown that many of the species that use caudal luring have tails that are a slightly different color or are brighter than the rest of their bodies, especially as juveniles. Caudal luring does come with a cost, though. Puerto Rican racers, *Alsophis portoricensis*, were found to have much more tail damage than is normally found in non-caudal luring species (Barun, Perry, Henderson, & Powell2007). This means that it is highly likely that many snakes are attacked by lured prey before successfully killing them. Also, it is highly possible that predation is higher in species with brightly colored tails used for caudal luring than it otherwise would be because the combination of bright color and conspicuous tail movement will make them easier to spot than similar species that don't perform caudal luring. Another possible form of aggressive mimicry in snakes is known as "lingual luring" (see Box 7.3 (Lingual Luring)).

7.1.5 Sexual Mimicry

Sexual mimicry, or mimicking an individual of the opposite sex, is different from most other forms of mimicry because the individual is mimicking another individual of its own species as opposed to one of a different species. Sexual mimicry is also one of the hardest forms of mimicry to understand because it seems to have very small benefits compared to the costs of posing as a member of the opposite sex. In snakes, the most well studied system of sexual mimicry is female mimicry among male garter snakes, *Thamnophis spp*. Certain males will give off pheromones that are very similar to the ones produced by females (Shine, O'Connor, & Mason 2000a).

The costs to this form of mimicry are relatively high, however, because the female mimics will often be courted by other males. This would not seem to be such a big cost in most mammal or bird courtship systems, but in garter snakes, the males form a large, writhing mass around the female, where the stronger ones can get closest to the female and therefore have the best chance of mating with it. While serious injury is rare for the female (or female mimic) being courted, it is still somewhat physically hard on the individual. So what could the benefits of female mimicry in garter snakes be that can outweigh these costs? Shine and his colleagues found several things that seem to help explain this phenomenon. One is that female mimics tend to be smaller than many other males. Another is that a large number of female mimics were found covered with soil compared to non-mimics. Being covered in soil at time of observation means the individual more likely emerged from hibernation closer to that time than a clean male.

Figure 7.7: Two-striped Garter snake, *Thamnophis hammondii*. Photo by rmceoin on Flickr.

These two general characteristics of female mimics show a likely reason for its benefit to the mimic. A small male is not very likely to reach the female in a mating ball. Also, males that emerge from hibernation late are also less likely to reach a female during courtship because so many other males will already be present in the courtship site. However, when a small, late emerging male mimics a female, it can move through the mating ball with relative ease, only having to fend off courting males who are much less likely to hurt a female they are courting than a competing male. By being able to reach the female, the female mimic greatly increases its chances to mate.

But reaching the female isn't the only obstacle to overcome in a garter snake mating-ball. The male must also be able to get the female receptive enough to mate. However, it was recently shown that the female may have less choice than previously thought. Although female garter snakes tend to be larger than males, especially female mimicking ones, and female mimics are more likely to court a large female than a small one (Shine, O'Connor, & Mason 2000a), males do have a distinct way to forcibly copulate with females (Shine, Langkilde, & Mason 2003). By pressing against the side of a female during courtship, the male can contract its muscles in certain ways that presses against the female's lungs and invokes a defensive response from the female due to a lack of oxygen (see Figure 7.8). During this response, the female's **cloaca** opens and excretes musk and excrement. This would very often get rid of a predator trying to attack the female, but the male uses the opportunity to forcibly inseminate the female with his sperm. Thus by mimicking a female and exploiting the anatomy of the species, a small male that emerges from hibernation relatively late can inseminate a female and pass on his genes to the next generation.

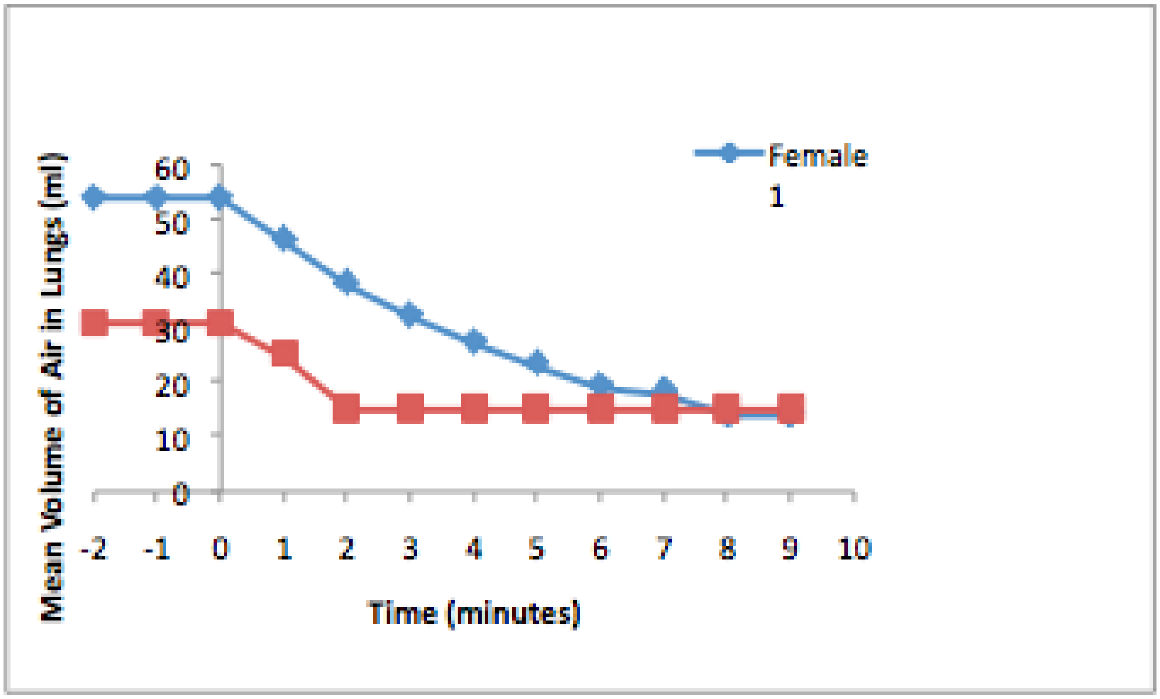

Figure 7.8: Mean volume fo air in lungs of two female garter snakes, Thamnophis sirtalis parietali, before and during courtship by several males (Recreated from Shine, Langkilde, & Mason 2003). The graph shows that females being courted by males lose a significant amount of air in their lungs during courtship. This loss of air is thought to be caused by the males in order to forcibly inseminate the female.

7.1.6 Discussion Questions

1. Why would mimicking a brightly colored venomous species not be entirely beneficial?
2. Why would a venomous species mimic another species that is less venomous?
3. How would wriggling one's tail help attract prey to eat?
4. What costs and benefits are likely to exist for having a tail that is more conspicuous than the rest of a snake's body?

Figure 7.9

7.1.7 Glossary

- **Aggressive Mimicry**- Having a similar appearance or behavior to another species which increases the ability of the individual to acquire food or other resources.
- **Batesian Mimicry**- Having a similar appearance or behavior to another species that is dangerous or unpalatable which decreases the individual's likelihood of being preyed upon, even if it doesn't have the trait that coincides with the mimicked trait.
- **Caudal Luring**- A form of aggressive mimicry in which a snake or lizard wiggles its tail to look like an insect larvae or worm in order to attract prey.
- **Cloaca**- The orifice near a snake's tail used for excretion of feces and urine as well as for mating.
- **Competitive Mimicry**- Having a similar appearance or behavior to another species in order to better access or defend resources.
- **Defensive Mimicry**- Having a similar appearance or behavior to another species which decreases the chance of an individual being attacked by a predator.
- **Sexual Mimicry**- Having a similar appearance or behavior to the opposite sex or another species in order to increase the individual's likelihood of mating.
- **Fitness**: An individual's ability to pass their genes on to the next generation.
- **Gene**- An amount of DNA such that it is likely to be inherited intact by the next generation during

reproduction.

- **Lingual Luring**- A form of aggressive mimicry in which an individual flicks its tongue against the surface of a body of water to simulate a small insect in order to attract prey.
- **Mertensian Mimicry**- Having a similar appearance or behavior to another species that is less dangerous than the individual because the predators learn not to attack organisms with that trait from the non-lethal species.
- **Mimicry**- Having a similar appearance or behavior to another individual which increases an organism's fitness in some way because it is mistaken for the individual being mimicked.
- **Mullerian Mimicry**- Mutual mimicry between two or more unpalatable species which decreases any given individual's likelihood of being the 'mistake' a predator learns to avoid the shared trait from.
- **Native Range**- The area in which a given species is known to naturally occur.
- **Olfactory Mimicry**- Having a similar smell to an individual of another species or another object in order to attract pollinators or possibly to repel predators
- **Reproductive Success**- The number of an individual's genes passed on during reproduction to offspring that have the ability to reproduce.

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Gives evidence that while Batesian mimicry is generally associated with bright warning colors, there is a decrease in predator attacks on non-venomous species that mimic venomous snakes lacking bright warning colors.

7.1.9 Images

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- Hognose Snake, Heterodon sp, By Benimoto: http://www.flickr.com/photos/benimoto/2788651836/
- Two-striped Garter snake, Thamnophis hammondii, By rmceoin: http://www.flickr.com/photos/rmceoin/3207412781/

7.1.10 Biography

Figure 7.10

Michael Schiff is currently a junior working towards a Bachelor of Science degree in Ecology and Evolutionary Biology at Rice University. He was born in Los Angeles, CA but raised in Las Vegas, NV. Michael spent the first two years of college at the University of Arizona, where as a freshman he studied for a B.S. in Aerospace Engineering, but quickly switched to Environmental Biology because engineering was too focused on the business side of science and bored him compared to his lifelong fondness for the natural and life sciences. He also found a severe dislike for calculus and physics, which would be essential to an engineering career. After receiving his degree, Michael hopes to move on to a career in either animal keeping and enrichment or environmental consulting for at least a few years before possibly attending graduate school. His hobbies include visiting zoos, computer games, and archery.

7.2 Prey Deception in Australian Crab Spiders[2]

Author: Claire Shorall

7.2.1 Introduction

Have you ever seen an advertisement for a food item that looked so scrumptious you had to have it? A flame-broiled burger, perhaps, with a juicy patty piled with fresh vegetables sandwiched between an artisan-bread bun. And then, once you had raced out of your house to the nearest drive-thru, you find the burger to be dismal – grayish meat, wilted veggies and tasteless bread; the lure of the image on television instantly unraveled after the first bite. Welcome to the world of false advertisement. Retailers who use this method use exaggerated and calculated imagery to convince consumers to buy their product, ever-so-sure of the negative benefits to their customers. Deceitful advertising is not a human invention, however. Species of **ultraviolet** (UV)-positive Australian crab spiders *Thomisus spectabilis* tactfully position themselves on floral surfaces with no or low UV-reflection in order to create the greatest amount of contrast between their body and the flower, a trick that makes the flower more attractive to pollinators such as honeybees (Bhaskara et al. 2009). Once lured to a plant, a crab spider will ambush the honeybee, trapping their prey with their powerful front legs and then paralyzing the unsuspecting pollinator with a venomous bite. But UV-contrast is not the only weapon in their arsenal of deceit. Australian crab spiders can also change their body color from yellow to white in order to attract honeybees to the white or yellow daisy they occupy, however this color change does not follow the logic of normal **crypsis** (Heiling et al. 2005). Spiders will both attempt to blend into the background, using color as a mechanism of **camouflage**, and also in some cases create high contrast with their background, a visual marker which proves intriguing to their **hymenopteran** prey.

All is fair in this game of love and war. Australian crab spiders thrive at prey deception, manipulating elements such as choice of floral species, floral color, position on the flower, and geographic location, all playing critical roles in their hunting success (Heiling et al. 2004, Heiling et al. 2005, Heiling et al. 2006). Winning crab spiders are essentially masterful marketers.

7.2.2 Who are these creatures?

Crab spiders (family: Thomisidae) are a fascinating subset of the **Araneae** order. They derive their name from their crab-like appearance and movements; their shape is flattened and angular, and they can even move sideways and backwards! Unlike many spiders, they forgo weaving webs to trap their prey in favor of an attack and ambush method. Accordingly, the front legs of crab spiders are powerful enough to trap their unsuspecting victims while they deliver a venomous bite.

Crab spiders are found all over the world. They come in abundant varieties; in fact, there are 170 genera in the family and over 2,000 known species! Differing species of crab spiders utilize flowers, plants and trees to hunt. While some spiders hide in deep crevices on tree bark and lurk until prey comes their way, others actively attract their victims using deception techniques. Their hunting technique and their physical qualities are strongly related.

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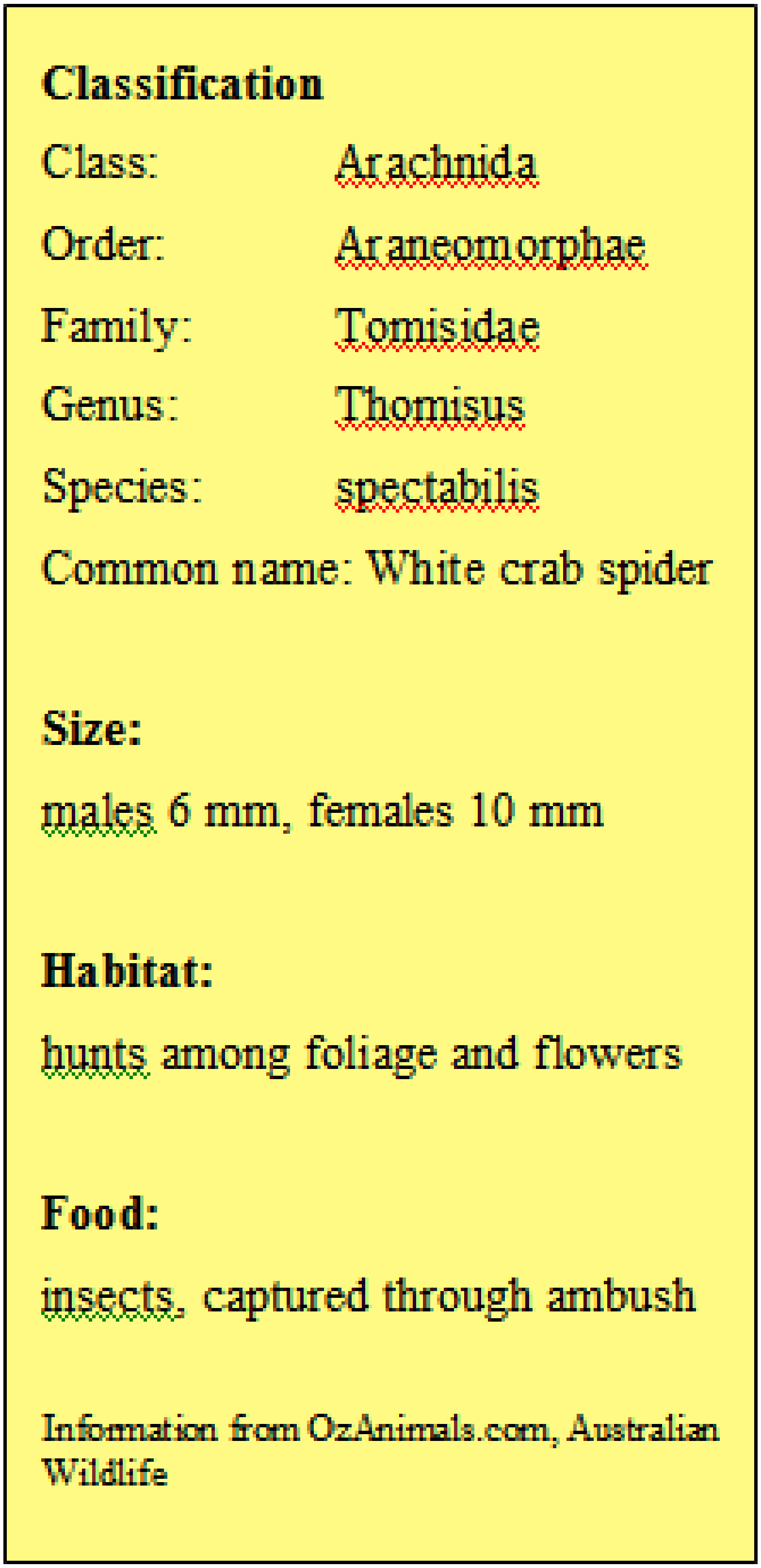
[2] This content is available online at <http://cnx.org/content/m34743/1.3/>.



Classification

Class: Arachnida

Order: Araneomorphae

Family: Tomisidae

Genus: Thomisus

Species: spectabilis

Common name: White crab spider

Size:

males 6 mm, females 10 mm

Habitat:

hunts among foliage and flowers

Food:

insects, captured through ambush

Information from OzAnimals.com, Australian Wildlife

Figure 7.11

Crab spiders (family: Thomisidae) are a fascinating subset of the **Araneae** order. They derive their name from their crab-like appearance and movements; their shape is flattened and angular, and they can even move sideways and backwards! Unlike many spiders, they forgo weaving webs to trap their prey in favor of an attack and ambush method. Accordingly, the front legs of crab spiders are powerful enough to trap their unsuspecting victims while they deliver a venomous bite.

Crab spiders are found all over the world. They come in abundant varieties; in fact, there are 170 genera in the family and over 2,000 known species! Differing species of crab spiders utilize flowers, plants and trees to hunt. While some spiders hide in deep crevices on tree bark and lurk until prey comes their way, others actively attract their victims using deception techniques. Their hunting technique and their physical qualities are strongly related.

The crab spiders from Australia, Thomisus spectabilis, and their hunting game

A variety of signals are transferred from plants to their pollinators. Many plants rely on other species to propagate their own. But what if you preyed on those pollinators? Would it not be advantageous to know exactly what looks most attractive to them? And could you be a more effective hunter if your presence added extra incentive? Combining these two concepts in hunting behavior is effective for the Australian crab spider, *Thomisus spectabilis.*

The Australian crab spider uses UV-contrast to attract their prey, the honeybee *Apis mellifera*, to the flowers they are occupying. The crab spiders must select the most likely flower a honeybee will possibly visit, however, to ensure the greatest levels of hunting success. The spiders use floral odor along with visual and **tactile** clues to pick the most enticing flower on which to sit. But what makes a flower particularly delectable to a honeybee?

As expected, honeybees use **olfactory** signals in selecting which flowers they wish to pollinate (Heiling et al. 2004). Crab spiders can also use scent in their hunting site decision. This was found in a study performed by Astrid M. Heiling et al. in 2004, where honeybees and crab spiders were presented the choice between two flowers in the presence and absence of olfactory cues. In their presence, crab spiders and honeybees selected the same flower for hunting and foraging, respectively, 75% of the time (n=60), however in the absence of the cues, the selection of the same flower boiled down to little more than chance.

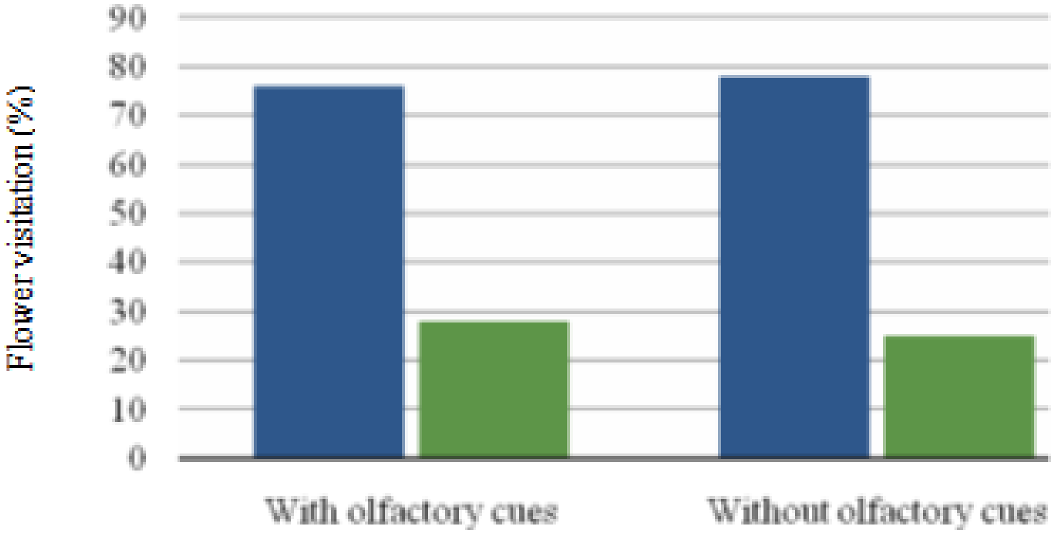


Figure 7.12

Of course, flower selection for both species is not as easy as a quick sniff. Both also use visual cues. For example, foraging honeybees have been found to prefer flowers with **radial symmetry** over **bilateral symmetry**, examples of both seen in the insert to the left, in tests where olfactory signals were removed (Wignall et al. 2005). Some visual signals are harder to detect. In particular, visual signals communicated at ultraviolet wavelengths are difficult to study as they are invisible to the human eye, but are the likely culprit for much of the manipulation of floral signals used by crab spiders to attract honeybees. It has been shown that honeybees are more likely to approach flowers occupied by crab spiders than those without (Heiling et al. 2003), although native Australian bees are less likely than introduced European bees to actually land on occupied flowers (Heiling and Herberstein, 2004).

In a spectral study conducted by Heiling et al. in 2003, it was shown that crab spiders sitting on white daisies have high UV contrast, thus making the signaling strategy of the Australian crab spider quite different than those who lurk in tree bark or blend into the background. In fact, this makes them particularly **conspicuous** in the insect visual spectrum when seen at close quarters. So why are honeybees attracted to these risky flowers? The findings of the study are consistent with empirical data that show that bees innately prefer flowers with strongly contrasting markings. Thus a contrasted spider, even with the known danger, makes a flower incredibly enticing.

Figure 7.13: Bilateral Symmetry Photo Credits: Denis Barthel and SiGarb

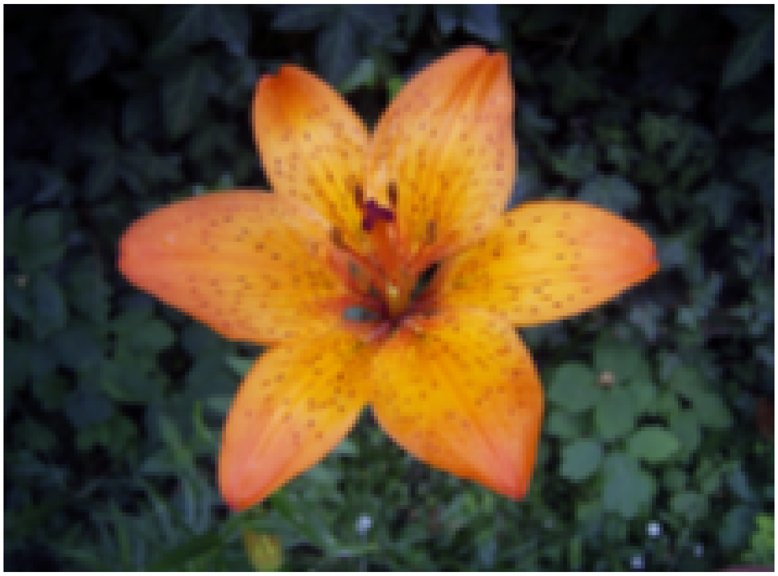


Figure 7.14: Bilateral Symmetry Photo Credits: Denis Barthel and SiGarb

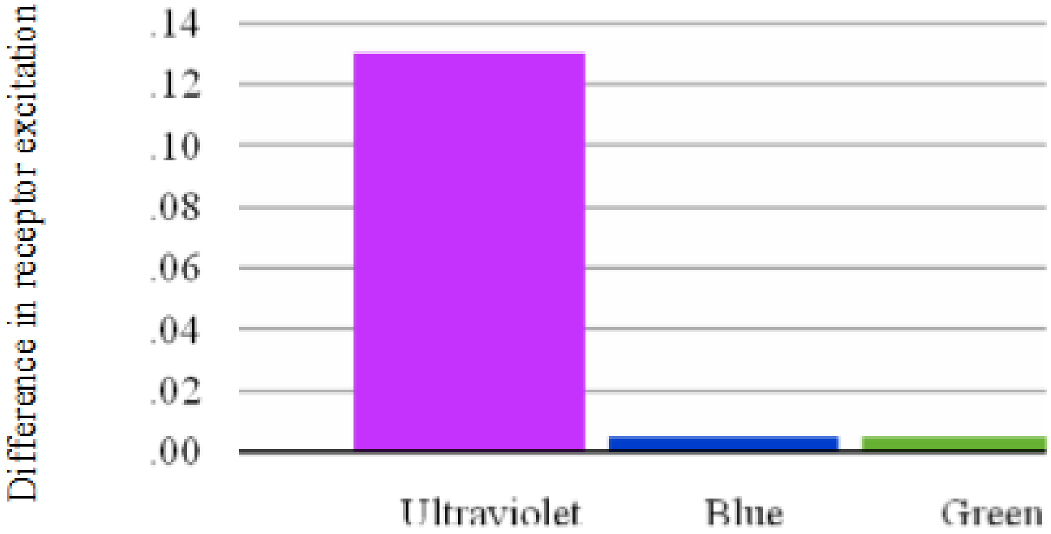


Figure 7.15

7.2.3 Playing the game: Australian crab spiders alter their behavior to attract prey

What do honeybees see?

Imagine you're a honeybee, flying around, looking for a delicious flower to pollinate. What would you see? This intriguing question is in the process of being answered by some of the world's top ecologists, physiologists, and evolutionary biologists.

Honeybees are UV-blue-green trichromats, a combination so popular that it must have appeared early in the evolution of insects. UV vision is the most common wavelengths detected by insects; in fact, not a single species of insects has a confirmed absence of UV vision.

Honeybees are capable of viewing their world at high sensitivity and enhance contrast, a capability that comes in handy in UV-rich environments where they often live such as meadows.

Honeybees prefer UV-blue and blue light, which they associate with high nectar. Green receptors are primarily used for the detection of motion, which is particularly helpful when bees are around or upon leaves. Briscoe and Chittka, 2001.

Figure 7.16

Figure 7.17

So it has been established that flowers look even more delectable to honeybees with an Australian crab spider sitting on top. But as aforementioned, Australian crab spiders cannot simply guess which flower is most attractive to a bee if they wish to have the most hunting success. They need to anticipate honeybee desires. This adds a twist to this predator/prey dynamic. Non-random selection of flowers is an evolved trait; however, just as Australian crab spiders are evolving to become better predators by anticipating honeybee preferences, honeybees are becoming smarter prey, learning to avoid crab spiders (Heiling and Herberstein, 2004) as described in the "Predator and Prey Coevolution" insert on the next page.

Example 7.5

Predator and Prey Coevolution

Australian crab spiders ambush the hymenopteran prey available to them on their continent, including native honeybees to Australia and an introduced "naive" European honeybee species. In a study performed by A. M. Heiling and M. E. Herberstein, native and naive honeybees were watched as they approached flowers with or without spiders. While both species were attracted to the flower with spiders occupying a petal, only the naive bees frequently landed on these flowers. The native species has coevolved with the Australian crab spiders and therefore has learned to avoid landing on spider-occupied plants.

The results of this study indicate that native pollinators, the Australian bees, currently have the upper hand in the coevolutionary arms race. The authors of the paper expect that the crab spiders will counter this advantage by either reducing conspicuousness or exploiting a different sensory modality to attract native prey. (Heiling and Herberstein, 2004)

Figure 7.18

Australian native bee.
Photo credit: Louise Docker

Figure 7.19

Apis mellifera. Photo credit: Scott Bauer, USDA/ARS

The aforementioned studies that confirmed that Australian crab spiders use olfactory signals, visual cues, and UV-contrast imply that spiders make a choice about where they want to sit. The ability to process these signals, especially those being sent by floral species to their pollinators, is an evolved exploitation. But beyond intercepting signals meant for their prey, Australian crab spiders can manipulate themselves in a way that makes them even more adept at trapping their meals.

Thomisus spectabilis have the ability to change their body color from white to yellow over the course of several days. Incredibly, these spiders choose what color they want their bodies to be depending on the color of the flower on which they are sitting! This implies that they have knowledge of their own body color and are able to discern the colors of their surroundings. Australian crab spiders use their body and the UV-contrast it provides in comparison to the petal on which it is sitting to send a signal to a receiver, the honeybee. Therefore, in changing their body color in relation to the flower, they are using a behavioral means to exploit the signal for their greatest hunting success.

In a study performed by Astrid Heiling et. al in 2005, yellow spiders were overwhelmingly found on yellow plants (93.7%, N=16), while white spiders were found on primarily white plants (69%), but also on yellow plants of the same species (31%, N=71). In order to test this pattern of distribution, the researchers conducted a choice experiment where it was found that spiders actively choose flowers, as opposed to just settling on what is available. They found that spider preference was due to reflectance properties of flowers. So why do yellow spiders overwhelming prefer yellow flowers, and white spiders have less of a preference? The researchers did further analysis of spider and flower coloration and by looking at reflectance and contrast found that while the white spider on white plant combination was visible by bees, the yellow on yellow pairing of the two species yielded a higher contrast. In fact, the yellow spider on a yellow plant combination yielded higher UV contrast than a yellow spider on a white flower! The combination of yellow spiders on yellow flowers and white spiders on either color of flowers are attractive to honeybees and correspond to the combinations that spiders choose most frequently. This shows that spiders are actively seeking to contrast highly with their background on the basis of perceived honeybee attraction (Heiling et. al, 2005).

Table 1. *Overview of the color contrasts between white and yellow* T. spectabilis *and white and yellow* C. frutescens, *and the visibility of this contrast by honeybees.* Modified from Heiling et. al, 2005.

Spider/flower combinations	Color contrast
Yellow/yellow	Detectable (very high)
Yellow/white	Detectable (high)
White/yellow	Detectable (very high)
White/white	Detectable (high)

Table 7.2

Beyond picking the right flower in comparison to their body to create a desired level of contrast, spiders can manipulate other variables, such as their position on a given flower, to attract their hymenopteran prey. In another experiment performed by Heiling et. al, researchers placed spiders on both the **ligulate florets** and the center of daisies to see how honeybees would respond. Expecting that spiders positioned naturally on the petals would deceive honeybees while those placed atypically in the center of the flowers would repel the prey, researchers found their predictions to be supported. Researchers hypothesized that the honeybees may have been less attractive to daisies with spiders over the center because it would make it more difficult for spiders to access their reward (i.e. nectar). Another hypothesis was that the spider-covered centers had inflorescences that did not visually resemble natural daisies, hence the rejection by honeybees. What was evident, however, is that deception by spiders and attractiveness to honeybees was greatest when spiders were placed on the petals, a behavior that spiders exhibit in nature. In this careful choice, spiders are able to position themselves to influence the behavior of their hymenopteran prey (Heiling et. al, 2006). This adds to a bevy of evidence that confirms that spiders act in a way that maximize their attractiveness to prey.

A selection of recent scholarship on coevolutionary arms races:

Natural selection drives the fine-scale divergence of a coevolutionary arms race involving a long-mouthed weevil and its obligate host plant.

Hirokazu Toju, BMC Evolutionary Biology 9:273. 2009.

Co-evolutionary arms race between brood parasites and their hosts at the nestling stage.

Manuel Soler, Journal of Avian Biology,3:237-240. 2009.

Intersexual Arms Race? Genital Coevolution in Nephilid Spiders (Araneae, Nephilidae).

7.2.4 Who will win the game?

Australian crab spiders and honeybees are in a **coevolutionary arms race**. But which is ahead? And how will this dynamic be shifted in the future?

To understand what's coming next, it is helpful to understand the underlying principals of this "arms race." This term is used in describing genes that are co-evolving, such as an Australian crab spiders ability to anticipate a honeybee's preference in flowers and a honeybees ability to identify crab spiders and avoid landing on the flowers they occupy. As these two species develop adaptations, they must then develop counter-adaptations as a result of the other species' advances. This **positive feedback** resembles a military arms race. There are numerous examples of these arms races in evolution, and while many have asymmetrical selective pressures, like those acting on the Australian crab spiders and the honeybees, there are symmetrical selection processes as well.

Even though Australian crab spiders are masters of prey deception, making the flowers they sit upon look even more enticing to a bee than less dangerous pollinating sites, scientists hypothesize that they have relinquished the upper hand in the arms race (Heiling and Herberstein, 2004). As more honeybees are able to recognize and combat the Australian crab spiders' trickery, they will be forced to try new tactics. One anticipated evolutionary response is that the Australian crab spiders will become increasingly less conspicuous to honeybees, which may occur even without becoming less conspicuous to the human eye. There is an increasing body of literature that explain how animals reinvent the common notion of camouflage, that is the their bodies match the colors or patterns of their backgrounds, to a newer definition that includes non-pattern matching body designs that creative disruptive coloration patterns that trick their prey in the same way. Therefore, concealment can occur even if the background is not matched (Stevens et. al, 2006). Or conversely, perhaps the Australian crab spiders might change the way they are ambushing their hymenopteran prey. Instead of pouncing from the petals of a flower, they could hide below the surface, waiting to ambush from their sheltered location. The Australian crab spiders have countless evolutionary paths that they could take, although they must expect the honeybees to be simultaneously fighting back, looking to preserve and advance themselves at the same time and only time will tell how the Australian crab spider responds to these evolutionary pressures.

7.2.5 Discussion Questions:

1. What are some other examples of effective prey deception in animals? How are these examples similar and different to the that of the Australian crab spiders?
2. What would you expect to be evolutionary more advantageous for the Australian crab spider: to become better at signal interception or to change their prey capturing method?
3. The flowers discussed in this chapter rely on honeybees to pollinate them in order to propagate the species. As honeybees become increasingly aware of a spider's presence on a flower and therefore choose not to visit it, a flower is less likely to pass its genes on to the next generation (Brechb*ü*hl, Rolf et al, 2010). What are the evolutionary implications for the flowers? What adaptions could the flower make to increase its likelihood of being pollinated?

7.2.6 Glossary:

- **Araneae** - spiders; air-breathing chelicerate arthropods with eight legs and venom-injecting fang
- **bilateral symmetry** - symmetry about one, and only one, plane (called the sagittal plane); bilateral flowers are known as zygomorphic
- **coevolutionary arms race** - competition between two co-evolving genes that develop adaptations in reaction to adaptations of the other based on a positive feedback model
- **crypsis** - the ability of an organism to avoid observation
- **hymenoptera** - one of the largest orders of insects, comprising of wasps, bees, sawflies, termites and ants
- **ligulate florets** - tongue-shaped petals
- **actory** - of or relating to the sense of smell
- **positive feedback** - an effect causes more of itself, an augmentation
- **radial symmetry** - symmetry about an axis; radial flowers are known as actinomorphic
- **tactile** - of or relating to the sense of touch
- **ultraviolet** - electromagnetic radiation with a wavelength shorter than that of visible light, but longer than x-rays (10 nm to 400 nm)

7.2.7 References:

Aronsson, Marianne and Gabriella Gamberale-Stille. 2009a. Importance of internal pattern contrast and contrast against the background in aposematic signals. Behavioral Ecology. 1-7. This study looks at the relation between internal pattern contrast versus contrast of prey against a background using domesticated chicks. The chicks were shown prey that was plain or striped, but neither yielded the significant avoidance results in comparison to contrast against the background.

Bhaskara, Ramachandra M., C. M. Brijesh, Saveer Ahmed, and Renee M. Borges. 2009a. Perception of ultraviolet light by crab spiders and its role in selection of hunting sites. Journal of Computational Physiology. 195:409-417. This article demonstrates that crab spiders (Thomisidae) are able to perceive UV light and use it to become more attractive to prey, thus enhancing their ability to capture honeybees. The crab spiders use *Spathiphyllum* plants.

Brechbühl, Rolf, Christian Kropf and Sven Bacher. 2009a. Impact of flower-dwelling crab spiders on plant-pollinator mutualisms. Basic and Applied Ecology. 1-7. This article explores the indirect effects of the spider crab preying behavior on the plants where they act. This study demonstrates that the crab spider praying behavior can negatively effect the fitness of the plant species, but primarily when the pollinators of the plants (ie honeybees) are specialized to avoid crab spider occupied plants.

Brechbühl, Rolf, Jéröme Casas and Sven Bacher. 2010a. Ineffective crypsis in a crab spider: a prey community perspective. Proceedings of the Royal Society of Biological Sciences. 277:739-746. Crypsis is the ability to avoid observation. It is a reasonable assumption to presume that predators that can avoid being recognized by their prey would have an advantage. In this study, however, it is shown that flowers with spiders on them are not visited more frequently than others. This demonstrates an indifference to predators, and in order to make sense of these findings, the authors of the paper suggest a community understanding approach.

Briscoe, AD and Lars Chittka. 2001. The evolution of colour vision in insects. Annual Review of Entomology. 46:471-510. A review of the physiological, molecular, and neural mechanisms of insect color vision.

Chittka, L. 1996. Optimal sets of colour receptors and opponent processes for coding of natural objects in insect vision. J Theoretical Biology. 181:179-196.

Chittka, L. 2001. Camouflage of predatory crab spiders on flowers and the colour perception of bees. Entomol Gen. 25:181-187.

Chittka, L and R Menzel. 1992. The evolutionary adaption of flower colours and the insect pollinators' colour vision. J Comp Physiol A. 171:171-181.

Chittka, L, A Shmida, N Troje, and R Menzel. 1994. Ultraviolet as a component of flower reflections, and the colour perception of hymenoptera. Vision Res. 34:1489-1508. Study shows that flowers colours fall into distinct clusters as viewed by bees. The article purposes a system of colours and naming.

Chittka, Lars and Nigel E Raine. 2006a. Recognition of flowers by pollinators. Current Opinion in Plant Biology. 9:428-435. This article explains the evolution of signal designs by plants to pollinators. It focuses on both visual and olfactory information processing.

"Crab-spiders manipulate flower signals." Nature 421 (2003): 334. Nature Publishing Group. Web. www.nature.com/nature[3] . This is a brief communication summary of a Heiling et. al study about pollinator attraction in Nature.

Dimitrova, Marina and Sami Merilaita. 2009a. Prey concealment: visual background complexity and prey contrast distribution. Behavioral Ecology. 176-181. This study is concerned with the use of camouflage and disruptive coloration by species to avoid predation. In the study, the background of the prey was manipulated and was found to aide in the concealment of prey. Visually complex backgrounds may provide prey with decreased predation risks.

Giurfa, M, J Núñez, L Chittka, and R Menzel. 1995. Colour preference of flower-naive honeybees. J Comp Physiol A. 177:247-259.

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[3] http://www.nature.com/nature

Guo, Wei and Yildirim Aktas. 2009a. Backaction of a detector on the field it measures. Optics Communications. 282:14-17. This article provides insight into the mechanisms of light scattering between a detector and a medium. It can be used in the understanding of how a crab spiders UV contrast mechanism works.

Heiling, A. M. and M. E. Herberstein. 2004a. Predator-Prey Coevolution: Australian Native Bees Avoid Their Spider Predators. Proceedings of the Royal Society of Biological Sciences. 271:S196-S198. This study compares the pollinating behavior of Australian honeybees and non-native honeybees on plants that are occupied by Australian crab spiders *Thomisus spectabilis*. Native bees approached spider occupied flowers more frequently, however landed on vacant flowers more frequently. The non-native bees did not show this anti-predatory response.

Heiling, Astrid M., Ken Cheng, and Marie E. Herberstein. 2004a. Exploitation of floral signals by crab spiders (*Thomisus spectabilis*, Thomisidae). Behavioral Ecology. 15:321-326. This study looked at potential signals to both crab spiders and honeybees to be attracted to a certain flower. The study found that honeybees use olfactory signals, which the spiders exploit to encounter prey.

Heiling, Astrid M., Ken Cheng, and Marie E. Herberstein. 2006. Picking the right spot: crab spiders position themselves on flowers to maximize prey attraction. Behavioral Ecology. 143:957-968. Position of the spider on a plant is important in prey attraction, such that spiders must sit on the petals and not a daisy's center.

Heiling, Astrid M., Ken Cheng, Lars Chittka, Ann Goeth and Marie E. Herberstein. 2005a. The role of UV in crab spider signals: effects on perception by prey and predators. The Journal of Experimental Biology. 208:3925-3931. In this study, the researchers took crab spiders, typically a UV+ species, and applied an UV-absorbing surface to the insects, creating a UV- spider. This is turn translated into less attraction by honeybees, thus changing the behavior of the prey.

Heiling, Astrid M., Lars Chittka, Ken Cheng and Marie E. Herberstein. 2005a. Colouration in crab spiders: substrate choice and prey attraction. The Journal of Experimental Biology. 208:1785-1792. This study combine observance of honeybee behavior and state-of-the-art knowledge about bee color vision to evaluate honeybee preferences for both white and yellow spiders on both white and yellow plants. The results showed that crab spiders select flowers adaptively in a way that attracts them to their flower, or minimally does not deter them from pollinating it.

Herberstein, M. E., A. M. Heiling and K. Cheng. 2009a. Evidence for UV-based sensory exploitation in Australian but not European crab spiders. Evolutionary Ecology. 23:621-634. This study looks at UV-reflection in crab spiders, which is common in Australian species, but absent in their European counterparts. It is unknown as to whether or not UV-reflection evolved in Australia or whether UV-reflective spiders are more recent arrivals to the continent.

Hoese, F.J., E.A.J. Law, D. Rao and M.E. Herberstein. 2006a. Distinctive yellow bands on a sit-and-wait predator: prey attractant or camouflage? Behavior. 143:763-781. Another example of crypsis in spiders. Spiders with yellow bands on their backs attracted more insects to their web than those with their yellow bands covered by black marker. This indicates that the yellow serves some purpose, whether it be camouflage through disruptive coloration or attractiveness to insects, and thus they are able to attract more prey.

Pasteur, Georges. 1982a. A Classificatory Review of Mimicry Systems. Ann. Rev. Ecol. Syst. 13:169-99. The purpose of this article is to give a definitive and comprehensive review of the types of mimicry systems known to biologists at the time. Special attention is given to semantics.

Reader, Tom, Andrew D. Higginson, Christopher J. Barnard, Francis S. Gilbert, and The Behavioral Ecology Field Course. 2006a. The effects of predation risk from crab spiders on bee foraging behavior. Behavioral Ecology. 933-939. This study evaluated bee reactions to crab spider presence on plants. The study found that plant-pollinator systems were not immune to the effects of predation.

Schaefer, H. Martin and Graeme D. Ruxton. 2009a. Deception in plants: mimicry or perceptual exploitation? Trends in Ecology and Evolution. 24:676-685. This article looks at mimicry and perceptual exploitation done by plants to animals. The suggestion is that perceptual exploitation is a potential lead in to the evolution of mimicry. Plants would want to manipulate animals in certain ways in order to be pollinated.

Stevens, Martin and Isabel S. Winney, Abi Cantor and Julia Graham. 2009a. Outline and surface disruption in animal camouflage. Proceedings of the Royal Society of Biological Sciences. 276:781-786. This study looks at disruptive coloration of prey as viewed by avian predators. The findings show that disruptive coloration is a helpful prey concealment tactic, provided that the disruption is not along the outline of the body, thus creating a surface disruption. Object detection is more difficult if the true-body outline is hard to distinguish.

Stevens, Martin, Innes C Cuthill, Amy M.M Windsor and Hannah J Walker. 2006a. Disruptive contrast in animal camouflage. Proceedings of the Royal Society of Biological Sciences. 273:2433-2438. This study looked at various types of disruptive coloration, including the counter-intuitive idea that conspicuous patterns might aid concealment. The findings showed that any disruptive contrast, including incomplete patterns, were of help to animals to avoid predation.

Théry, Marc. 2007a. Colours of background reflected light and of the prey's eye affect adaptive coloration in female crab spiders. Animal Behavior. 73:797-804. This article looks at how crab spiders are able to change colors, including through the ingestion of certain prey. The suggestion that pigment ingestion is not just used to change color, but to signal to females the hunting abilities of potential mates, was also made.

Théry, Marc and Jérõme Casas. 2009a. The multiple disguises of spiders: web colour and decorations, body colour and movement. Philosophical Transactions of the Royal Society of Biological Sciences. 364:471-480. This article discusses the potential camouflage and mimicry done by spiders for prey attraction and predator deterrence.

Théry, Marc, Martine Debut, Doris Gomez and Jérõme Casas. 2004a. Specific color sensitivities of prey and predator explain camouflage in different visual systems. Behavioral Ecology. 25-29. This study looked at the chromatic contrast (viewing from close range) and achromatic contrast (viewing from long-range) of female crab spiders on daisies. From this study, more questions about bird predators' ability to constrain spider crypsis arise.

Wignall, Anne E., Astrid M. Heiling, Ken Cheng and Marie E. Herberstein. 2005a. Symmetry Preferences in Honeybees and their Crab Spider Predators. Ethology. 112:510-518. This article looks at honeybee and spider symmetry preferences when choosing where to pollinate. The study removed olfactory clues, which is likely to be used in foraging decisions.

"White Crab Spider (Thomisus Spectabilis)." *OzAnimals - Australian Wildlife*. Web. 20 Apr. 2010. http://www.ozanimals.com/Spider/White-Crab-Spider/Thomisus/spectabilis.html[4] .

7.3 The Real Deal?: Behavioral Mimicry in Hymenoptera[5]

Author: Shalin S. Patel

7.3.1 Introduction

The theory of mimicry has been of interest to ecologists and evolutionary biologists for years, and has been called the "greatest post-Darwinian application of Natural Selection" (Rettenmeyer 1970). Mimicry has a fascinating role in affecting animal behavior and an even more amazing impact on the ecological and evolutionary success of organisms. Just about any characteristic or attribute can be mimicked, and the permutations for the roles of these mimetic behaviors in the lives of organisms are endless. In this chapter, we will explore behavioral mimicry within the **Hymenopteran** insect order, focusing heavily on ants, wasps, and to some degree, bees.

In order to adequately study mimicry, we must first establish a basic understanding of mimicry itself, and the model organisms we will be discussing. Insect mimicry made its debut into the primary literature in 1862,

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[4] http://www.ozanimals.com/Spider/White-Crab-Spider/Thomisus/spectabilis.html

[5] This content is available online at <http://cnx.org/content/m34751/1.3/>.

when Bates first proposed his theory of mimicry (Rettenmeyer 1970). Bates astutely realized that certain insects resembled another, and thus dubbed these imitations "mimics." **Batesian mimicry** is based on six principles: 1) predators find the model organism unpleasant, 2) predators find the mimic to be acceptable but because it resembles the model closely, they leave it alone, 3) the models vastly outnumber the mimics, 4) the models and mimics are found in the same place at the same time, 5) predators find the models and mimics noticeable, and 6) the predators learn to correlate the model with dislike (Rettenmeyer 1970). Since then, the field has blossomed with the development of other types of mimicry, including **M*ü*llerian mimicry**, **Aggressive mimicry**, and **Wasmannian mimicry** (Box 7.6 (Distinguishing common types of mimicry and an introduction to a unique form, imperfect mimicry), Pasteur 1982). These will be discussed later in the chapter.

The Hymenoptera are one of the largest orders of insects. They are **holometabolous** insects named for their membranous wings. Ants, wasps, bees, and sawflies comprise the Hymenopteran order, and many species within this order are eusocial insects. We will consider specific examples of Hymenopterans throughout this chapter as they relate to behavioral mimicry.

Box 7.6: Distinguishing common types of mimicry and an introduction to a unique form, imperfect mimicry

The different types of mimicry commonly discussed can be confusing if not adequately differentiated. In order to make understanding this chapter easier, definitions and examples of the major mimetic categories are outlined below, followed briefly by a discussion of imperfect mimicry, a unique type of mimicry that differs from the commonly recognized ones.

Mimicry	Definition	Example
Batesian	Mimic shares protective signals with model but does not have anti-predator attribute	Hoverflies mimic vespid wasp color patterns, but do not have a stinger
M*ü*llerian	Mimic shares protective signals and anti-predator attributes with model	Bees, vespid wasps, and sphecoid wasps have the aposematic yellow and black stripes, and also have stingers*
Aggressive	Predators or parasites that share attributes with their harmless prey so as to avoid detection	Social parasitic ants *Acromyrmexinsinuator* avoid detection by their hosts *A. echinatior* via chemical insignificance***
Wasmannian	Mimic resembles model with which it lives in a social nest or colony	Social insects: ant, bee, wasp inquilines

Table 7.3

*Females of these species are harmful to predators. In most of these species, males are harmless and are considered automimics of females.

**Definitions and examples from Rettenmeyer 1970.

***From Lambardi et al. 2007.

7.3.2 Chemical Insignificance vs. Chemical Mimicry

In the leafcutter ants, *Acromyrmex insinuator*, a unique form of mimicry is employed in order to usurp a host colony of the heterospecific *A. echinatior* (Lambardi et al. 2007). While some **social parasites** use force to take over a colony, most use a less aggressive form of chemical disguise to trick the host colony into allowing the thievery. **Chemical mimicry** is the production of recognition cues similar to the host that allows for an intruder species to be falsely accepted as a member of the host species. Most insects that mimic behaviors and intrude on host colonies use this method of chemical disguise in order to avoid being caught. However, the *Acromyrmex* ants utilize a special variant of this chemical mimicry known as **chemical insignificance**. In this form, the ants use stealth rather than trickery to take over a host colony (Lambardi et al. 2007). They minimize the production of all recognition cues to reduce the intruder response elicited by the resident colony workers and soldiers (Figure 7.20). Due to this chemical stealth, the specialized social parasites *A. insinuator* were able to significantly avoid aggressive encounters – menacing threats, bites, and fatal attack – when compared to a similar amount of neutral inspection in the form of attenuation by the host *A. echinatior*.

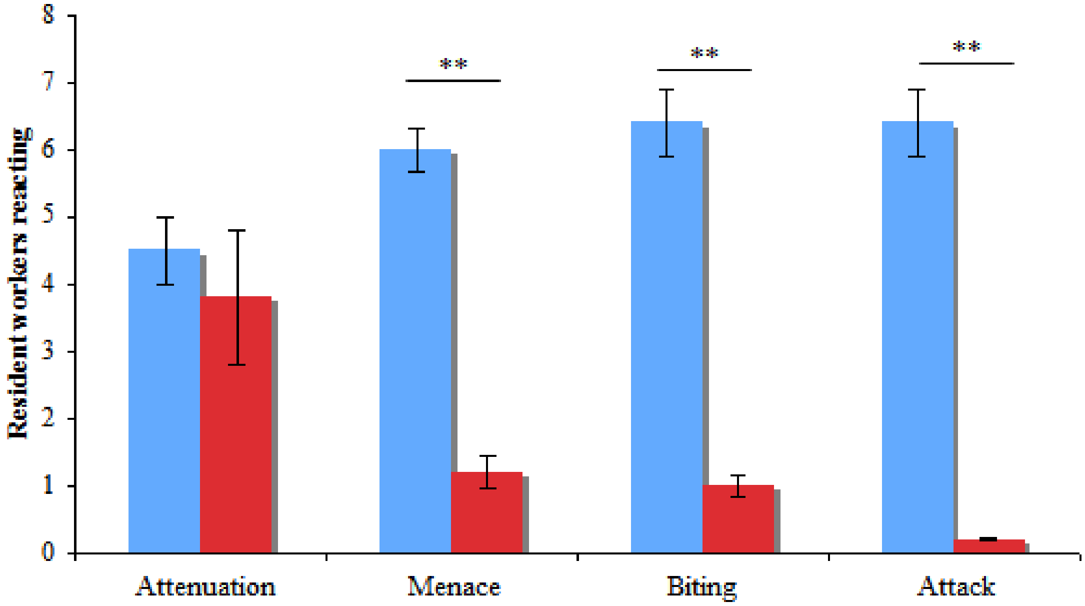


Figure 7.20: The number of resident colony workers of Acromyrmex echinatior (mean ± SD) reacting to random intruder species (blue columns) and the social parasites A. insinuator (red columns) in behavioral samples during 5 min of observation. **p<0.001
(Modified from Lambardi et al. 2007).

Most Hymenopteran social parasites, however, utilize chemical mimicry in order to usurp a host colony. One of the best examples of this occurs in the paper wasps. It has been well documented and substantiated that social parasite paper wasps modify their **cuticular hydrocarbon** profiles in order to falsely establish nestmate recognition between themselves and the host species. This has been successfully shown by studies delineating that *Polistes sulcifer* parasitizes *P. dominulus* (Dani et al. 2001, Howard & Blomquist 2005, Sledge et al. 2001, Turillazzi et al. 2001) and that *P. atrimandibularis* parasitizes *P. biglumis* (Lorenzi 2003, Howard & Blomquist 2005, Bagnères et al. 1996) using this mechanism of chemical mimicry. These parasite wasps enter host nests, fight the queens for control as the alpha-individual, and then alter their cuticular hydrocarbon profiles in order to establish nestmate recognition amongst the worker wasps (Figure 7.21).

The parasite wasps literally disguise themselves in order to obtain control of and parasitize host nests before moving on to the next!

It has been shown that in *P. dominulus*, *n*-alkanes are the common hydrocarbons present on the cuticles of the wasps (Bonavita-Cougourdan et al. 1991, Dani et al. 1996a, Dani et al. 1996b). Studies have shown that application of *n*-alkanes to residents of *P. dominulus* does not increase the aggressive response by other residents. However, in experiments applying either 40 μg or 200 μg of synthetic *n*-alkanes to the bodies of *P. dominulus* wasps, results showed that with an increase in the amount of synthetic *n*-alkanes applied, there were significantly more aggressive encounters with control residents, indicating that *P. dominulus* can recognize higher levels of cuticular hydrocarbons. Furthermore, when residents were treated with methyl alkanes and monoenes, the number of aggressive responses from other control residents was significantly higher, suggesting that the cuticular hydrocarbon profiles are colony-specific for nestmate recognition (Bonavita-Cougourdan et al. 1991, Dani et al. 1996a, Dani et al. 1996b).

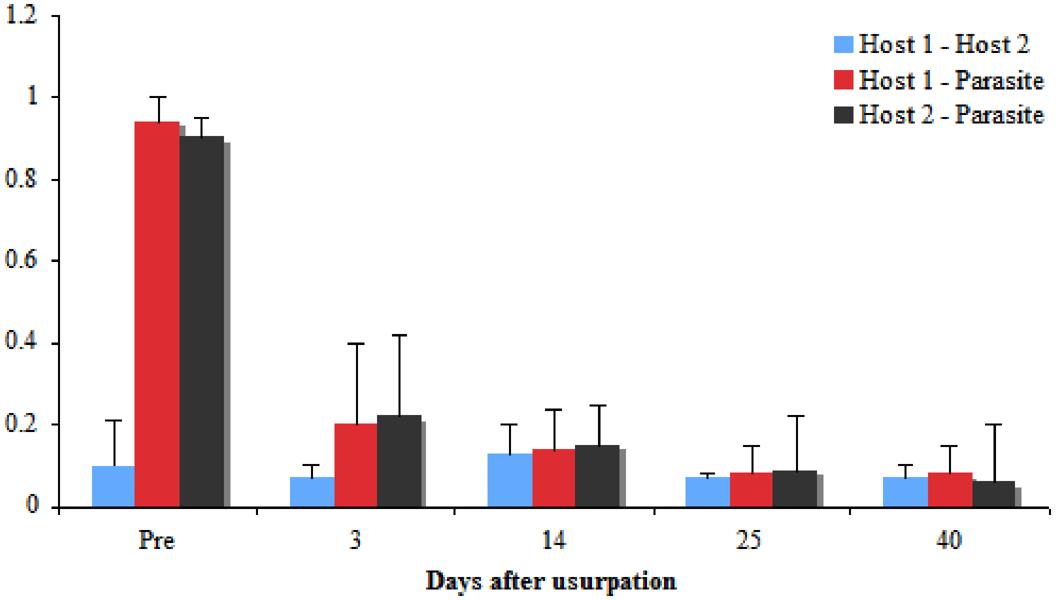
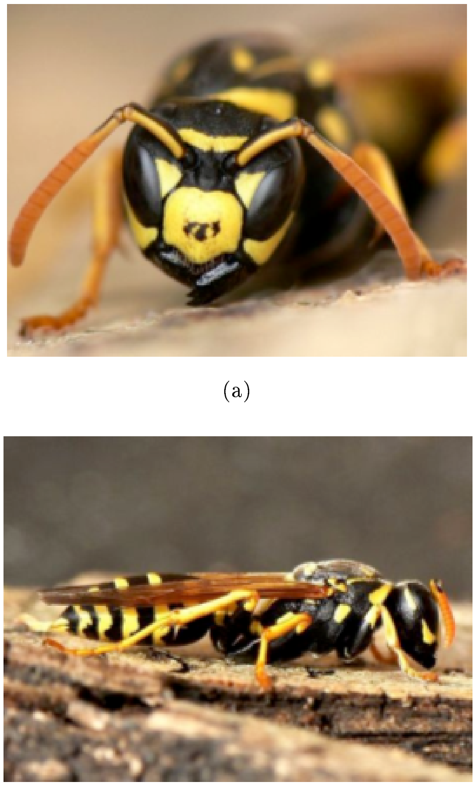


Figure 7.21: The mean (+ SD) chemical differences of cuticular hydrocarbon profiles between individual *P. sulcifer* social parasites and two host individuals of *P. dominulus* within usurped nests before and after parasitization. Measurement of cuticular hydrocarbons was performed via nondestructive solid-phase micro-extraction. The chemical differences were measured as dissimilarities in the quantities of individual hydrocarbons between individuals.
(Modified from Turillazzi et al. 2000).



(a)

(b)

Figure 7.22: Polistes dominulus. Copied from http://www.eol.org/pages/31072. Copyright Public Domain.

Ants also exhibit chemical mimicry, and species of ants have been known to pick up and reproduce colony odors to allow for nestmate recognition (Bagnères et al. 1991, Kaib et al. 1993, Lenoir et al. 1997, Lahav et al. 1999, Monnin et al. 1998). One mechanism by which ants and other Hymenopterans can mimic recognition cues of their hosts is through passive means. Gas chromatographic profiles of hexane soaks of increasingly developed stages in the ectoparasitic wasp's, *Orasema sp.*, relationship with the host fire ant, *Solenopsis invicta*, showed that false nestmate recognition developed passively over time, as the parasitic wasp acquired the ant colony odor via basic contact (Vander Meer et al. 1989). Aphid-parasitoid wasps have also exhibited chemical mimicry as a means to appease the ants that usually protect aphids (Liepert & Dettner 1993). This allows for them to bypass ant attack while they parasitize aphids.

Chemical mimicry has also been shown to be a developed behavior that is achieved during adult life and is not innate or inherited (Lenoir et al. 1997). Besides passive means of chemical mimicry, cuticular hydrocarbon profiles can also be actively synthesized by the mimic (Bagnères et al. 1991). In this study, two ant species that do not share many commonalities in their colony odors were raised in separate and mixed colonies. *Formica selysi* ants have unsaturated compounds, mainly monoenes and dienes, in their cuticular hydrocarbon profiles, whereas *Manica rubida* ants have almost exclusively saturated alkanes in theirs. In mixed colonies, a new odor was achieved that was a mix of both saturated and unsaturated hydrocarbons and was an intermediary odor that shared characteristics with both individual profiles. Because the quantities of these mixed hydrocarbons were similar to what the donor ants normally produced, it was suggested that the ants had to have actively synthesized the compounds. If the compounds were passively transferred from the donor ant to the recipient, it was expected that the quantity picked up would be less than what the donor normally produced, but this was not the case (Bagnères et al. 1991). Another study of cuckoo wasps that parasitize beewolves showed that an active synthesis of cuticular hydrocarbons occurs by demonstrating the presence of isomeric forms of compounds on the mimic that are not present on the host (Strohm et al. 2008). These cases serve as behavioral evidence that Hymenopteran insects are versatile chemical mimics and are capable of both passively and actively obtaining chemical recognition cues of their nestmates, by either simple contact or synthesis, respectively (Bagnères et al. 1991, Lahav et al. 1999).

In all of the examples discussed above regarding this mimetic behavior, **aggressive mimicry** is elucidated. In this form of mimicry, a predator or parasite imitates certain characteristics and attributes of the host in order to avoid detection.

7.3.3 Female Mimicry and Sexual Success

Another topic of much interest within the context of mimicry and behavior is how the sex of organisms affects their sexual and reproductive success. This has been widely studied, and has become important with regard to mimicry because examples of conspecific gender mimicry have evolutionarily arisen as a means of optimizing sexual success.

One very interesting example of this conspecific gender mimicry occurs in the parasitic wasp species, *Cotesia rubecula* (Box 7.7 (Female mimicry as post-copulatory mate-guarding behavior); Ayasse et al. 2001, Field & Keller 1993). This species is polygynous, and therefore, males mate with more than one female. This causes competition to arise between males as they vie for female mates, and thus, behavioral adaptations evolutionarily developed as a means to address this competition. One such adaptation that has impacted individual *C. rubecula* male sexual success is female mimicry. In this species, the majority of the females mate only once. Occasionally, if enticed, they will mate again in the post-copulatory period. During this period, the first male to mate becomes very protective, and has the desire to ensure that the female does not mate with another rival male. This will increase his personal reproductive success by maximizing the chances that his genes propagate. This mate-guarding behavior has been observed by Field and Keller (1993). In laboratory observations of *C. rubecula*, the first male to mate mimics a female's receptive mating position upon being approached by a rival male either before, during, or immediately after copulation. This, in combination with the female's sex pheromones being transferred onto the first mated male, usually distracts the rival male into futile attempts to mate with the mimic, during which time the actual female becomes unresponsive to post-copulatory advances (behavior and outcome pictured and explained in detail in Box 7.7 (Female mimicry as post-copulatory mate-guarding behavior)). Thus, female mimicry serves as a method of mate-guarding behavior in *Cotesia rubecula*, and directly increases the sexual and reproductive success of males (Ayasse et al. 2001, Field & Keller 1993).

A genus of army ants, *Eciton spp.*, also exhibits female mimicry, but rather than mimicking female posture and sex pheromones, these male ants anatomically mimic their female counterparts (Ayasse et al. 2001). Worker males, who are not reproductively capable, have the ability to choose which male enters the colony and inseminates the queen. Therefore, this audition per se, has caused an evolutionary shift towards larger males that resemble queen shape and morphology. These reproductive males also have exocrine glands located on certain parts of their bodies similar to where they lie on the queen, further developing the anatomical female mimicry (Ayasse et al. 2001).

Reproductive strategies are also influenced by chemical mimicry in the tropical ant species, *Cardiocondyla obscurior*. Winged males exhibit conspecific female mimicry in this ant species (Anderson et al. 2003, Howard & Blomquist 2005). Wingless males are aggressive by nature due to competition for mates. However, by mimicking the cuticular hydrocarbon profiles of queens, winged males are able to court virgin queens without being attacked by aggressive wingless males. As such, wingless males also falsely court these winged males. Since both male species can reproduce with females, this female chemical mimicry is taken into a behavioral evolutionary context when considering the two very different reproductive strategies employed by males (Anderson et al. 2003, Howard & Blomquist 2005). Why do winged males get off the hook from attack from wingless males, especially since they are stiffer competition for mates? Anderson et al developed a mathematical model to answer this question (2003). Because winged males chemically resemble females, wingless males are subdued because letting winged male imposters live has been overall less costly than accidentally killing a virgin queen. Therefore, this explicates why chemical female mimicry has led to the development of two reproductive strategies that affect male *C. obscurior* sexual success (Anderson et al. 2003).

Box 7.7: Female mimicry as post-copulatory mate-guarding behavior

In the polygynous parasitic wasp species, *Cotesia rubecula*, several males compete for a single female. One of the three competitive mating tactics employed by these males is to distract the rival male using female mimicry, lure the rival into a false mating situation, and then to court the actual female (Field & Keller 1993). Although most females mate only once, there is a brief post-copulatory period during which females have been shown to respond to courting advances by males. In 64 out of 84 laboratory observations of mating behavior, the first-mating male employed a post-copulatory female-mimicking behavior to distract 55 of 64 rival males. Panel (a) shows a female (left) accepting the male's (right) courtship, with the characteristic lowering of the antennae. Panel (b) shows the male and female copulating. As shown below in the bottom left panel (c), most rival males approach a mating pair *in copula*, and the copulating male immediately lowers his antennae and begins to mimic a female in an attempt to confuse the rival male (right). Following copulation and separation, as shown in panel (d), the female (left) moves away and the rival male (right) attempts to mate with the female mimic (center). This attempt at mating continues unsuccessfully for a short period of time, after which the female mimic leaves, having successfully warded off the rival male from copulating with his female. This suggests that female mimicry is a mate-guarding mechanism (Field & Keller 1993).

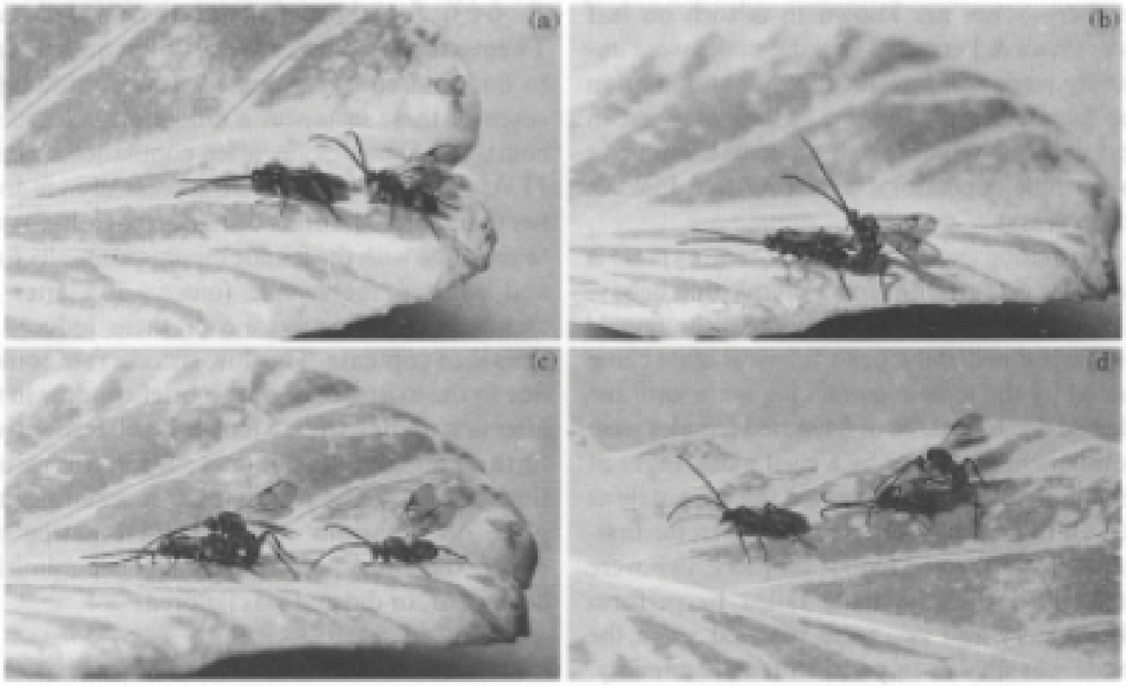


Figure 7.23

7.3.4 Interspecific Mimicry

All of the examples discussed in the previous section dealt with intraspecific female mimicry and how it affected the organisms' reproductive success. This section will discuss a unique case of interspecific mimicry that requires cross-gender interactions to achieve social parasitism.

In the **cleptoparasitic** cuckoo bee genus, *Nomada*, females gain entry into the host nests of *Andrena* bees, where they lay their eggs so that their larvae can eat and survive based off of the pollen stores in *Andrena* nests (Dettner & Liepert 1994, Ayasse et al. 2001). This is necessary because *Nomada* cuckoo bees lack pollen baskets, or **scopa**, on their hind legs, and therefore are unable to gather their own pollen. This cleptoparasitic behavior is accomplished in *Nomada* bees through chemical mimicry of *Andrena* nest odors secreted from female Dufour's glands. The *Nomada* females do not produce these *Andrena* odors on their own. However, *Nomada* males produce the compounds in their mandibular glands, and during mating, spray them onto the *Nomada* females. This is a very unique circumstance, in that the chemical mimicry occurs in one sex of the parasitic species, but the actual cleptoparasitic behavior is performed by the other sex, and is entirely dependent on a behavioral interaction between the two sexes. The compounds that allow for *Nomada* females to enter *Andrena* nests undetected are specific to pairs of hosts and parasites. For example, the compound *trans*-farnesyl hexanoate is released from the Dufour's gland of the hosts *Andrena haemorrhoa* and *Andrea caratonica*, and is also chemically mimicked by *Nomada* males specific to these hosts. Likewise, *geranyl octanoate* is released by *Andrena helvola* and *Andrena clarkell*a and is specifically mimicked by other *Nomada* males (Dettner & Liepert 1994, Ayasse et al. 2001).

(a)

(b)

Figure 7.24: The cleptoparasitic cuckoo bee, Nomada succincta (left) and a host bee Andrena sp. with a load of pollen on its body (right). Left image copied from [6]. Right image copied from [7]. Copyright Public Domain.

Box 7.8: Chemical mimicry allows for Hymenopteran insects to serve as model organisms for interspecific co-evolutionary arms races

We have established in this chapter that the chemical mimicry Hymenopterans utilize to modify their cuticular hydrocarbon profiles allows for social parasitism. This phenomenon has also been recognized in avian systems for years (Cervo 2006). When social parasites exhibit cleptoparasitic behavior in order to raise their young, it is known as brood parasitism. Birds and brood parasitism have long been considered together as a driving mechanism for co-evolutionary arms races between the host and parasite. In these arms races, host and parasite species continuously adapt and counter-adapt to one another via positive feedback loops, with both species trying to gain the upper hand in their interaction. Up until relatively recently, social insects, such as the Hymenoptera, were largely only considered as model organisms for studying sociobiological interactions; however, they also make suitable models for co-evolutionary arms race studies (Cervo 2006). *Polistes* paper wasp

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[6] http://en.wikipedia.org/wiki/File:Wespenbiene_Nomada_succincta_2.jpg
[7] http://en.wikipedia.org/wiki/File:Bee_February_2008-3.jpg

species are phylogenetically similar, rare, present in high local populations, and are capable of exerting strong selective pressure on each other, all key factors in serving as a model organism for co-evolution. Most importantly, and what distinguishes paper wasps as possibly better models than avian brood parasites, is that *Polistes* parasites and hosts have similar population sizes and generation times (Cervo 2006). Thus, Hymenoptera can serve as good models for co-evolutionary arms races and sociobiological studies.

Another example of interspecific co-evolution in Hymenoptera and their hosts is facilitated by chemical mimicry. In Central America, acacia trees play host to an ant, *Pseudomyrmex ferrugineus* (Espelie & Hermann 1988). The social wasp *Parachartergus aztecus* chemically mimics the ant's cuticular hydrocarbon profile and the acacia tree's thorn wax lipids in order to nest peacefully in the acacia with the ants. This strongly suggests that biochemical co-evolution occurs between the two Hymenopterans, the ant and wasp, and their host plant (Espelie & Hermann 1988). Both of the examples discussed here illustrate convincingly that Hymenoptera can serve not only as good models for social behavior, but also for co-evolution.

7.3.5 Mimicry as Self-Defense

An example of Müllerian mimicry in Hymenoptera is elucidated by a protective mechanism in *Parachartergus colobopterus*, a social wasp species. Workers of *P. colobopterus* sting only in self-defense, not for the protection of the colony (Strassmann et al. 1990). Workers have stingers, but do not sting the antagonist unless individually threatened. Instead, if the colony is disturbed, workers simply fly around and heavily beat their **gasters**, the bulbous portion of the Hymenopteran abdomen. One explanation for this behavior that is being debated is that these wasps mimic more aggressive species, such as vespid wasps, to achieve their protection. *P. colobopterus* do have alternating stripes of yellow and brown, which could serve as aposematic signals to deter predators. In this regard, the *P. colobopterus* wasps act as Müllerian mimics because they use the signaling to avoid predation and possess effective stingers, however, they seldom use their stings in colony defense. Other possible explanations for this interesting behavior include that it is a warning to predators that the larvae are distasteful or that nestmates have a low level of relatedness, suggesting that it is not within an individual's interest to fight aggressively to defend the colony. Though all of these theories could explain this mimetic behavior, it is still widely unknown as to why *P. colobopterus* uses its sting sparingly in defense of the colony. It is possible that this occurs because vertebrate predation of these wasp species is rare in areas where *P. colobopterus* is found (Strassmann et al. 1990).

Box 7.9: Wasmannian anatomical mimicry increases organismal success

Wasmannian mimicry refers to a type of mimicry in which the mimic resembles the host that it commensally lives with in a colony. These mimics are dubbed inquilines, and occur mostly in the social insects of Hymenoptera. One striking example of this kind of mimicry occurs in the myrmecophilous (ant-loving) wasp species *Paralypsis enervis* and *Aclitus sappaphis* (Wojcik 1989). These wasps live peacefully in ant colonies and parasitize the aphids that the ants usually protect. This occurs largely because *P. enervis* and *A. sappaphis* have over time come to mimic ant mouthparts, and with these modified mouthparts are able to engage in successful trophallaxis, or the transfer or food and other liquids among members of a colony or nest via mouth-to-mouth or anus-to-mouth mechanisms, with the ants. This is a primary example of how anatomical mimicry can significantly impact the behavior and success of a species, in this case in terms of getting food, a habitat, and other resources (Wojcik 1989).

7.3.6 Discussion Questions

1. Name three kinds of mimicry, define them, and give an example of each.

2. What is the difference between chemical insignificance and chemical mimicry? What type of mimicry are organisms that utilize these methods illustrating, and for what purpose?
3. For what behavioral purposes can mimicry be beneficial?

7.3.7 Glossary

- **Aggressive mimicry** – Resemblances that allow a predator or parasite to avoid detection by their prey by sharing the same attributes as the harmless model they parasitize or prey on (Rettenmeyer 1970).
- **Batesian mimicry** – Resemblances that allow a mimic to share signals with the model host while lacking the attributes that make it unprofitable or unpalatable to predators (McIver & Stonedahl 1993).
- **Chemical insignificance** – The production of as few chemical recognition cues as possible in order to avoid recognition as an intruder species by a host (Lambardi et al. 2007).
- **Chemical mimicry** – The production of chemical recognition cues similar to the host in order to avoid recognition as an intruder species by a host (Lambardi et al. 2007).
- **Cleptoparasitism** – A method of feeding where the parasite steals food or other resources from the host (Dettner & Liepert 1994).
- **Cuticular hydrocarbons** – Organic molecules consisting of primarily carbon and hydrogen that are present on the tough outer coverings of the insects. These usually serve as recognition cues (Howard & Blomquist 2005).
- **Eusocial** – A term describing the highest level of organization in a hierarchal social structure. Eusocial organisms exhibit reproductive division of labor with and without sterile castes, overlapping generations, and cooperative care of the young (Sherratt 2002).
- **Gaster** – The bulbous section of the abdomen present in Hymenoptera (McIver & Stonedahl 1993).
- **Holometabolous** – A term describing insects that go through complete metamorphosis between their larval and mature adult stages (Ayasse et al. 2001).
- **Hymenoptera** – One of the largest orders of insects comprising the ants, bees, wasps, and sawflies. The name Hymenoptera refers to the heavy membranous wings that these insects share (Sledge et al. 2001).
- **M*ü*llerian mimicry** – Resemblances that allow a mimic to share warning signals with the model host with both species also sharing honest anti-predation attributes (Rettenmeyer 1970).
- **Scopa** – Modifications, usually on the hind legs, of bees that serve as pollen-carrying baskets (Dettner & Liepert 1994).
- **Social parasite** – An organism that benefits from and takes advantage of interactions between members of social organisms at the expense of these social hosts (Lorenzi 2003).
- **Solid-phase micro-extraction** – A sample preparation technique involving the use of a fiber coated with a solid extraction phase that can extract both volatile and non-volatile analytes from either liquid or gas samples. After extraction, the fiber is transferred to a gas chromatograph, where separation of the analyte and analysis occurs. Also known as SPME (Turillazzi et al. 2000).
- **Wasmannian mimicry** – Commensal or mutualistic resemblances that facilitate a mimic living with its host (Rettenmeyer 1970).

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7.3.9 About the Author

I was born in Minnesota, but have spent almost my entire life growing up in Sugar Land, TX. One of my favorite activities is to spend quality time hanging out with my friends and family. As a proud son of Texas, I also love football and all sports. My favorite sport to play, however, is tennis. I wrote this chapter as a result of an interest in Hymenoptera that I developed after taking an insect biology class at Rice University. When I started learning about animal behavior, I became very interested in how mimicry, something so common in my favorite order of insects, could affect their behaviors. This paper is what came of that interest. I truly learned a lot from writing this chapter, and I hope it was helpful for those of you who chose to read this far!

Chapter 8

Host - parasite interactions

8.1 Host Interaction and Regulation in Parasitoid Wasps[1]

Author: Jennifer Pan

8.1.1 Introduction

Successful **parasitism** by insect parasitoids is a complex evolutionary process. The **parasitoid** insect must locate a host, overcome the host immune response, and adapt to a constantly changing environment to satisfy the metabolic and nutritional needs of the immature parasitoid. Parasitic organisms have diverse origins and have evolved a variety of developmental strategies to exploit their host (Brodeur and Boivin, 2004). While several orders of insects include parasitoids, the **Hymenoptera** are a particularly diverse order of **holometabolous** insects that are abundant in terrestrial areas throughout the world (Whitfield, 1998). Parasitoid **wasps** belong to the Hymenoptera order and are important for biological control since they reduce pest populations by parasitizing various species of insects. Not only are they ecologically important, parasitoid wasps greatly contribute to insect diversity. Recent estimates indicate that around 10% to 20% of all insects are parasitoid wasps (Quicke, 1997). Just as they demonstrate extensive species diversity, parasitoid wasps display a wide variety of interactions with their hosts.

Wasps commonly parasitize other insects by attacking a particular host life stage, such as the eggs, larvae, pupae, or adults. Parasitoids are classified into two groups: **idiobionts** and **koinobionts**. The difference between these two types is that a host ceases to develop after being infested by an idiobiont, whereas a host will continue to develop after being infested by a koinobiont (Askew and Shaw, 1986). Iodobionts are either **ectoparasitoids** that develop outside the host or **endoparasitoids** that develop inside the host. Koinobionts are usually endoparasitoids of **larval stage** insects, and only a few are ectoparasitic. Both ectoparasitoids and endoparasitoids have developed a variety of strategies to escape or overcome their host's immunity defenses and regulate the host's physiology to allow for their own development (Beckage and Gelman, 2004).

Understanding the evolution of parasitoid wasps is essential to explaining the observed diversity of relationships between parasitoid wasps and their hosts. The interactions between parasitoids and hosts are primarily controlled by genetic factors. Therefore in order to understand the occurrence of parasitoid diversity we must trace the evolutionary history of these organisms by considering the ecological constraints that affect parasitoid development and the observed physiological traits parasitoids use to infest other organisms (Pennacchio and Strand, 2006). This paper will focus on the evolution of the parasitoid lifestyle, ecological constraints that shape parasitoid development, methods of host location and oviposition, and the physiological tools parasitoid wasps use to regulate their hosts.

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[1] This content is available online at <http://cnx.org/content/m34732/1.3/>.

8.1.2 Evolution of Parasitoid Lifestyle

Hymenopteran insects first appear in the fossil record around 220 million years ago and the first parasitoids appear around 160 million years ago (Whitfield, 1998). The evolution of hymenopteran insects paralleled that of plants and other insects. As **angiosperms** became increasingly diversified, the Hymenoptera underwent substantial radiation such that all the major lineages of Hymenoptera present today exist by 65 million years ago (Whitfield, 1998).

Recent studies of hymenopteran **phylogeny** have used comparative **morphology** and DNA sequencing to provide a thorough understanding of this order (Whitfield, 1998). Phylogenetic hypotheses have since been formulated to investigate the evolution of various parasitoid lifestyles. Current evidence indicates that parasitism evolved once in a common ancestor of the Orrussoidea and **Apocrita**. After the occurrence of the original life history transition, many developmental strategies that facilitate parasitism have evolved independently multiple times (Whitfield, 1998).


(a) (b)

Figure 8.1: Examples of parasitoid wasps. (a) Female parasitoid wasp using ovipositor to inject her eggs into moth pupa; (b) Female parasitoid wasp injecting her eggs into aphids.

Orrussoids and several basal apocritan lineages share biological habits and developmental strategies, tending to be ectoparasitic idiobionts of beetles. Thus, the ancestral parasitoid was most likely an ectoparasitic idiobiont that lived on concealed wood-boring beetle larvae (Wharton, 1993). Developmental strategies evolved after the original appearance of ectoparasitic idiobionts. The Ichneumonoidea is divided into the Braconidae and Ichneumonidae. While most ectoparasitic ichneumonoids are idiobonts that develop on concealed hosts, a few groups, such as the Polysphinctini, are koinobionts that parasitize mobile hosts such as spiders (Shaw, 1994). Many aculeates are ectoparasitic idiobionts or have evolved closely related developmental strategies. Novel habits such as pollination, predation, and sociality also evolved in the aculeates (Whitfield, 1998).

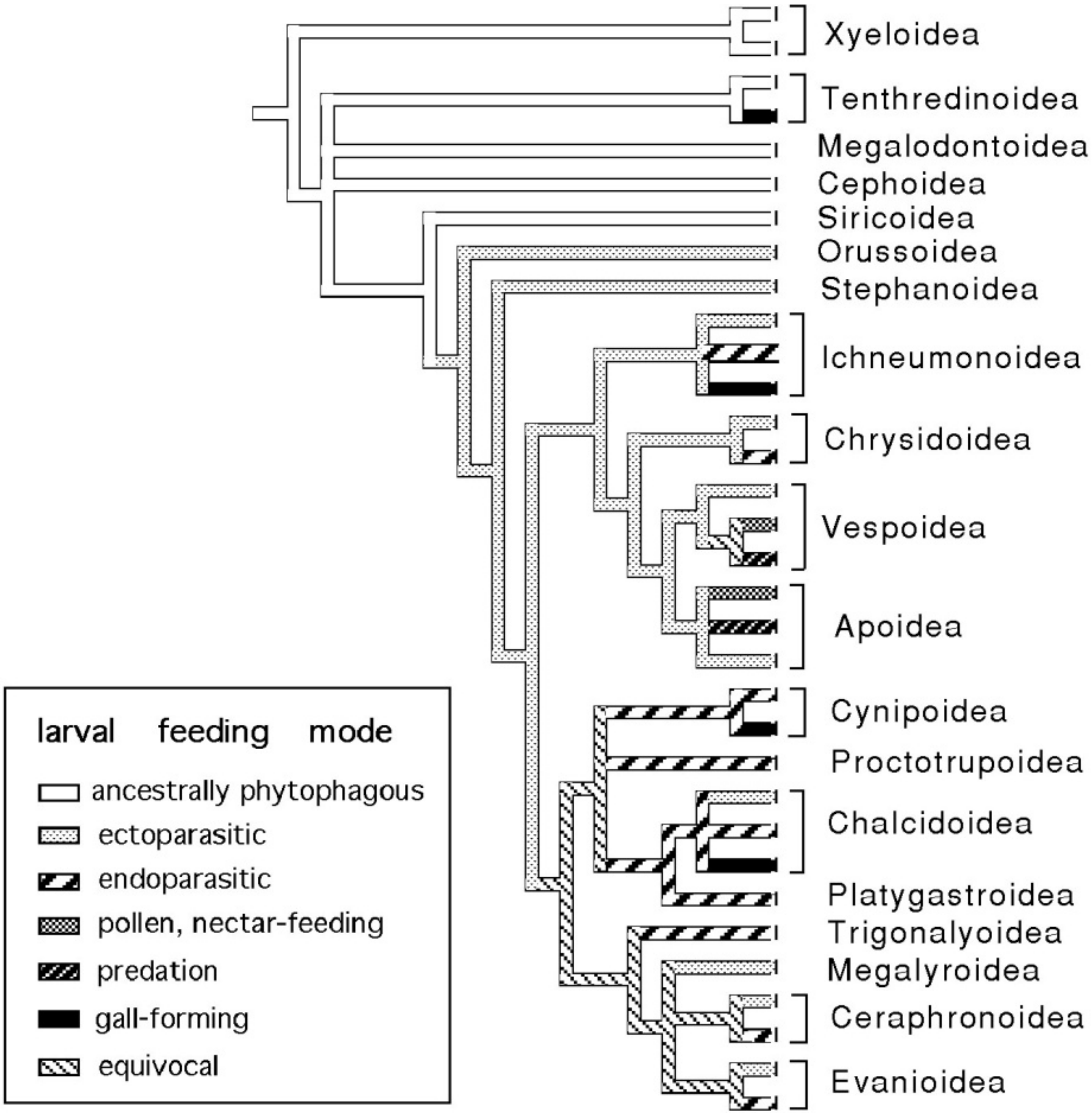

Figure 8.2: Phylogentic hypothesis for the Hymenoptera based on current evidence (Courtesy of Whitfield, 1998).

SuborderSuperfamily	Estimated number of species	Biological habits and developmental strategies
		continued on next page

Symphyta		
Xyeloidea	60	Phytophagous as immature
Megalodontoidea	300	Phytophagous as immatures
Tenthredinoidea	7,000	Phytophagous as immatures, some gallformers, some predators as adults
Cephoidea	100	Stem-boring herbivores as immatures
Siricoidea	200	Phytophagous and mycophagous as immatures
Orussoidea	70	Idiobiont ectoparasitoids of beetles(Buprestidae)
Apocrita		
Stephanoidea	100	Idiobiont ectoparasitoids of woodboringbeetles and wasps
Megalyroidea	100	Ectoparasitic idiobionts of beetles
Trigonalyoidea	100	Parasitoids oviposit on plants. Eggs eaten byLepidoptera but only develop if lepidopteranlarva is parasitized and thus developendoparasitically, possibly ashyperparasitoids

continued on next page

Aculeata	92,000	Basal lineages idiobiont ectoparasitoids. Nestprovisioning with adults providing multipleprey to offspring that feed as ectoparasitoidsalso common. Other species are predators orpollin/nectar feeders; many social species
Evanioidea	1,200	Ectoparasitic idiobionts or cleptoparasites(Gasteruptiidae), endoparasitic koinobionts ofbeetles (Aulacidae), or egg predators(Evaniidae)
Ceraphronoidea	2,000	Both ectoparasitic and endoparasitic; biologypoorly known
Ichneumonoidea	100,000	Basal lineages ectoparasitic idiobionts;multiple origins of endoparasitic koinobionts;polydnaviruses associated with selectedadvanced lineages
Chalcidoidea	100,000	Extremely diverse habits that includeectoparasitism, endoparasitism, predation,gall formation, seed feeding, and other formsof phytophagy

continued on next page

Platygastroidea	10,000	Endoparasitic idiobionts of eggs (Scelionidae)or endoparasitic koinobionts of larvae(Platygastridae)
Cynipoidea	4,000	Basal lineages of endoparasitic koinobiontsthat complete their development asectoparasitoids. Derived lineages includeendoparasitic koinobionts (Figitidae) or gallformers (Cynipidae)
Proctotrupoidea	6,000	Endoparasitic koinobionts of diverse hosts
Total	280–320,000	More than 75% of known species areparasitoids

Table 8.1: Species richness and biological habits of the major superfamilies of Hymenoptera (Courtesy of Pennacchio and Strand 2006).

*Data extracted from Whitfield 1998, Whitefield 2003 and Dowton 2001

8.1.3 Ecological Constraints and Parasitoid Development

Parasite lineages tend to parallel those of their hosts (Brooks and McLennan, 1993). A number of studies have shown patterns of coevolution between parasitoid wasps and their hosts. Fig-pollinating wasps, which originated from a parasitoid ancestor, appear to have evolved in response to their host plants (Machado et al., 2001).

Figure 8.3: Co-speciation of figs and their pollinators (Courtesy of Cook and Rasplus, 2003). Phylogenies of *Ceratosolen* pollinators show significant congruence with their host figs.

The relationship between parasitoid and host is attributed to mortality risk (Strand, 2000). A trade-off exists between size and development time – an organism must choose between growing larger at the cost of greater mortality risk due to increased development time and developing rapidly to reduce mortality risk at the cost of reduced size (Abrams, 1996). Thus, conditions that increase development time increase risk of mortality for both the host and parasitoid. Because of this trade-off, parasitoids that face high mortality risk favor shorter development times and are smaller. Conversely, species that face low mortality risks favor size at the cost of increased development time. Parasitoids that attack exposed species appear to experience higher levels of intraguild competition than parasitoids that attack concealed hosts (Blackburn, 1991). In response to this increase in mortality risk, parasitoids that attack exposed hosts have shorter development times.

Box 8.1: Nonpollinating Fig Wasps

Although this paper focuses on parasitism of insect hosts, wasps also parasitize plants. Like many other mutualisms, the fig-pollinator association has been exploited by wasp parasites (Yu, 2001). One fig species can host up to 30 different species of nonpollinating fig wasps. Niche space within the syconium is separated by different subsets of flowers, timing of oviposition, and by larval diets. Nonpollinating fig wasps can be split into different functional groups (Cook and Rasplus, 2003):

- Large gall-inducers and their parasitoids: these wasps are much larger than pollinator wasps and oviposit from outside the syconium at or before pollination.

- Small gall-inducers: these wasps oviposit from outside at or mostly after pollination, but the wasps are similar in size to the pollinations.
- Internal parasites: these wasps only occur in the old World and enter figs along with similar sized pollinators.

> It has been hypothesized that figs do not exclude nonpollinating fig wasps because defenses against these parasitoid wasps might also exclude necessary pollinators (Cook and Rasplus, 2003). Some parasitoid wasps use the same cues as pollinators to oviposit at the same time, and defenses against these wasps might come at the cost of attracting pollinators to disperse seeds.

Another factor related to development time is fecundity. Parasitoids must compensate for the increase in mortality risk that accompanies host exposure. Therefore, parasitoid fecundity is expected to rise as opportunities of finding hosts increases and the probability of offspring surviving to adulthood declines (Price, 1980). Early host stages such as eggs and young larvae are more abundant and exposed than later host stages, so parasitoids that attack young hosts are expected to have larger fecundities than those who attack older hosts. Conversely, parasitoids that attack concealed hosts are predicted to have lower fecundities (Price, 1980). As predicted, wasps that parasitize young larvae are associated with higher fecundities and are typically endoparasitic koinobionts, while wasps that parasitize pupae are associated with lower fecundities and are typically idiobionts (Mayhew and Blackburn, 1999).

Examination of phylogenetic data and ecological constraints on parasitoid wasps reveals three main points. The first is that ectoparasitic idiobionts provided the original framework for parasitoid lifestyle from which other developmental strategies evolved. The second is that endoparasitoids developed physiological responses to overcome host immune and developmental factors, which allowed for greater specialization in endoparasitoid wasps. Finally, ecological factors such as host mortality risks have affected developmental traits such as offspring development times and parasitoid fecundities (Pennacchio and Strand, 2006).

8.1.4 Host Location and Oviposition

Once an adult parasitoid wasp emerges from its host, it must have an efficient way of finding its next host. Parasitoid wasps respond to a series cues to locate their next potential host. The adult parasitoid is able to determine the general area of their host using various environmental cues, namely temperature, shade or humidity, and semiochemicals associated with plants or other organisms in the place where the host might occur. Thus, adult parasitoids respond to either physical or chemical stimuli associated with the host's habitat (Gauld and Bolton 1988). This response has been observed in numerous studies of braconids. The braconid *Cardiochiles nigriceps*, which parasitizes budworms, have been shown to respond to lighting cues in order to determine their host's location. In an experiment conducted by Vinson, *C. nigriceps* eagerly searched for tobacco plants in sunlit places but rarely visited the same plants if they were located in heavily shaded areas (Vinson 1975).

The majority of parasitoid wasps locate hosts by responding to particular chemical stimuli, such as chemicals emitted from the host's food source. For example, Read and colleagues found that the aphidiine braconid *Diaretiella rapae*, which parasitizes the cabbage aphid, is attracted to the odor of brassicas, the aphid's food source (Read et al 1970). As a result of parasitoid reliance on physical or chemical cues, hosts that feed on relatively unusual foodplants can escape parasitism. Salt examined the ability of the parasitoid *Cotesia glomerata* to locate and attack the larvae of their host, the cabbage butterfly *Pieris brassicae*, based on the host's source of food. *C. glomerata* easily located and parasitized pierid larvae when they fed on their normal foodplant, cabbage. However, the pierid larvae were able to escape parasitism by this parasitoid wasp if the larvae developed on sea rocket or on capers (Salt 1958).

Once a female parasitoid has located a potential host, she chooses whether or not to lay eggs on or inside the host using host-associated semiochemical cues. She initially examines the host by doing a simple physical exam using her antennae. As a result, the size, shape and surface texture of the prospective host are important characteristics involved in eliciting an oviposition response. Many females then probe the prospective host with their ovipositor and use semiochemical cues to determine that the correct host has been located prior to oviposition (Gauld and Bolton 1988).

Box 8.2: Beneficial Branconids

Braconidae is one of the largest families of parasitic wasps in the Hymenoptera and is estimated to include at least 40,000 species, although only about a 15,000 of these species have been described. The Braconidae family has been divided into about 35 subfamilies, and the subfamilies of greatest interest are: Agathidinae, Alysiinae, Blacinae, Braconinae, Doryctinae, Euphorinae, Homolobinae, Microgastrinae, and Opiinae (Quick 1997). Wasps belonging to the Braconidae family exclusively parasitize other insects and are therefore greatly beneficial for pest control. Braconids are found throughout the world, but most species prefer warm, dry climates. As a result, braconids have been extensively used in biological control programs in tropical and subtropic areas (Gauld and Bolton 1988).

The braconid wasp Toxoneuron nigriceps is an endoparasitoid of the tobacco budworm that uses polydnaviruses, to control its host's development. After T. nigriceps injects venom containing polydnavirus into its host, teratocytes produce a chitinase just before the parasitoid larva emerge from the host. The chitinase is involved in facilitating the emergence of parasitoid larva by digesting the host cuticle since parasitoid larva lack mandibular apparatus (Consoli et al 2005).

In addition to polydnaviruses in the female ovary, several different types of virus-like particles (VLPs) have been discovered in the accessory glands of various braconid species. In a recent study by Luo and Zeng (Luo and Zeng 2010) a new rod-shaped virus was found in the accessory gland filaments of the parasitoid wasp D. longicaudata. This braconid parasitizes several species of fly pests and has been used to control fly populations in Thailand.

8.1.5 Venom and its Impact on Host Regulation

In order to successfully parasitize the host, parasitoid wasps must generate and release gene products at oviposition that alter the physiology of the host (Vinson and Iwantsh, 1980). One of the most important morphological adaptations in Hymenoptera that arose to accommodate parasitoid lifestyle was the venom gland (Quicke, 1997). All female hymenopterans internally store poisonous venom in their ovaries and secretory organs. The venom gland appears to produce factors that are injected into hosts or prey that can also be injected into intruders as defensive secretions. Ectoparasitic idiobionts inject venom into hosts that is often paralytic and causes developmental arrest of the host, which benefits the externally developing parasite (Doury et al., 1995). Parasitoid wasps produce a wide range of venoms that could serve as models for developing synthetic chemical insecticides.

One species that has been extensively studied for its venom is the fly ectoparasitoid *Nasonia vitripennis*. This parasitoid wasp feeds and lays eggs on large flesh fly pupae. Adult females of this species inject venom prior to oviposition and the envenomated fly eventually dies from venom toxicity (Danneels et al 2010).

Figure 8.4: Female Nasonia vitripennis injecting venom in a pupa of the bloyfly Calliphora vomitoria. (Picture courtesy of Professor Dirk C. de Graaf)

Box 8.3: Ovarian Antidote to Deadly Venom

Female parasitoids produce and release venom in order to regulate their host's immunity and physiology. The venom is injected along with the parasitoid egg during oviposition, and in many species of ichneumonid and braconid families, symbiotic polydnaviruses or virus-like particles are also injected at oviposition as agents of controlling the host's physiology. In a study on the effects of parasitism by Asobara japonica on Drosophila melanogaster larvae, this parasitoid wasp demonstrated a unique means of avoiding encapsulation, using both venom and ovarian fluids to foster the success of parasitoid development (Mabiala-Moundoungou et al 2010).

A. japonica venom is injected by the female wasp into fly larvae at oviposition and induces permanent paralysis followed by death of M. melanogaster larvae (Mabiala-Moundoungou et al 2010). However, these paralytic effects can be reversed by injection of ovarian extracts from female wasps. Thus, the venom of the endoparasitoid can have a deadly effect on hosts, but ovarian extracts can act as an antidote and reverse the effects of the parasitoid wasp's venom. This finding shows that A. japonica produces factors from both the venom gland and ovary that are required to regulate host physiology in a synergistic manner.

The venom secreted by *Nasonia vitripennis* is lethal to a wide range of manure-breeding flies and the common house fly, *Musca domestica*, which is a major vector of human disease. The venom is also toxic to multiple developmental stages of several mosquitoes that are vectors of diseases such as malaria, encephalitis, yellow fever and West Nile fever (Rivers 2004). The evenomation of the host fly results in a number of changes in the fly's physiology that leads to cell death. David B. Rivers and his colleagues performed bio-assays of *Nasonia* venom and found that the venom operates by nonparalytic means to induce arrested development in evenomated hosts. The venom was found to alter the fly's lipid metabolism, leading to lipid accumulation in the host fat body, and change plasma membrane permeability leading to an increase in sodium influx. Venom also suppressed the host fly's immune response and was essential for successful parasitization by the developing wasp larvae (Rivers et al 2002).

A powerful weapon of parasitization, venom has evolved to produce both immunosuppressive and stimulatory properties to create the optimal host environment for parasitoid offspring. In order to maximize progeny production, female parasitoids must regulate the host without totally suppressing the host's physiology and creating an unregulated host environment. Should the host become immune-compromised, the parasitoid's progeny is subjected to unregulated microbrial attack and invasion. Thus, the female wasp must evade the host immune response without compromising the host's immune system. To accomplish this difficult task, parasitoid wasps use a venomous mixture that includes virus-like particles, such as the **polydnavirus**, at the time of oviposition to subdue the host (Danneels et al 2010).

The shift from ectoparasitism to endoparasitism has greatly diversified developmental strategies among parasitoid wasps as novel traits evolved in response to offspring developing inside the host (Pennacchio and Strand, 2006). In order to evade the host's immunity reaction of encapsulation, some species release "hidden-self" recognition molecules so that the parasitoid egg or larva avoids recognition and attack from host **hemocytes** (Schmidt and Strand, 2001). Other species have evolved mechanisms of inhibiting or destroying the host's cellular immunity system (Strand and Pech, 1995). Endoparasitoid wasps regulate the host's physiology either by targeting hormones or the **hemolymph** protein content of the parasitized host (Bae and Kim, 2004). These parasitoids produce and release active factors in the host hemocoel that may be synthesized by the female parasitoid in venom glands and injected along with the parasitoid egg during oviposition, or they may be released by the offspring during the course of development (Mabiala-Moundoungou et al., 2010). Many species of the ichneumonid and braconid families use symbiotic polydnaviruses (PDVs) to infect the host tissues and control the host's physiology with the acquired virus (Schmidt et al., 2001).

8.1.6 Conclusion

Hymenopteran insects show an immense range of biological diversity and employ various strategies to escape or overcome their host's immunity defenses and regulate their host's physiology to foster the success of their own development. The presence of parasitoid wasp diversity can be better understood by tracing the evolution of the parasitoid lifestyle and discussing the ecological constraints on parasitoid development. In addition, analyzing of the different mechanisms of wasp parasitism sheds light on the evolution of biological diversity in this group of insects. Although a great amount of research has been done on wasp venom and related symbiotic polydnaviruses used to infect host tissues, these re remains plenty of room for research on these secretions. Parasitoid wasps produce a wide range of venoms that could serve as models for developing synthetic chemical insecticides and effectively reduce the spread of human diseases via insect vectors. Parasitoid wasps are a diverse and fascinating group of insects that continue to have a significant global impact.

8.1.7 Discussion Questions:

1. What factors select for the evolution of a parasitoid lifestyle?
2. Why would an ectoparasitoid lifestyle evolve before an endoparasitoid lifestyle?
3. What are the advantages of having a parasitoid lifestyle over a predatory lifestyle?
4. What are the dangers of having a parasitoid lifestyle?
5. What defense mechanisms can hosts utilize to escape parasitism?

8.1.8 Glossary

- **Angiosperms**- A plant that produces flowers.
- **Apocrita**- A suborder of insects in the order Hymenoptera that includes wasps, bees and ants.
- **Ectoparasitoid**- A parasitoid that develops on the outside of the host's body.
- **Endoparasitoid**- A parasitoid that develops inside the host's body.

- **Hemocytes**- A cell that plays a role in the immune system of invertebrates; phagocytes found within the hemolymph of invertebrates.
- **Hemolymph**- The liquid that fills the interior of the body and surrounds all cells in arthropods; analogous to the fluids and cells that comprise blood in higher animals.
- **Holometabolous**- A term applied to insect groups that exhibit complete metamorphism in which the insect undergoes a series of physical changes during development; includes four life stages – an embryo, a larva, a pupa, and an adult.
- **Hymenoptera**- one of the largest orders of insects; comprised of sawflies, wasps, bees, and ants
- **Idiobiont**- A parasitoid whose host ceases to develop after parasitism.
- **Koinobionts**- A parasitoid whose host continues to develop as the parasitoid's offspring matures.
- **Larval stage**- A distinct juvenile stage in an insect's life that occurs before it undergoes metamorphosis into an adult.
- **Morphology**- Descriptive structures used to identify an insect.
- **Parasitism**- A type of relationship between different organisms wherein on organism benefits at the expense of the host.
- **Parasitoid**- An organism that lives internally or externally on its host and ultimately kills its host.
- **Phylogeny**- A tool that shows the evolutionary relatedness among various organisms.
- **Polydnavirus**- A type of insect virus that is secreted with venom at the time of oviposition and aids in immune suppression of the host.
- **Wasp**- Any insect of the order Hymenoptera and suborder Apocrita that is neither a bee nor ant.

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8.1.10 About the Author

Jennifer Tina Pan is a graduating senior at Rice University currently living in Oak Park, California. Originally born in Houston, TX, Jennifer's family moved to California when she was four years old. A rambunctious and energetic child, Jennifer began playing various sports at the age of five and eventually focused on tennis at the age of ten. Among her friends, Jennifer was called "Panda Express" for being the token Asian girl on the team. Their team made it to the state championships two years in a row, and Jennifer went on to play Varsity tennis her freshman year at Rice University.

Jennifer enjoys sampling foreign cuisine and baking in her spare time. An avid fan of Food Network, she recently made chocolate soufflé for twelve friends and is embarking on a quest to make crème brûlée so that her set of ceramic soufflé dishes are put to good use. In addition to sweets, Jennifer has a weakness for sushi and has been to nine different sushi restaurants while living in Houston for the past four years. Her younger sister, Rachel, is also an active sushi connoisseur and the sisters are known to frequent their favorite hometown sushi restaurant, Sushi Gen, multiple times each week. Although she also grew up playing tennis, Rachel discovered a passion for pole vaulting in her freshman year of high school and plans to pole vault for UCI after graduating from Oak Park High School. An important year of transition for both, Jennifer and Rachel plan to finally take a summer vacation together after graduating from their respective places of learning.

Jennifer's multiple sports-related injuries led her to become interested in Sports Medicine in her sophomore year of college. In addition to majoring in Kinesiology, Jennifer continued to pursue her interest in ecology by taking various biology classes and labs. To this day, Jennifer cites Plant Diversity with Tom Miller as her favorite class at Rice University. She is thankful for the wealth of information she gained from her professors while at Rice, and is excited for the next step in her career.

8.2 Mind Games: Acanthocephalan infection and behavioral modification[2]

Author: Dina Yangirova

8.2.1 Introduction

Parasitism is a long-term, durable interaction between two species, in which one uses the other as a source of nutrients, a transport vehicle, or a habitat without providing anything in return (Combes 2001). The parasite's activities lack the glory and drama of a predator eating its hard-won prey. Instead, the parasite works quietly and diligently behind the scenes, often hidden, but nevertheless profoundly influential in the life of its host. For instance, the parasite might literally, physically change the host, because some of its genes become expressed by the host. Moreover, the parasite influences the host by consuming the resources that it would otherwise use for its own growth, repair, or reproduction. It may also influence the dynamics of the host population by killing individuals susceptible to infection, and thus indirectly increasing the number of infection-resistant individuals. By doing so, the parasite is creating strong selective pressures for the host to develop defenses against exploitation, which in turn causes selection for parasites that can bypass these defenses. In this way, the host and the parasite find themselves in an evolutionary arms race, which has wide-ranging effects on both organisms (Combes 2001).

Effective transmission to another host or transmission of the eggs to another host is an important task for parasites, because otherwise when the host dies due to the parasite's activities or otherwise – the parasite, its offspring, and most importantly its genes will perish as well. Transmission can occur through contact, consumption, or an active **free-living stage**(Combes 2001). This task becomes especially important if the parasite requires more than one host to complete its development and reproduce. In such cases, one of the most extreme cases of host manipulation by a parasite can be observed, in which the parasite turns

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[2] This content is available online at <http://cnx.org/content/m34741/1.4/>.

its host into a veritable zombie by radically changing its behavior and appearance to increase the chance of transmission to the next host. An organism that vividly demonstrates this phenomenon is a thorn-headed worm of the phylum Acanthocephala, which causes radical changes in the life and behavior of its invertebrate **intermediate host** in order to improve the chances that it will be consumed by its next, vertebrate **definitive host**. A relationship between parasitic worms of the phylum Acanthocephala and their hosts provide great insights into the dynamics and complexity of parasite-induced behavioral modifications, and provide a great demonstration of the **extended phenotype**.

8.2.2 Life cycle

The acanthocephalans are one of the smallest and least diverse metazoan parasites, yet they can be found on all continents and in a variety of environments, including sea and fresh water (Kennedy 2006). They are thorn-headed parasitic worms whose life cycle requires two hosts. They begin their development when an intermediate host (typically an isopod, amphipod, or an insect) inadvertently consumes the acanthocephalan eggs. Once inside, the parasite grows in the host's alimentary canal, avoiding significant mechanical damage to the host's body. Once the parasite reaches the **cystacanth** stage, it needs to transfer to a new, definitive, vertebrate (generally a bird or a fish), in order to be able to reproduce and complete its life cycle. Inside the definitive host, they reproduce sexually and the eggs are released with the host's feces. The transfer requires that the definitive host consume the intermediate host (Bierbower et al 2007, Benesh et al 2008, Moore 1983, Kennedy 2006).

The cystacanths do not leave such a crucial step in their life cycle to fate and work to modify the behavior and physiology of the invertebrate so as to maximally increase their chance of being eaten by the definitive host (Bakker 1997). The parasite makes the intermediate host more vulnerable to predation by variety of ways such as by decreasing its stamina, making it highly conspicuous, making it disoriented, and inversing its responses to environmental stimuli that indicate definitive host presence (Moore 1983). For acanthocephalans like *Pomphorhynchus laevis,* the level of behavior manipulation is higher if two parasites infect an individual rather than one, but the manipulation level does not increase for higher number of parasites. They cystacanths also have to be of the right age during transmission, i.e. older than 30 days. If they infect the definitive host too early, they might not be able to remain in the intestine. On the other hand, they usually do not survive longer than a year if not passed on to the next host (Kennedy 2006). Behavioral changes are more intense if the host is infected with older cystacanths (Franceschi 2008), reflecting the urgency to move on.

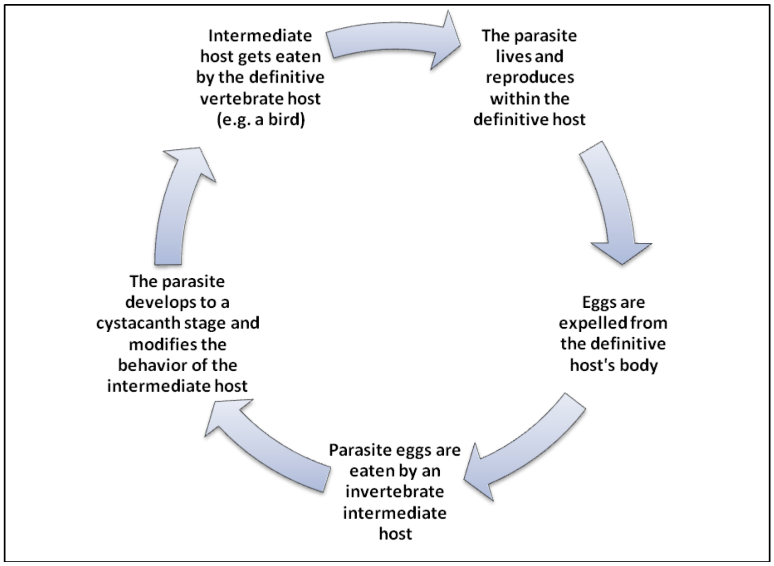

Figure 8.5: Acanthocephalan life cycle (Moore 1983, Kennedy 2006)

The size of the parasite population may follow an annual cycle (Brattey 1988). For instance, adult *Acanthocephalus lucii* living in Scotland are most abundant in late spring and summer, decline in numbers during autumn, and reach a minimum during winter. There is only one generation per year and there is a continual flow of parasites through the population of its final host, the European perch, *Perca flaviatilis*. The cycle may be driven by seasonal changes in the number of infective larvae, host's resistance to infection, or host feeding behavior (Brattey 1988).

8.2.2.1 Parasite-host dynamics

Along with serving as a mode of transmission to the final host, the intermediate host's other role in the parasite's life is as a source of nutrients. It is in the parasite's interest to consume as many nutrients (i.e. eat as much of the host) as possible in order to grow and develop, but it is also in its interests to keep the host alive and fit, in order to escape predation until the parasite is ready to be transmitted. Thus, the parasite must find an optimum level of exploitation that maximizes growth and also maximizes the chances eventual of predation on the host (Benesh 2000). One method of dealing with this conflict is to infect a larger host in the first place, so that there are more nutrients to consume and more room to grow (Hasu 2007).

The conflict is exacerbated when multiple parasites infect a single host and find themselves in competition for the host's resources. One might expect that each would try to consume as many of host's nutrients as possible and grow as much as possible to maximize its own fitness. Instead, the growth of parasites in crowded conditions appears to slow down over time. One possible explanation may be that the parasites are related and they are sharing the resources equally to ensure that all the relatives have maximum possible fitness and pass on the genes (Benesh 2007).

Box 8.4: Conflicts of Interest

If another type of parasite, like the microspordium *Dictyocoela* (roeselum), infects the same host as the acanthocephalan (e.g. *P. minutus*), a competition between two survival strategies may ensue (Haine 2005). The microspordia are transmitted vertically, from infected parent to offspring, so they are highly invested in the reproductive fitness of their host. On the other hand, the

> acanthocephalans are transmitted horizontally, that is between unrelated hosts, and thus are not invested in their hosts' reproductive success. In fact, they sometimes manipulate the behavior or physiology of their host in order to use the resources like time, energy, and nutrients that would normally go toward reproductive activities to increase their own fitness. So, when these two parasites infect the same host, an obvious conflict of interest occurs. In these situations, the microspordia are not above sabotage, and cause *P. minutus* to have less success in manipulating the behavior of the host (Haine 2005).

In order to inhabit the host's body for significant amount of time, the parasite has to bypass the immune system defenses (Rigaud 2000). The fact that they often manage to do so may indicate **co-evolution** of the two organisms. If the host's immune system were able to kill the parasites, then there would be strong selective pressures for the acanthocephalans to develop anti-immune system defenses, because only those parasites that have these defenses would be able to survive and pass on their genes. However, a growing prevalence of immune system resistant parasites would put selective pressures on the host to develop new mechanisms against infection, especially since the parasite dramatically decreases the host's reproductive fitness. Thus, the two organisms are in an arms race. Furthermore, the parasite's ability to suppress an immune response is specific to a particular host species, and does not work on invasive species (Rigaud 2000).

Parasite Species	Intermediate Host	Definitive Host
Acanthocephalus dirus	Isopod: *Caecidotea intermedius*	Chub: *Semotilus atromaculatus*
Acanthocephalus lucii	Isopod: *Asellus aquaticus*	Perch: *Perca fluviatilis*
Pomphorhynchus laevis	Amphipod: *Gammarus pulex*	Perch: *Perca fluviatilis*
Corynosoma constrictum	Amphipod: *Hyalella azteca*	Variety of waterfowl
Echinorhynchus borealis	Amphipod: *Pallasea quadrispinosa*	Burbot: *Lota lota*
Plagiorhynchus cylindraceus	Isopod: *Armadillidium vulgare*	Starling: *Sturnus vulgaris*
Polymophus paradoxus	Crustacean: *Gammarus lacustris*	Mallard ducks, muskrats, and beavers
Polymorphus minutus	Crustacean: *Gammarus roeseli*	Waterbird

Table 8.2: The intermediate and definitive hosts of the parasite species discussed (Bierbower 2007, Brattey 1988, Benesh 2005, Benesh et al. 2008, Helluy 1990)

8.2.2.2 Acanthocephalan host specificity

Acanthocephalans are highly successful in causing elaborate changes in the behavior of their intermediate host; however, their mechanisms of manipulation are often highly specific to that particular host and do not work on other species. Consequently, parasites that are adapted to a local host may have little to no influence on an **invasive host** (i.e. one that has recently arrived to the area). For instance, the *P. laevis* parasite, whose local host is the amphipod *G. pulex*, fails to alter the behavior and immune system of a recent invader which is also an amphipod, the crustacean *G. roeseli* (Moret et al 2006). The invading population's resistance to parasitism gives it a selective advantage over the native population, and helps it invade the area successfully. This finding suggests that the two amphipod species have evolved due to parasite-mediated competition with each other, which demonstrates a profound effect a parasite's specificity may have on its host in terms of its species evolution (Bauer 2000).

Two acanthocephalans may have different behavioral effects on the same intermediate host. For instance, *P. laevis* and *P. minutus* have the same intermediate host, *G. pulex*. However, the definitive host of *P. laevis* is freshwater fish, while the definitive host of *P. minutus* is a waterbird. In the presence of a fish predator, the amphipods infected with *P. laevis* remained outside of refuge more and spend more time in areas with the predator 'odor' than the amphipods infected with *P. minutus*, (Kaldonski 2007).

8.2.2.3 Physiological effects of an acanthocephalan infection

Acanthocephalan infection can cause drastic changes of the host's physiology and distribution of resources. In particular, the parasites often decrease the reproductive capability of the intermediate host because their transmission to the definitive host does not depend on the survival of the intermediate. The significant amount of resources and time that the host spends on finding a mate and producing offspring could be used instead to maximize the parasite's own fitness and chances of advancing to the next host.

For example, the acanthocephalan *Pomphorhynchus laevis* causes its intermediate amphipod host, *Gammarus pulex*, to have lower lipid content in pregnant females. Females need lipids for yolk synthesis, and cannot successfully reproduce without them. The parasites instead use the energetic resources to increase the intermediate host's survivorship until it is eaten by the parasite's definitive host (Plaistow 2001).

The parasites can also reduce reproductive capability of its male hosts. When the isopod, *Caecidotea intermedius*, is parasitized by *Acanthocephalus dirus*, the host males still develop sperm and have the same fertilization ability as noninfected males. However, they are less likely to initiate mating in noncompetitive situations and are less responsive to females (see Figure 8.7) (Bierbower 2007). Likewise, acanthocephalan infection causes the amphipod *G. pulex* males to have significantly lower pairing success and to be less likely to engage in competition with other males for females (Bollance 2000). The parasite can use the energy that the host would spend on competition and mating for its own growth.

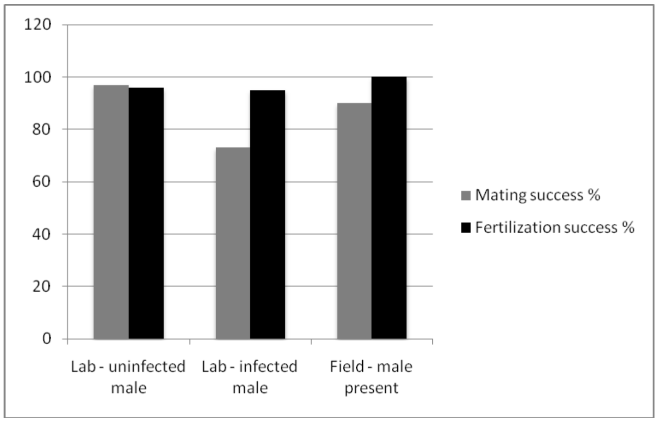

Figure 8.6: C. intermedius male mating and fertilization success is lower when infected with an acanthocephalan A. dirus compared to uninfected males in the lab and field (Drawn from Table 1, Beirbower 2007)

Acanthocephalans also use physiological changes to directly make their intermediate hosts more vulnerable to predation by final host. For example, the acanthocephalan *P. laevis* has a conspicuous yellow-orange color (see Figure 8.6), caused by the pigments called carotenoids. They are readily visible through the transparent cuticle of its host *G. pulex*, which makes the infected host become more vulnerable to predation due to enhanced visibility (also called **oddity selection**), as well as due to parasite-induced behavioral changes (Bakker 1997).

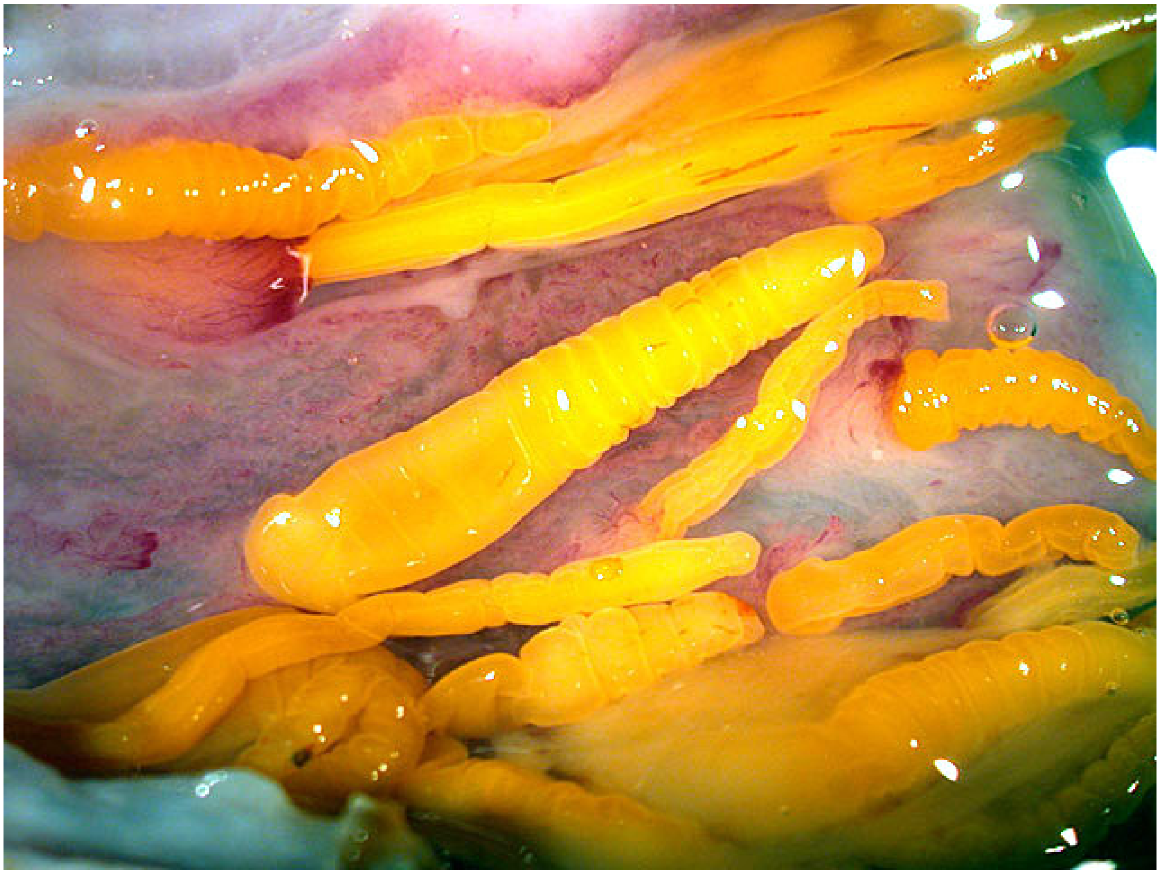

Figure 8.7: P. laevis (Raschka 2007)

8.2.3 Parasite-induced Behavioral Changes Result in Predation

Acanthocephalans alter the behavior of their hosts in many ways to make them more vulnerable to predation. First, they can manipulate their hosts' response to various aspects of light stimuli, including light and wavelength. For example, the acanthocephalan *Corynosoma constrictum* alters its amphipod intermediate host *Hyalella azteca*'s response to higher red (600-700 nm) and green (500-550 nm) wavelength regions. The host uses properties of light to identify various microhabitats, and acanthocephalan infection causes the amphipod to become lost and enter foreign microhabitats. The host also becomes less photophobic and begins to prefer dangerous, well-lit areas (Benesh 2005). Uninfected amphipods usually stay away from such sunlit areas, as well as from areas disturbed by duck movement. However, acanthocephalan infection interferes with such self-preserving tactics and increases the chance of their intermediate host being eaten by their final host (Bethel 1976).

Deep under water, the sense of smell is often more important than sight in detecting aquatic predators. Infection by acanthocephalans reduces the ability of the host to respond to olfactory signals that indicate the presence of predator. For example, acanthocephalan *Echinorhynchus borealis* causes its host, amphipod *Pallasea quadrispinosa*, to spend less time hiding, and thus is more exposed, in water containing strong chemical cues from its predator (Benesh et al 2008).

Another way in which acanthocephalans like *Plagiorhynchus cylindraceus* manipulate their host (isopod

Armadillidium vulgare)is by increasing their tolerance to low humidity (Moore 1983). As the result, the infected isopods spend more time in exposed, dry spots, which causes them to be isolated from the group and more visible to predators. The parasites also increase the visibility of the host by increasing its affinity to light-colored areas, so that they stand out more (Moore 1983).

8.2.3.1 Serotonin and Behavior Manipulation: A Mechanism of Action

One mechanism by which acanthocephalan parasites alter the behavior of their host is through manipulation of **neuromodulators** (Adamo 2002). For example, *P. laevis* changes the **serotonin**(5-HT) levels in the brain its host *G. pulex*, which causes it to have an inverse reaction to light. Laboratory injection of serotonin into an amphipod, such as *G. pulex*, causes the same inversed reaction to light, which indicates that the change in serotonin levels is the reason for the behavior and not merely byproduct of the invasion (Tain 2006).

Another effect of high serotonin levels is demonstrated by crustacean *Gammarus lacustris*, which display an abnormal response to disturbances in the water by swimming up the surface and clinging to solid objects when infected with the acanthocephalan *Polymorphus paradoxus* (Helluy 1990). When uninfected amphipods were injected with serotonin, they displayed the same behavior. The increased serotonin levels might have influenced chemical pathways related to the precopulatory clinging of the male amphipod (Helluy 1990).

Box 8.5: Behavior Manipulation in Vertebrates: Rabies

Rabies is a disease caused by the lyssa virus that affects many vertebrates, such as dogs, bats, monkeys, foxes, and humans (Easmon 2005). It is found on all continents and between 40,000 and 70,000 people die of the infection every year.

As with acanthocephalans, the rabies virus requires transmission from one host to the next for survival. One of the mechanisms of transmission is through saliva, with the current host biting the next one to transfer the virus. After the initial penetration into the new host's body, the virus bypasses the immune system and travels through the nervous system into the brain, skin, mucous membranes, and salivary glands. The virus causes inflammation in the brain and interferes with many of its functions. The new host becomes aggressive and prone to biting, which helps further transmission of the virus.

Rabies infection proceeds through several stages. The time that it takes for the virus to reach the brain constitutes an incubation period, which can last months. Following incubation is a preliminary stage during which the individual develops various gastrointestinal and respiratory problems, such as loss of appetite, fever, nausea, and vomiting. The individual also experiences copious salivation and tear production. Then, during the neurological stage, the infected host begins to suffer from paralysis, throat spasms, fear of water, anxiety, hyperactivity, confusion, uncontrolled movement, and delirium. After the appearance of symptoms, the mortality rate is nearly one hundred percent. However, a vaccine has been developed that treats the infection if administered before or soon after the transmission (Easmon 2005).

8.2.3.2 Behavior Modification to Avoid Non-host Predators

While the acanthocephalans work hard to improve the chances of their intermediate host being eaten, the last thing that they want is for someone besides the definitive host taking advantage of the situation and getting an easy meal. Thus, the parasites also modify the behavior of their hosts in various ways to prevent consumption by non-host predators. For example, uninfected crustacean *Gammarus roeseli* usually resides in the benthic (i.e. bottom) areas of the lake. However, when infected by *Polymorphus minutus*, they appear in higher concentrations near the water surface, often clinging to floating material, in the presence of non-host predators, such as another aggressive crustacean near the bottom of the lake (Medoc et al. 2006). The parasites also improve the host's performance when it comes to escaping non-host predators, so that infected *G. roeseli* have higher average and maximum swimming speeds, greater speeds during the moment of escape, and cover greater distance while fleeing. This counterintuitive effect on the host's fitness may increase the chances of the intermediate host being eaten by an appropriate definitive host (Medoc 2007).

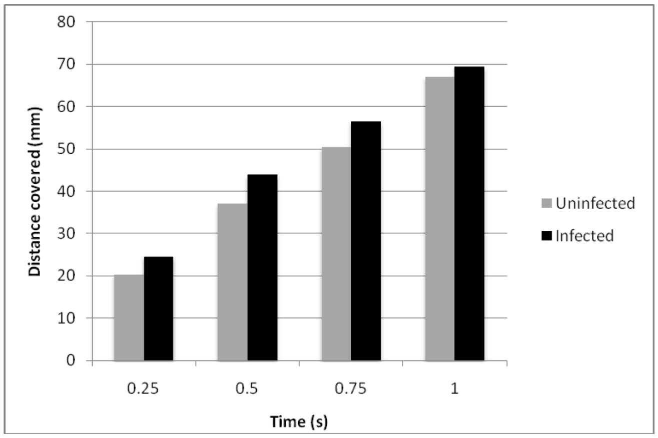

Figure 8.8: Cumulative distance (mm) covered by uninfected and P. minutus infected G. roeseli after contact with non-host predator D. villosus (redrawn from Table 1, $p < 0.001$, Medoc 2008).

8.2.4 Discussion Questions

1. How can a parasite both increase the possibility of being eaten by a definitive host and decrease the possibility of being consumed by a non-host predator?
2. Why is behavior modification so important for many parasites?

8.2.5 Glossary

- **Cystacanth**- developed acanthocephalan larva, which is able to infect its definitive host (Moore 1983).
- **Co-evolution**- phenomenon when a change in one species causes a change in another species, which triggers a counter-adaptation in the first species again, so that the two species evolve together.
- **Definitive host**- an organism in which parasite reproduces and resides until death.
- **Extended phenotype**- term coined by Richard Dawkins to describe the phenomenon of genes not only determining physical phenotypes but also various behaviors of an organism.
- **Free-living stage**- a stage in parasite's life when following a signal from the environment or the host's body the parasite escapes the host's body and lives outside (Sukhdeo 1995).
- **Intermediate host**- an organism that contains the parasite for a limited amount of time, when the parasite life cycle requires more than one host.
- **Invasive host**- a potential host for a parasite that is not native to the area, often harder to invade than local hosts
- **Neuromodulators**- can alter the neural circuits and allow the organism to be flexible in its responses to the environment (Adamo 2002).
- **Oddity selection**- when conspicuous appearance of an organism causes it to becomes more vulnerable to predation.
- **Serotonin**- a neurotrasmitter and hormone, also known as 5-HT, that is known to constrict blood vessels and have an effect on mood (Medicinenet.com)

- **Parasitism**- a relationship between two species in which one benefits and another suffers losses to fitness.

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[5] http://en.wikipedia.org/wiki/File:Acanthocephala_Pomphorhynchus.jpg

8.2.7 About the Author

Figure 8.9: Dina Yangirova

I was born in Russia, but have lived in Houston, Texas for nine years. I am a junior biochemistry major and I have taken the Animal Behavior class because I dearly love all animals, even the ugly ones. In my spare time, I like to dance, take pictures, draw, watch movies, and read. The hardest part of writing this chapter was putting together all the disparate, disjoined pieces of information and constructing a coherent picture of how the acanthocephalans operate. In the process, I have realized yet again that even the smallest and slimiest creatures can be incredibly complex and exciting.

Chapter 9

Learning

9.1 The Social Factor in Song Learning in American Sparrows[1]

Author: Lu Yang

9.1.1 Introduction

The ability to communicate is an **adaptive trait** that has evolved many times. Songs, in particular, are very complex signals found in insects, frogs, and birds and are most predominantly used by males to attract mates and/or compete with other males (Searcy & Anderson 1986). Among the animal taxa that use songs as a means of communication, songbirds (suborder Passerini) are unique in that their songs are not entirely genetically based (unlike a cricket chirp or a frog croak). Instead, songbirds learn songs through social interactions. We know this because juveniles raised in acoustic isolation develop abnormal songs (Marler 1970b). In this way and many others, songbirds' songs are similar to human speech (see Box 4; Doupe & Kuhl 1999). Furthermore, song learning in birds is a great model for studying social learning in other animals, especially humans (see Box 4; Brainard & Doupe 2002).

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[1] This content is available online at <http://cnx.org/content/m34754/1.3/>.

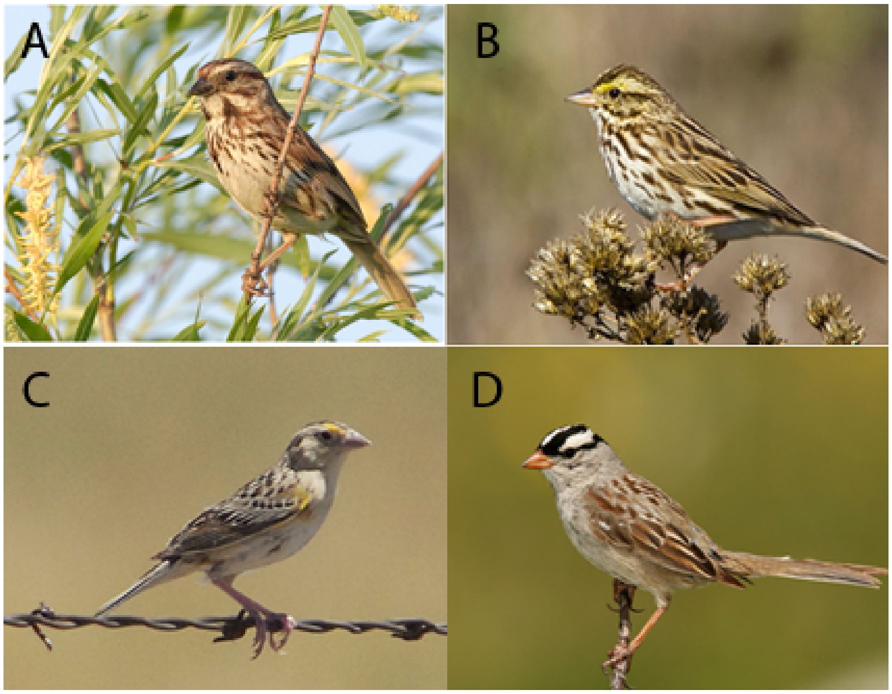

Figure 9.1: Four species of American sparrows. A) song sparrow (Melospiza melodia), B) savannah sparrow (Passerculus sandwichensis), C) grasshopper sparrow (Ammodramus savannarum), D) white-crowned sparrow (Zonotrichia leucophrys).

Image A : <http://commons.wikimedia.org/wiki/File:Melospiza-melodia-001.jpg>.
Image B: mikebaird <http://www.flickr.com/photos/mikebaird/39066219/>.
Image C: jerryoldenettel <http://www.flickr.com/photos/jroldenettel/2543533860/>.
Image D: <http://commons.wikimedia.org/wiki/File:White-crowned-sparrow.jpg>.

Biologists have been trying to decipher the meaning behind bird songs since the 18th century (Baker 2001). Like many areas of biology, studies of bird songs have been greatly influenced by Darwin's theory of evolution by natural selection, which spurred biologists to investigate deeper into the adaptive value of songs as form of communication. Only recently has serious progress been made in understanding song learning in songbirds, incited by Marler's claim that song learning in birds has many parallels with speech learning in humans (Marler 1970a). Since then, numerous studies have been done on songbirds, although song learning, especially the **social learning** of songs, is still a relatively poorly understood topic.

In this chapter, we will focus on four species of American sparrows (family Emberizidae). We will cover recent theories and findings regarding why song learning occurs, who songs are learned from, when (i.e. at what stages of development) songs are learned, and how songs are learned, while focusing on the social factors involved. Figure 9.1 and Table 9.1 describe the species of sparrows covered.

Species	Habitat	Nesting	Breeding season	Clutch size	Age at leaving nest

continued on next page

Song sparrow(M. melodia)	Low shrubby, swampy areas.	Early: groundLate: shrubs/trees	April – August	3-5	10 days
Savannah sparrow *(P. sandwichensis)*	Grassy, open areas	Ground	Mid-March – early June	4-5	8-14 days
Grasshopper sparrow (A. savannarum)	Grassy areas	Ground	Early April – early June	4-5	9 days
White-crowned sparrow (Z. leucophrys)	Cleared, open areas	GroundSometimes bush/low tree	Early March – early August	2-5	9-11 days

Table 9.1: Selected Natural History of Species of American Sparrows (Baicich & Harrison 1997).

9.1.2 Why Do They Learn? – The Adaptive Function of Song Learning

Songs are an important communicative tool for songbirds, but do they make sense as an evolutionary adaptation? It seems that all of the costs associated with song learning, such as time and energy (which can be diverted towards foraging, for instance), can be avoided if songs are completely **innate**, like a cricket chirp. From an evolutionary point of view, it follows that song learning can only evolve if its benefits outweigh these costs.

Figure 9.2: A song sparrow singing during breeding season (beginning of spring). Image: Almiyi <http://www.flickr.com/photos/2070909>

So what are these benefits? Learning is usually a tool used when external circumstances are variable, because it has the potential to help individuals adapt their behaviors to changing environments. For example, humans have the ability to learn languages, which is beneficial when a baby is born into a country that does not speak the language of its parents or when a person moves to a country that speaks a foreign language. Therefore, songs are most likely an important tool used by songbirds to adapt to their changing social environments. Examining differences between **sedentary** and **migratory** white-crowned sparrows in song learning from neighbors illustrates this concept. The songs migratory birds learn from **tutors** are more **plastic**, while the songs sedentary birds learn are more accurate (Nelson et al. 1995). Such differences may be explained by the fact that migratory birds have more uncertainty in where they will breed. Therefore, their songs remain more plastic, allowing the birds to easily adjust their songs to those of their neighbors where they decide to breed (Nelson et al. 1995). See *Sharing Hypothesis of Song Learning* below on advantages of adjusting songs to those of neighbors. More on the role of neighbors as song tutors will be discussed in a later section.

The importance of social learning can be explained by two hypotheses: the repertoire hypothesis and the sharing hypothesis (Beecher & Brenowitz 2005).

9.1.2.1 Repertoire Hypothesis of Song Learning

The repertoire hypothesis states that song learning allows birds to acquire a large **song repertoire**, which aids them in attracting mates, since females prefer males with large repertoires (Searcy & Anderson 1986). Gil and Gahr (2002) explain that song repertoire is an **honest communication** and can be used for **sexual selection** because it directly correlates with the amount of neural space in an individual, which is a measure of intelligence in songbirds. However, this hypothesis has been under much criticism, as most birds have just a few songs; many have just one. To explain this observation, Garamszegi (2004) claims that limited neural space acts as a strict limitation to the size of song repertoire. Therefore, the cost of having a large repertoire (taking up neural space) balances the benefit (attracting females).

9.1.2.2 Sharing Hypothesis of Song Learning

The sharing hypothesis says that through song learning, birds can share songs with their neighbors, which enhances communication (Beecher & Brenowitz 2005). This is beneficial because territorial neighbors are usually important individuals in a songbird's life. In fact, Beecher et al. (2000) found that greater song sharing among neighbors, but not repertoire size, predicted longer territorial possession. This sharing hypothesis, however, directly conflicts with the repertoire hypothesis, since sharing songs with neighbors is easier if both sides have a small repertoire.

Box 9.1: Song Developmental Stages

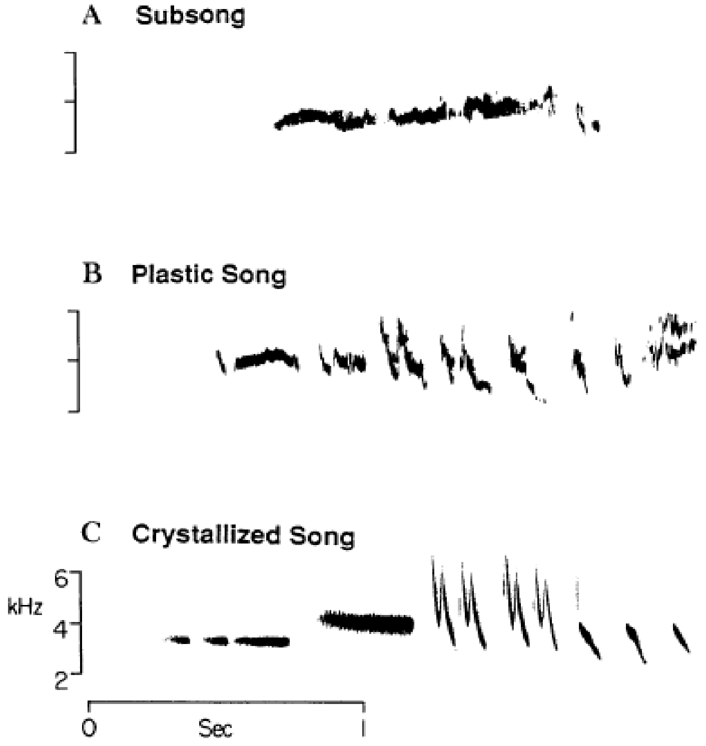

Figure 9.3: Developmental stages of white-crowned sparrow song, visualized in frequency of sound, over time.

DeWolfe BB, Baptista LF, Petrinovich L. 1989. Song development and territory establishment in Nuttall's white-crowned sparrows. Condor. 91:397-407. ©1989 by the Cooper Ornithological Society. Reprinted with permission from the University of California

A songbird's song goes through many developmental stages before arriving at the final, crystallized song (DeWolfe et al. 1989; Marler 1970b). Prior to this final stage, the developing song is considered plastic and subject to alteration. In fact, in many species, songs remain plastic for much of an adult's life, allowing the bird to alter his songs throughout his life, perhaps to imitate his neighbor (Lehongre et al. 2009; Nordby et al. 2001). Many biologists recognize three stages of song development: subsong, plastic song, and crystallized song (Fig.3; DeWolfe et al. 1989).

- Subsongs are the first syllables uttered by juvenile birds. These can vary in length and are generally incomprehensible.
- Plastic songs vary greatly among individuals of a species, but can be recognized as belonging to a certain species.
- Crystallized songs are songs used by breeding adults. These are species-stereotyped although there may still be some variations among individuals, such as in addition or deletion of certain syllables.

9.1.3 Who do They Learn From?

Tutors, or sources of songs, are very important in social learning. Marler (1970b) shows that **juvenile** male songbirds that are acoustically isolated develop abnormal songs, while those that are raised with tape-recordings of songs develop songs normally. Juveniles usually learn their songs from older adults and show a tendency towards preferring **conspecific** models (Beecher & Brenowitz 2005). Soha & Marler (2001) found that white-crowned sparrow juveniles began showing preference toward conspecific songs prior to 20 days of age, when they are just beginning to memorize songs. Interestingly though, juvenile white-crowned sparrows can successfully learn the song of another species, such as the strawberry finch (*Amandava amandava*) provided that the tutors are live, as opposed to tape-recordings (Baptista & Petrinovich 1984). It seems that social interaction between tutors and tutee can even overcome genetic preference for conspecific songs. There is a general consensus among researchers that social interaction, and not mere exposure to a tutor song, is required for the best song-learning results in juvenile songbirds. For instance, in grasshopper sparrows, learning from live tutors results in more accurate **imitation** than learning from tape-recordings (Soha et al. 2009).

Box 9.2: General Development of Young Passerines

Passerines, or perching birds, are birds of the order Passeriformes. Songbirds (Passeri) are a suborder of passerines, and include the family Emberizidae (American sparrows).

Juveniles have many different choices of tutors. Usually, juveniles choose many adults to be their tutors, each with varying importance. In song sparrows, for instance, the number of tutors for each juvenile can vary from two to five (Beecher et al. 1994; Nordby et al. 1999; Nordby et al. 2000). According to Wheelwright et al. (2008), male savannah sparrows choose social fathers to be their most important tutor 12% of the time, **natal** neighbors (neighbors when the learner hatched) 35% of the time, 1-year-old breeding-year neighbors (neighbors when the learner first begins to breed) 26% of the time, and older-breeding neighbors (neighbors long after the learner began to breed) 26% of the time. In this case, the most important tutor is defined as the tutor that shares the most number of songs with the subject. Such variations in importance of tutor, especially among the different types of neighbors, suggest that learning allows songbirds to adapt to their social environment.

There are many reasons why a juvenile bird may choose a particular tutor to be his primary tutor over another. One may be the repertoire size of the tutor. Soma et al. (2009) has found that juvenile Bengalese finches (*Lonchura striata domestica*) learn from both their father and a subtutor when the two models have small repertoire sizes; but when the father has a smaller repertoire size, they tend to learn from the subtutor; in either case, the presence of a subtutor led to a larger repertoire. This is in accordance with the repertoire hypothesis of song learning. In Wheelwright et al. (2008)'s study, the juveniles tend to pick neighbors as the most important tutor. This result is in accordance with the sharing hypothesis of song learning, and is explained further in the following subsections.

9.1.3.1 Learning from Fathers

Although fathers are a logical choice as tutors for juvenile songbirds, since chicks are exposed to the songs of their fathers from birth; however, fathers are often not important tutors at all. Baptista (1985, described in Petrinovich & Baptista 1987) found that songbirds usually do not sing the songs of their fathers. Instead, as described above, neighbors are much more important tutors. This suggests that juvenile birds choose tutors not simply to learn how to sing, but to learn how to communicate with an individual. Juvenile songbirds leave their natal nests just a few weeks after hatching, so they never need to communicate with their fathers as adults. On the other hand, communicating with neighbors is important to territory possession (described below) and breeding (recall earlier discussion on sedentary versus migratory white-crowned sparrows).

9.1.3.2 Learning from Neighbors

Neighbors are one of the most important tutors to sparrows and can be much more important than fathers. Figure 9.4 shows that song sharing increases the closer two neighbors are to each other, suggesting that song learning from neighbors is important for social interactions with those neighbors. Social interaction, in turn, is important to learning from neighbors. DeWolfe et al. (1989) show that juvenile white-crowned sparrows that socially interact with adult territorial neighbors develop songs faster than those that do not.

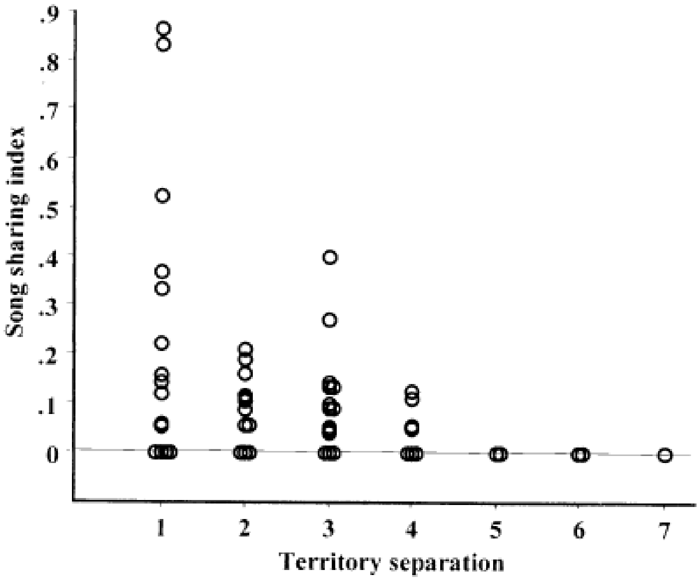

Figure 9.4: Song-sharing index, or repertoire overlap, between pairs of territorial males versus the number of territories separating them in a population of song sparrows.
Wilson PL, Towner MC, Vehrencamp SL. 2000. Survival and song-type sharing in a sedentary subspecies of the song sparrow. Condor. 102:355-363. ©2000 by the Cooper Ornithological Society. Reprinted with permission from the University of California Press.

Juveniles learn songs from more than one neighbor and preferable learn songs that their neighbors share (Beecher et al. 1994; Nordby et al. 2000). A possible explanation for this observation is that juveniles eventually set up their own territory next to these neighbors, sometimes even replacing one (Beecher et al. 1994; Nordby et al. 1999). Nordby et al. (2000) also points out that juvenile song sparrows preferably learn songs their first-year fellow juveniles learn. In fact, juvenile cohorts' songs can even be more similar to each other than to those of the early tutor (Kroodsma & Pickert 1984). This is more evidence showing the importance of sharing songs with neighbors, because there is a good chance that cohorts will become neighbors once they settle their own territory.

Box 9.3: Territoriality in Songbirds

Settling and maintaining a territory is very important to male sparrows. Territory ownership affects major areas in a bird's life, including nesting, inter- and intraspecies competition, and food collection, all of which have implications for mate attraction and offspring survival (Nice 1941). In song sparrows, males (and their partner) essentially gather all of his food from within his territory and males with a good territory often come back to it year after year. This illustrates the importance of finding a good territory (Nice 1941).

Best (1977) studied the field sparrow (*Spizella pusilla*) to see the effects of territory quality on mating success. He found that males with better territories mated more frequently. Territory quality was measured based on territory size and presence of certain favored plant species. Other factors that affected territory quality include snake and mammalian predation and cowbird parasitism (cowbirds have been observed to place their eggs into the nests of many species of sparrows). The presence of these factors often led to the female's desertion (Best 1977). Much of these findings can be applied to our sparrow species.

Songbirds also exert great effort to learn songs of their neighbors; juveniles hone their songs continuously after settling a territory to better match those of neighbors. DeWolfe et al. (1989) notes that juvenile song sparrows that are first settling a territory have up to four songs, but after settling, they keep only two of the closest songs to those of their neighbors. This suggests that juveniles anticipate becoming territorial neighbors to their tutors, and therefore learn from them to ease communication, since territorial neighbors are required to interact with each other in many ways. Wilson et al. (2000) argue that the amount of song-sharing indicates a male's competitive ability to obtain a preferred territory near his tutors. Song sharing may also determine a male's effectiveness in using songs to communicate aggressively. To provide further evidence, another Beecher group showed that the number of songs a sparrow shares with his neighbors is correlated with length of possession of his territory, because neighbors depend on shared songs to regulate territories and interactions with each other (Beecher et al. 2000, Burt et al. 2001). A bird that does not share songs with its neighbors will have a hard time communicating with them and be successful in his territory (Beecher et al. 2000). This shows the importance of learning as an adaptive function. Without learning, there is no guarantee that a songbird will share songs with its territorial neighbor.

9.1.4 When Do They Learn?

Over the past few decades, the exact timing of song learning of whole songs (as opposed to song elements or parts of songs) has been a much-debated topic. No conclusive decisions have been reached among the scientific community on a proposed **sensitive period** for learning, specifically the strictness of this sensitive period (whether juveniles can only learn whole songs during this period) and the age that it occurs at. The overall theme, however, is that social interactions seem to play an important role in determining when songbirds learn songs. The rest of this section is a summary of recent discussions.

Marler (1970b) introduces the idea of a strict sensitive period for white-crowned sparrows in his discussion of the sensorimotor model of song learning. In this model, sparrows memorize songs between the ages of 20 and 50 days old; afterwards, they no longer memorize or learn any new songs. Instead, during their first spring, when they choose their territories for the first time, birds begin producing these songs from memory and compare them, via auditory feedback, to the songs of their neighbors. The birds then modify the songs stored in their memory to closely match the songs of their neighbors. In this model, the memorization/learning phase is called the sensory phase, while the reproduction phase/modifying phase is called the sensorimotor phase. The songs that are first produced during the sensorimotor phase are called plastic songs, because they are still subject to change or crystallization (Marler 1970b; see Box 9.1 (Song Developmental Stages)). The action-based model of song learning also indicates a sensitive period. In this model, a juvenile bird learns a large repertoire of songs and produces all of them during the plastic song developmental stage (Marler & Nelson 1993). When the bird meets its neighbor, it only selects the songs that most closely match those of its neighbors to keep.

Figure 9.5: A parent feeding its fledgling, which is not yet 50 days old.
Image: gerrybuckel <http://www.flickr.com/photos/91515698@N00/37288>

Baptista and Petrinovich (1984) provided the first evidence against the strict 50-day sensitive period. They found that juvenile white-crowned sparrows can learn songs even though tutoring did not start until the juveniles were at least 50 days old, as long as social interaction between student and tutor is involved. In Marler (1970b)'s experiments, the juveniles were only taught by tape-recorded songs (no social interaction). Therefore, Baptista and Petrinovich conclude that using live tutors is a more effective way to teach juveniles, allowing them to learn songs after they reach 50 days of age. Juveniles, which in nature are tutored by live birds, can therefore be expected to be able to learn songs past 50 days of age as well.

Baptista and Petrinovich (1984)'s results were also a topic of debate. Cunningham and Baker (1983, described in Baptista & Petrinovich 1986) argue that the experiments performed by Baptista & Petrinovich simply shifted the sensitive phase. They claim that by not exposing juveniles to acoustic stimuli during their first 50 days of life, the sensitive phase for song learning is delayed. Then, when Baptista and Petrinovich reintroduced the live tutor stimuli after age of 50 days, the sensitive phase reopened. In response, Petrinovich and Baptista (1987) performed an experiment in which juveniles birds received song stimulation during their first 50 days of life and found that they were still able to learn after they became 50 days old. Nelson and Marler (1994) show just a bit of concession to Petrinovich and Baptista's findings, arguing that not all birds can learn songs past their sensitive period of 50 days, and no bird can learn past 100 days old.

In 2001, Nordby et al. note that there is something logically wrong with the strict 50-day sensitive period. They reasoned that since it is advantageous for songbirds to share songs with neighbors (for reasons explained in previous sections), song learning should continue into the first fall and winter, when juvenile songbirds have a better idea of who their neighbors will be the following spring. Nordby et al. performed their own experiments and found that song sparrows can learn songs as late as 147 days old. In fact, half of the chicks in their experiment learned most of the songs in their repertoire from the tutor that they were exposed to only during their first fall. Songs learned during this time were also very accurate. This kind of learning (learning after the supposed sensitive period) is called de novo late learning. In most studies, tutors during the early sensitive period are conveniently called "early" tutors, while tutors for de novo late learning are called "late" tutors.

Burt et al. (2007), however, are unable to show that juveniles actually learn more from tutors they are exposed to later in life, a finding that appears to contradict Nordby et al. (2001)'s argument for the importance of learning from late tutors. The group performed an experiment where juvenile song sparrows are exposed to two song tutors only during their natal spring and summer (when they are less than 50 days old) and to two different song tutors only during their first winter (when they are at least 200 days old). In their experimental setup, the two late tutors each had similar songs to one of the two early tutors; one of the late tutors interacted with the juveniles, while the other one did not. However, while the authors found that juveniles learn more from the early tutors, the late tutors still have a large effect on song learning. Juveniles learned more songs from the late tutor and its early counterpart if they interacted with the late tutor (Burt et al. 2007).

Whether songbirds learn whole songs when they are young and then modify and trim their song storage once they meet their neighbors (selective attrition) or learn whole songs throughout the first year of their life (de novo late learning) is still under debate. Most researchers agree, however, that there is a sensitive period for song learning and it varies with each individual bird (Baptista & Petrinovich 1986; Nelson & Marler 1994). Also, songbirds become less and less able to acquire songs as they age; even within the so-called sensitive period, sensitivity to song learning decreases with time (Baptista & Petrinovich 1986; Baptista et al. 1993). This decrease in the ability to acquire songs with age supports theories on the adaptive function of song learning. Song sparrows often return to their same territory year after year to nest (Nice 1941). Therefore, it is likely that as they age, birds come across the same neighbors every year. So once they are old, it is no longer adaptive to learn songs from neighbors because they already share songs with them.

9.1.5 How Do They Learn?

Previous sections suggest that songbirds learn whole songs from their tutors. Marler and Peters (1987), however, propose that songbirds learn parts or elements of songs from various tutors and fuse them together to form their own unique song. Although there is some debate regarding this topic, recent research all seem to support that songbirds learn complete song types (Beecher 1996, described in Nordby et al. 2000; Nordby et al. 2000; Nordby et al. 2001).

The previous sections also hint that songbirds are exposed to and memorize more songs that they keep for their final repertoire. As explained before, while they are young, juveniles amass a great number of songs and goes through a selection process to weed out the songs they do not need once they are more mature (regardless of whether they continue to learn new songs during this time or not). There are two social ways for a juvenile songbird to learn and select songs. One is by directly interacting with an adult tutor; the other is by eavesdropping on singing interaction between two other birds.

9.1.5.1 Direct Interaction

As noted throughout the previous sections, interacting with a tutor (i.e. receiving **countersinging** feedback) leads to better song learning in juvenile songbirds than no interaction.

9.1.5.2 Eavesdropping

Eavesdropping is another important tool used by songbirds to learn songs, and is perhaps even more important than direct interaction. Juvenile song sparrows learn more by eavesdropping on an adult teaching another juvenile than by directly interacting with a tutor (Beecher et al. 2007). Furthermore, during the song-learning phase, juvenile song sparrows are more attracted to countersinging interactions between two or more birds than to the singing of a single bird (Templeton et al. 2010). The eavesdropping hypothesis explains these observations. As described in Burt et al. (2007), the eavesdropping hypothesis states that one of the advantages of eavesdropping over direct interaction is that by observing countersinging interactions, a juvenile bird can pay attention to both sides of the interaction and pick out the dominance relationship (Beecher & Burt 2004). The juvenile can then decide to learn the song of the more dominant bird. The juvenile can also use this dominance information in the future to make decisions regarding challenging other males. Furthermore, a juvenile bird can learn how to reply appropriately to certain songs. The eavesdropping hypothesis predicts that a juvenile bird will not only learn songs from a chosen tutor, but also from birds that sing to the tutor (Burt et al. 2007). Eavesdropping, therefore, is an important adaptive trait that allows songbirds to not only learn songs, but to learn ones that are most beneficial for their fitness.

Box 9.4: Birdsong and Human Speech

Now, having described song learning in songbirds, we can compare it to speech learning in humans. Marler (1970a) is one of the first to argue that birdsong learning parallels human speech learning. He compares babbling in infants to subsongs in birds in that both are initial, elastic precursors to their final forms of vocalization. Also, both infants and songbirds have a preference for learning conspecific vocalizations and both use vocal imitation and auditory feedback in the learning process. Furthermore, both infants and songbirds seem to derive some sort of intrinsic reward for imitating they sounds they hear with vocalizations (Marler 1970a).

In addition, speech learning in humans has a large social component, just like song learning in birds (see previous discussions). Golstein et al. (2003) performed speech experiments on 8-month old human infants, who are at a speech developmental stage that parallels the subsong developmental stage in songbirds (see Box 9.1 (Song Developmental Stages)). They found that infants that received immediate social feedback after a vocalization showed a significant increase in the number and quality of vocalizations. Meanwhile, infants that received the same amount of random social feedback (not necessarily after a vocalization) showed an increase in number but not quality of vocalizations. These results show that social feedback can affect speech development, just like song development (Goldstein 2003).

The eavesdropping hypothesis also explains Burt et al. (2007)'s finding that juveniles learn more songs from an early tutor than its late counterpart. At the end of their experiment, juveniles selectively retain the songs from early tutors that are appropriate replies to the late tutor. Since the juveniles have a better memory for songs earlier in life, they are able to remember more appropriate replies and therefore retain more songs.

9.1.6 Conclusion

There has been much recent progress on the social aspects of song learning in songbirds. Research has shown the importance of interaction, eavesdropping, tutors, and tutor types in the song learning process. However, there is still room for much more research on topics such as song culture, dialects, imitation, maintenance, and the effects of brood size and rearing environment on song learning. Studying such topics will not only help us understand song learning in birds but also speech learning in humans.

Figure 9.6: A healthy sparrow hatchling!
http://www.megavideo.com/?v=0QNHN4JV09314>.

9.1.7 Discussion Questions

1. What are the adaptive advantages of learning of bird songs?
2. What is de novo late learning of songs and how is it different from selective attrition?
3. Why is eavesdropping the preferred method of song learning over direct interaction in sparrows?

9.1.8 Glossary

- **Adaptive trait** – a genetically coded characteristic that has evolved because of its benefits to the fitness of individuals in a species
- **Conspecifc** – pertaining to the same species
- **Countersinging** – the act of singing in response to the song of another bird. Occurs during song learning and communication
- **Eavesdropping** – observing the interaction between two other birds without being directly involved in the interaction
- **Honest communication** – a signal from one organism to another that reveals a characteristic of the sender, usually pertaining to its fitness. A sender might want, for example, to let the recipient know that it is a fast runner, so the recipient will not waste time chasing it

- **Imitation** – technique used by songbirds to copy some characteristic of the song of another bird; can be conspecific or heterospecific
- **Innate** – a characteristic that is inherently part of an organism; heritable by genes
- **Juvenile** – a young bird that has yet reached sexual maturity
- **Migratory** – describes a bird species or subspecies that participates in seasonal journeys to different regions for food, habitat, mates, etc.
- **Natal** – refers to the hatching of a bird. For example, natal summer refers to the summer a bird hatches
- **Plastic** – describes a song that is still subject to alteration; not fully crystallized
- **Sedentary** – describes a bird that is non-migratory
- **Sensitive period** – the period in a young songbird's life when the bird is particularly sensitive to songs and song learning
- **Sexual selection** – selection that works on characteristics that affects an individual's ability to obtain mates
- **Social learning** – learning a new behavior through observation of others in the learner's social environment; may involve models, imitation, and operant learning
- **Song repertoire** – the number of songs a bird has learned and uses regularly
- **Tutor** – a bird, usually an older bird, that shares his songs with another, whether knowingly or unknowingly

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9.1.10 About the Author

I am an Ecology and Evolutionary Biology and Psychology double major at Rice University (as of 2010). I like birds, especially my pet African Gray parrot, Goose (some know me as the "bird-man" in high school). Unlike juvenile sparrows, Goose can learn the vocal productions of just about any species, plus things like telephones, ice cream trucks, and, unfortunately, fire alarms. Interestingly, I have never caught Goose using birdsongs to try to gain territory status among sparrows.

Figure 9.7: A picture of me and Goose, my African Gray parrot. Goose is a bit camera shy.

9.2 Host Learning as a Defense Against Avian Brood Parasitism[2]

Author: Mary Mao

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[2] This content is available online at <http://cnx.org/content/m34735/1.4/>.

9.2.1 Introduction

Figure 9.8: Hatchling cuckoos eject the chicks and eggs of hosts.
Credits M. Honza (upper left), M. Bán (right), and C. Moskát (lower left).

Seven taxa comprising approximately 80 species of birds around the world reproduce as **obligate interspecific brood parasites**, which means that they must make use of the nests of other species of birds in order to reproduce (Sorenson and Payne 2002). Such behavior is detrimental to the fitness of the hapless hosts, frequently **passerines** or perching birds, who sacrifice part or all of their own brood when deceived by parasitic species. The high cost of parasitism has spurred an evolutionary arms race, with hosts developing mechanisms by which to recognize and reject parasitic eggs and hatchlings, and parasites developing techniques such as mimicry, or protective and deceptive imitation, and bullying to thwart such defenses. Evolution is based on costs and benefits; hosts will only learn to recognize or reject hatchlings when the potentially beneficial fitness gains outweigh costs such as erroneously rejecting the wrong eggs. One important consequence of selectively rejecting eggs, for example, is that certain parasitic birds will return to depredate such nests in what has come to be called the "**Mafia hypothesis**" (Hoover and Robinson 2007). This system of costs and balances is one of the most robust examples of **coevolution**, where related parties exert selective forces on each other to spur evolution, known to occur in the natural world.

Since many factors are involved in the success of learned behaviors, the method by which a host is parasitized greatly affects the resulting behavior; some birds are more likely to simply accept the parasitic eggs and cut losses, while others are far more discriminatory (Rothstein 1975). We focus on host responses to parasitism by the brown-headed cowbird (*Molothrus ater*) and the common cuckoo (*Cuculus canorus*). The brown-headed cowbird is a **generalist** and has been known to parasitize over 200 species of birds (Marchetti, H. Nakamura, H. L. Gibbs 1998; Friedmann and L.F. Kiff 1985). On the other hand, the common cuckoo is more of a **specialist**; although it has been known to parasitize a handful of species, each female acquires specificity to only one (Vogl et al. 2002). Selection for learned host recognition and rejection behavior is determined by a number of factors including whether host chicks remain in the nest; extent of mimicry of parasitic eggs, hatchlings, or begging; and the experience of the host breeder. We will hope to elucidate these factors for a better explanation of how host learning has adapted to selection pressure from brood parasites.

9.2.2 Body

9.2.2.1 The Basics of Avian Brood Parasitism

(a)

(b)

Figure 9.9: (a) common cuckoo
Credits: Wikimedia Commons (b) brown-headed cowbird
Credits: Wikimedia Commons

Avian brood parasites such as the brown-headed cowbird and the common cuckoo are known as “obligate” brood parasites, meaning that they must parasitize other birds in order to reproduce. They do not build nests of their own to house their eggs or raise any of their own nestlings. As a result, whether hosts choose to reject or accept parasitic eggs controls the reproduction of these species of birds.

Parasitic birds watch for opportunities to exploit hosts in the nesting season. When host birds leave the nests, they approach the nest and lay their own eggs inside. Several differences may occur at this point depending on the species of parasite, such as the time in the laying period when the parasites act and whether host eggs are eaten or ejected. The common cuckoo, for instance, pushes out a host egg before laying its own. Its young hatch before the other nestlings and eject the other eggs, monopolizing the food source. Brown-headed cowbird hatchlings, on the other hand, do not exhibit this behavior and are raised with the host's own hatchlings. These will result in different strategies by hosts in responding to reduce the costs imposed by parasitism.

Figure 9.10: Reed warbler feeding a parasitic cuckoo chick.
Credits: Wikimedia Commons

9.2.2.2 Preying Upon the Naïve

9.2.2.2.1 Evidence for Imprinting

Just as experience in humans helps us to avoid being duped, there is some evidence suggesting that experienced breeders are less likely to be fooled into accepting and raising parasitic chicks. In one of the first studies investigating breeder age, Lotem et al. (1992, 1995) introduced and removed eggs from nests of reed warblers (*Acrocephalus arundinaceus*) and then observed rejection of cuckoo eggs and artificial painted eggs.

The authors argue for a learning-based mechanism for rejection; that is, breeders memorized their own eggs through the instinctual learning process called **imprinting** in order to reject dissimilar eggs. When eggs were introduced, false eggs were accepted more often by mid-season breeders, which are younger on average than early-season breeders Replacing all of a reed warbler host's eggs rather than one, and therefore reducing the host's exposure to its own eggs, caused the naïve mid-season breeders to accept more false eggs, but had no effect on experienced early-season breeders. As further support for learning through experience, returning an original egg to the experienced early breeders prompted rejection of an entire clutch of eggs, but had no effect on less inexperienced mid-season breeders. The experienced breeders were better able to detect sudden changes in their clutches than the naïve breeders and were able to respond accordingly.

Box 9.5: An Alternative to Imprinting

A species may reject parasitic eggs by one of a number of methods. For example, the yellow-browed leaf warbler (*Phylloscopus inornatus*) accepts eggs based on size and then adjust their preferences based on variations within the clutch (Marchetti 1999). When clutches were entirely replaced with large artificial eggs, the birds would accept and incubate them. The birds would also completely accept the original eggs if they were exchanged for the batch of artificial eggs. However, the presence of even one large artificial egg resulted in its rejection. Although it is parasitized by cuckoos, this warbler has a very brief learning period since it judges based on size instead of appearance. This is opposite of the predictions by Strausberger and Rothstein, but the bird's dynamic ability to adjust preference depending on the variation between its eggs at any given time offers a distinct advantage against cuckoo eggs.

9.2.2.2.2 The Dangers of Misimprinting

Imprinting is an irreversible sort of learning that is commonly seen between nestlings and their mothers. Mallard drakes will take this farther, choosing to mate with females that resemble their mother when they become of breeding age (Kruijt et al. 1982). Problems may arise even in such situations, such as imprinting on the incorrect organism. If a mallard drake imprinted on a different species of female, he would be unable to produce offspring later on. Similarly, imprinting can be a harmful strategy for birds that imprint on their own eggs since there is always the chance of **misimprinting**, or falsely recognizing parasitic eggs as own.

Imprinting as a defense has different implications due to the different strategies adopted by the common cuckoo and brown-headed cowbird. Strausberger and Rothstein (2009) investigated the frequency at which parasitic species took advantage of imprinting by parasitizing early on before naïve birds had learned the appearance of their own eggs. Both the gray catbird (*Dumetella carolinensis*) and brown thrasher (*Toxostoma rufum*) accepted more parasitic cowbird eggs when the eggs were placed early in laying or incubation stages in areas where cowbirds were more abundant, which would also increase the frequency at which naïve birds are parasitized, suggesting that hosts were induced to misimprint. However, misimprinting increasing with parasite frequency is not observed in cuckoo hosts. Since cuckoos are host-specific rather than generalistic like cowbirds, their eggs more closely resemble host eggs and therefore select for finer tuning of recognition and rejection behavior rather than a short period of imprinting. Many cowbird eggs, on the other hand, do not resemble host eggs at all, so a short period of imprinting is sufficient to distinguish between one's own eggs and parasitic eggs (See Figure 9.11).

Figure 9.11: Brown-headed cowbird egg in a phoebe (*Sayornis phoebe*) nest.
Credits: Wikimedia Commons

9.2.2.2.3 Genetic and Environmental Components to Learning

While it is assumed that recognition behavior among hosts of brood parasites is related to genes, there is evidence that recognition has both a genetic and a learning component. Soler et al. (1999) performed a study on magpie rejection rates of cuckoo eggs and found evidence for flow of genes regulating rejection behavior between populations. Magpies living in areas where they were not parasitized by cuckoos were still able to reject cuckoo eggs, suggesting that there is some innate genetic component to host recognition that did not rely on previous exposure to selection by parasitism. However, the rejection of mimetic eggs was found to be strongly correlated with the geographic component, which would result from exposure to selective pressures. The authors concluded that while all magpies with genes for recognizing eggs could reject nonmimetic eggs, a learning process for fine-tuning was needed to explain the ability for magpies to reject mimetic eggs.

9.2.2.2.4 Not All Egg Rejection is Explainable by Learning

While authors have found evidence that experience affects the ability of host birds to reject eggs, there are other systems where learning is not a sufficient explanation for how birds reject eggs. Amundsen et al. dispute the finding that breeder age affects egg rejection rates in another species, the bluethroat (*Luscinia svecica*). Through egg replacement and return experiments, no evidence was found suggesting that that age of breeder played any role in egg rejection rates (2002). Instead, the authors postulated that differences in acceptance or rejection are better explained by the **evolutionary lag hypothesis** rather than learning. This hypothesis states that rejection is adaptive but the behavior may not yet have spread to all members of the species, which is why some will still accept parasitic eggs. Although learning may be a method that some species use to defend against parasitism, it is certainly not the only explanation for differences among individuals within a species.

9.2.2.3 Choosing when to Reject Eggs

9.2.2.3.1 Acceptor versus Rejector Strategies

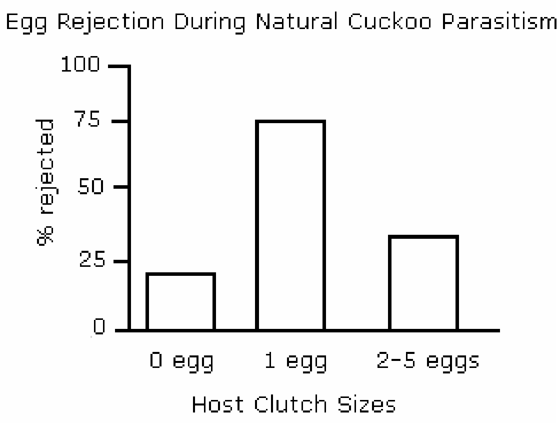

Figure 9.12: Rejection frequency of cuckoo eggs by the great reed warbler at various clutch sizes. Redrawn from Moskat and Hauber 2007.

As previously discussed, cowbird and cuckoo hosts exhibit different responses to learning their own eggs due to the specialist and generalist strategies of the two parasites. The result is that some species are far more willing to accept a parasitic egg than to reject it. Stokke et al. (2007) constructed a model to show how variation in egg appearance can affect whether a host species adopts an **acceptor** or **rejecter** approach. While acceptors accept all eggs, regardless of whether they are their own, rejecters will attempt to discriminate and reject parasitic eggs, risking misrecognition and rejection of own eggs. The model predicts that hosts that may potentially suffer greater losses from mistakes in recognition and rejection will be more likely to adopt an acceptor strategy. However, in cases where clutches have very similar eggs, hosts are more likely to reject since they are less likely to mistake their own eggs for a parasitic egg. The authors conclude that an increased learning period is more adaptive for clutches that have high variation between eggs since there is a greater risk of mistakes. A similar experiment corroborates these findings, revealing that females were much more successful at rejecting false eggs when mimicry is low and their eggs are more similar, situations in which learning one's own eggs becomes more advantageous and the cost of losing an own egg is much lower (Rodriguez and Lotem 1999).

9.2.2.3.2 The Effect of Intraclutch Variation

This dynamic ability of hosts to adjust their thresholds for egg acceptance or rejection is well-illustrated in one experiment by Moskat and Hauber (2007). Reed warblers reject cuckoo eggs more often when they had only laid one egg, but less often when several eggs or no eggs existed in the clutch (Figure 9.12). The authors hypothesized that reed warblers adjust their **acceptance thresholds**, or point at which eggs are accepted as own, based on the traits of the eggs in the clutch. When no eggs have been laid, the birds have no criteria on which to base their acceptance behavior. When only one egg has been laid, there are only a few traits that the hosts have to recognize as characteristic of their own eggs, so parasitic eggs that fall outside of this narrow range of traits are quickly rejected. However, as more eggs are laid by the host, variation between eggs results in a greater number of acceptable traits, and it becomes easier for a parasitic egg to slip in.

To protect against mistaken rejection of their own eggs, hosts expand their acceptance thresholds to allow eggs with a greater variety of traits, resulting in greater acceptance of parasitic eggs as well. As predicted by Stokke et al., greater **intraclutch variation**, a greater difference between the eggs in the same clutch, prompted hosts to accept more eggs because the costs of misrecognition and misrejection increased. As a result, the birds were more willing to accept parasitic eggs than risk the loss from rejecting their own eggs

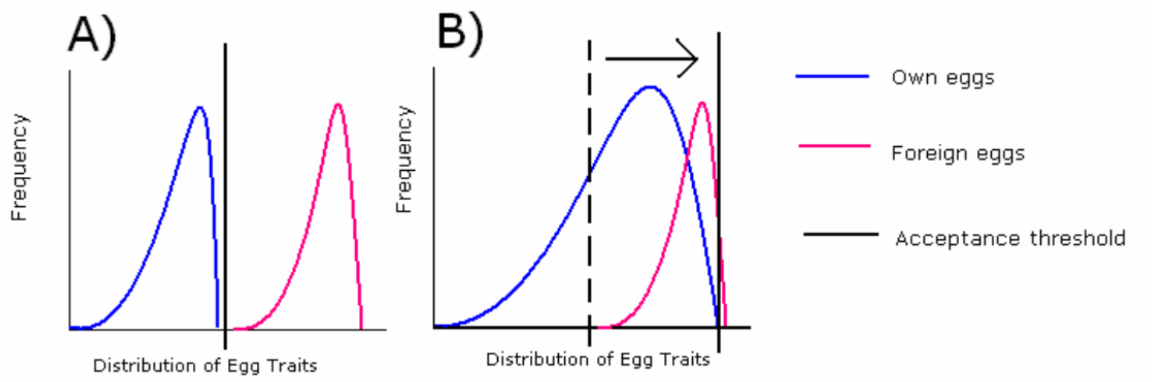

Figure 9.13: Relative trait distribution at A) one-egg and B) many egg stages of laying in the reed warbler. As more eggs are laid, the variation among eggs also increases. The birds increase their acceptance threshold to reduce costs of misrecognition if it is more likely that foreign eggs will resemble their own, which results in decreased rejection rates of parasitic eggs that once fell outside of their range of acceptable traits.
Redrawn from Moskat and Hauber 2007.

The importance of intraclutch variation in affecting the costs of mistaken recognition explains the success of another type of host bird. One species that shows great success against cuckoo eggs is the blackcap (*Sylvia atricapilla*). Within clutches, the birds' own eggs show very little variation, so rejection decisions are based on the degree of mimicry of cuckoo eggs when compared to own eggs. In this case, there is very little cost to learning to distinguish own eggs and foreign eggs, so learning to recognize and reject is adaptive (Honza et al. 2004).

9.2.2.3.3 The Effect of Parasitism Probability on Egg Rejection

The likelihood that a host will be parasitized will result in differences in frequency of egg rejection. If the threshold for accepting eggs is too low, then many of the host's own eggs will be rejected along with the parasitic eggs. However, if the threshold is set too high, then the host will accept many of the parasitic eggs, but retain its own eggs. Among reed warblers, this threshold is set depends on the stage of egg laying as described above as well as their perceived probability that the nest has been parasitized. Birds that recognized a cuckoo at their nest usually rejected an egg afterward because the probability of benefitting from rejection was much greater than if no cuckoo had been observed at the nest (Davies et al. 1993) (See also Box 9.6 (How to Recognize a Cowbird)). On the other hand, the rejection behavior of reed warblers that did not observe a parasite at the nest was best explained by the parasitism level in the area. As parasitism level decreases overall, the benefit of rejecting eggs diminishes since it is more likely that a bird will mistakenly reject its own eggs. Therefore, lower parasitism levels results in increased acceptor behavior.

Box 9.6: How to Recognize a Cowbird

While species such as reed warblers will reject eggs based on whether they see a parasite at the nest, it is unclear how host birds learn to recognize parasites. One study performed on yellow warblers (*Dendroica petechia*), a species that suffers heavily from brown-headed cowbird parasitism, found several cues that elicited defensive responses such as sitting in the nest. Female yellow warblers responded strongly to stuffed cowbirds, which had shorter bills than models that had been modified with a longer bill. The authors suggest that recognition of shape confers an advantage since parasitism usually occurs in low light conditions.

Additionally, yellow warblers respond differently to male and female cowbirds even though their physical appearances are quite similar. When female cowbird chatter and male cowbird songs were played, female yellow warblers responded much more intensely to the female vocalizations, suggesting that difference in sexes is recognized by sound.

9.2.2.4 When Learning is Hindered

As before described, whether learning is adaptive or maladaptive depends on the relative costs, benefits, and level of parasitism within a system. In many cases, the cost of mistaken recognition and rejection is too high, especially when intraclutch variation is high, so the acceptor approach is favored. One special case, explained by the **mafia hypothesis**, is one in which parasitic birds raise the costs for rejection behavior to pressure hosts into acceptor schemes (see Box 9.7 (Mafia Hypothesis)).

Box 9.7: Mafia Hypothesis

One study investigated the high levels at which the prothonotary Warbler (*Protonotaria citrea*) accepted cowbird eggs and concluded that rejection of eggs provoked retaliatory, mafia-like behavior from cowbirds. Nests which rejected eggs would later be depredated (Hoover et al 2006). In this case, the high cost of losing everything leads hosts to accept parasitic eggs, even if it reduces their own clutch sizes. In the case of cowbirds, where some of the host nestlings typically grow up in the nest with the parasites, it is to the host bird's benefit to save some of the brood by accepting the parasitic chick than to lose all chicks (see Figure 9.14).

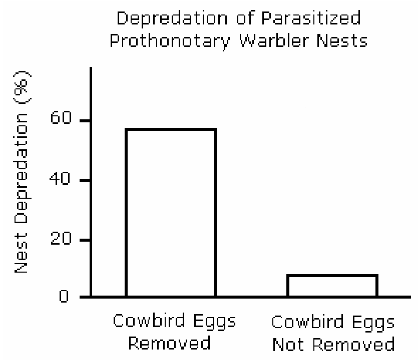

Figure 9.14

As before described, rejection behavior is less common as parasitism levels decrease because the costs of mistaken rejection increase. Laws and Marthews 2003). created a model for which learning to recognize and reject parasitic nestlings would be beneficial for cowbird hosts (2003). When parasitism levels are high, the chance of properly rejecting parasitic eggs increases as well, so the rejecter strategy is favored. Additionally, low host nestling survival when raised with parasitic nestlings increases the benefit of adopting rejecter strategies because rejection of parasitic eggs would allow more of a host's own nestlings to survive. In such cases, the benefits of choosing to reject would outweigh the costs of false rejection or accepting the parasitic eggs.

Even though rejection behavior produces a greater benefit when parasitism levels are high due to greater chance of correctly rejecting parasitic eggs, high levels of parasitism still inhibit selection for learning. Hauber et al. (2004) showed that repeated parasitism and increased costs of parasitism affect evolution of learning-based strategies simply because fewer offspring that possess the genes for learned behavior survive. One result they describe is that cowbird hosts that are smaller in size are more likely to adopt acceptor strategies. The small size results in greater costs from parasitism and fewer of their own nestlings survive. As a result, the appearance of learning-based rejection lags far behind for these smaller birds than it does for larger ones if the pressure is too high and prevents adaptive genes from surviving to the next generation.

Learning is beneficial for hosts of avian brood parasites only under certain conditions such as low parasitism rate and low intraclutch variation. Under other conditions, there may be other alternatives that are better. With the spread of many brood parasites, many previously naïve species have been exposed to the threats of parasitism and have been observed to display non-learned defenses (See Box 9.8 (Non-learned Defenses in Naïve Populations of Songbirds).)

Box 9.8: Non-learned Defenses in Naïve Populations of Songbirds

The hooded warbler (*Wilsonia citrine*), a bird that has relatively recently become a target of parasitism by brown-headed cowbirds, is significantly more responsive to stuffed cowbirds than to the stuffed veeries (*Catharus fuscescens*). Even young, naïve breeders were able to differentiate between the cowbird threat and the harmless veery, and this ability did not vary with the age of the birds. This suggests that the basis for determining the cowbird threat is not learned since age and experience seem to play no part in recognition of cowbirds, but is instead based primarily on a non-learned, genetic component. Given the short time in which the bird has served as host to cowbirds, it is likely that non-learned behavior has evolved quickly as a defense. If such behavior is sufficient to ward off parasites, then learning to differentiate between eggs may not even be necessary.

9.2.3 Discussion Questions:

1. Explain the meaning of each word in the term “obligate interspecific brood parasite.”
2. What is the difference between a generalist and a specialist brood parasite?
3. Why is the concept of coevolution important for understanding avian brood parasitism?
4. How have imprinting experiments demonstrated learning among host birds?
5. What is an explanation for rejection behavior that is not based on learning through experience?
6. Explain a situation in which parasitic birds have been known to exploit defensive imprinting.
7. Describe how experimenters have shown unlearned defensive strategies against parasitism.
8. Explain how costs and benefits affect whether birds adopt an acceptor or rejecter strategy.
9. What is the response of birds to different levels of intraclutch variation, and why is this adaptive?
10. How do levels of parasitism affect adopted acceptor/rejecter strategies?
11. Explain how the Mafia Hypothesis explains the importance of cost in rejection decisions by hosts.
12. How do levels of parasitism affect the selection for learning-based defenses?

9.2.4 Glossary

- **acceptor**- In terms of avian brood parasitism, a strategy of response to foreign eggs in which a species always accepts parasitic eggs. This usually occurs when the cost of mistaken recognition and rejection are high, so it is more advantageous to accept all eggs.
- **rejecter**- In terms of avian brood parasitism, a strategy of response to foreign eggs in which a species attempts to distinguish parasitic eggs from its own eggs and then reject them. In cases where the risk

of mistake are low, such as in species with low intraclutch variation, learning to reject foreign eggs is favored even at low levels of parasitism.

- **obligate interspecific brood parasite**- A species of bird that must parasitize nests of other species in order to reproduce. Brood parasites fool host birds into accepting their eggs and then raising the young as their own.
- **passerine**- A member of the order Passeriformes, which comprises a number of small perching birds. This group makes up a majority of bird species.
- **coevolution**- a system of interactions in which multiple parties exert selective forces upon each other and drive each other's evolution.
- **mimicry**- an imitation of something for purposes of protection or deception. In this context, parasitic birds have varying levels of egg mimicry; while cuckoos can have highly mimetic eggs, cowbird eggs can be extremely different from their hosts.
- **acceptance threshold**- the point at which eggs satisfy a host bird's criteria for "self" eggs and are accepted
- **intraclutch**- characteristic of eggs that were laid in the same clutch. For example, intraclutch variation refers to the extent to which eggs laid in one clutch vary from each other.
- **mafia hypothesis**- Sometimes, when hosts reject eggs, the parasitic birds return to depredate nests. The cost prompts some hosts to adopt an acceptor approach as it is better to accept a few parasitic chicks than to lose everything.
- **generalist**- In this context, a species of bird that parasitizes many different species of hosts, such as the brown cowbird.
- **specialist**- In this context, a species of bird that parasitizes specific hosts. The common cuckoo's females each specialize on a certain species of host, though each female's preference may be different.
- **evolutionary lag hypothesis**- Hypothesis on why some birds in a species adopt acceptor strategies while others adopt rejecter strategies. It states that rejection is always adaptive but the behavior may not yet have had enough time to become fixed within the species, which is why some will still accept parasitic eggs.

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9.2.6 About the Author

Figure 9.15

Mary Mao grew up as the daughter of immigrants in the small town of Oxford, Mississippi. It was in this rural setting that she was first exposed to wildlife in the surrounding woods and forests and became interested in the ecosystems in which local fauna and flora. She now resides in Houston, Texas as an undergraduate at Rice University majoring in Biochemistry and Cell Biology and hopes to attend medical school after graduation in spring 2010.

9.3 Sex Differences in Learning Processes of Rats[3]

Author: Vanessa Lippay

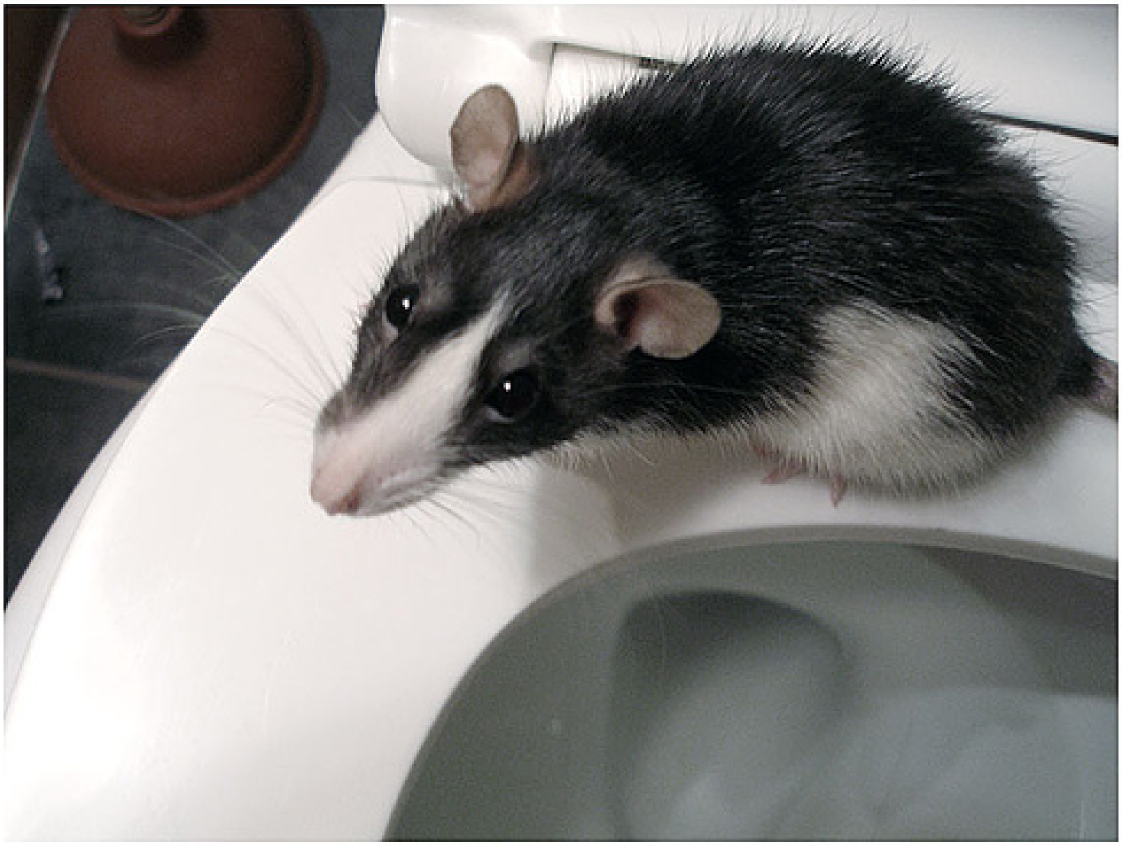

Figure 9.16: Photo courtesy of Flickr and Big_Fat_Rat

9.3.1 Introduction

Rodents share many features at the anatomical, cellular, biochemical, and molecular level with humans. The rat (*Rattus norvegicus*[4]) is a particularly useful as a neurological model and source of primary cell cultures because of their relatively large organs and suborganellar structures. Also, the rat shares similar brain functions to humans, such as anxiety, hunger, circadian rhythm, aggression, memory, sexual behavior and other emotional responses (Beatty, 1979). Therefore many studies use rodent models to approximate human behavioral responses under physiological and pathological conditions.

Differences between male and female non-reproductive behaviors in rodents have been frequently observed in laboratory studies. Among the behaviors that are sexually dimorphic in the rat are activity, aggression,

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[3] This content is available online at <http://cnx.org/content/m34748/1.3/>.

[4] http://www.wordiq.com/definition/Rattus_norvegicus

pain, taste sensitivity, food intake and body weight regulation, avoidance responses, taste aversion, performance on certain schedules of reinforcement, and the learning and retention of information relevant to certain kinds of mazes (Beatty, 1979).

The standard for measuring spatial learning and memory ability in mammals is the **Morris water maze (MWM).** This maze requires subjects to use the spatial arrangement of objects or cues outside of a circular pool to find a submerged goal platform located in a fixed location in the pool. It is presumed that with repetition rats learn to find the platform by remembering the visual cues surrounding the pool (Perrot-Sinal, 1996). Created 20 years ago, the MWM is currently one of the most frequently used laboratory tools in behavioral neuroscience.

Learning in spatial tasks takes place via two strategies, **denominated taxon** and **local strategies**. In denominatedtaxon, the animals always begin in the same location and learn to reach the end location by repeating the same set of movements each trial. When using localstrategies, the animal moves directly to the target location from any starting position guided by distant cues outside of the maze (Cimadevilla, 1999). Memory and spatial learning can also be divided in rodent models into working versus reference memory. Reference memory is similar to local strategies, and depends on the recall of a set of static objects that can then be referred to. Working memory occurs when objects are mobile or exhaustible, this type of memory requires the ability to update and retrieve information (Puts, 2007).

Spatial learning in general and MWM performance in particular appear to depend upon the coordinated action of different brain regions and neurotransmitter systems (D'Hooge, 2001). Gonadal hormones also seem to be responsible, in part, for behavioral sex differences, but their contribution varies greatly with the particular behavior (Beatty, 1979).

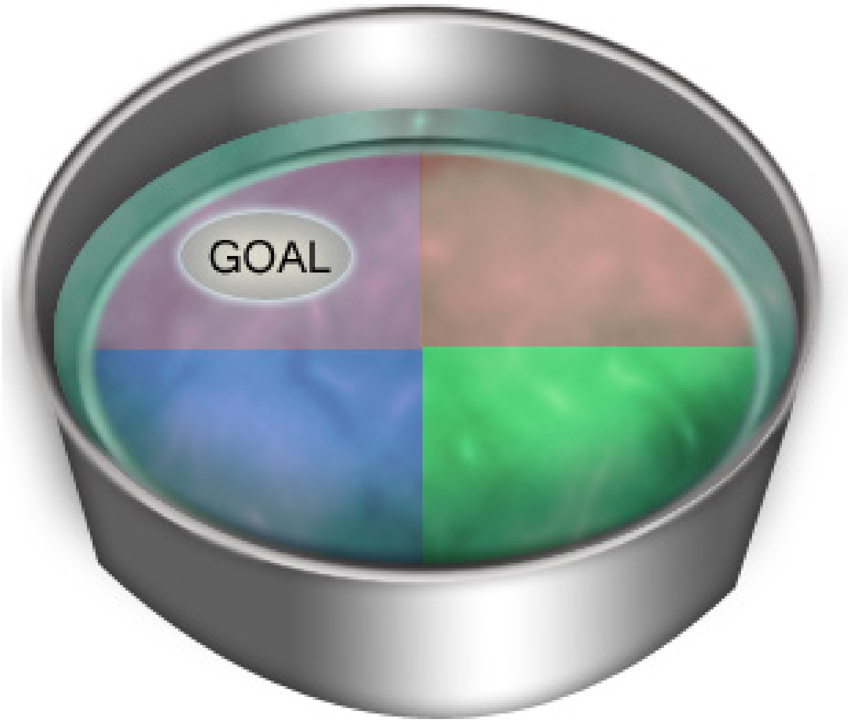

Figure 9.17: The Morris Water Maze (MWM) is commonly used to test spatial learning and memory in rats. Mice are dropped at selected locations on the outside edge of the pool and must locate a submerged goal platform on which a visual cue is placed. In later trials, the cue is removed and rats must locate the goal platform using visual cues outside the pool.
Original image http://www.biochemj.org/bj/389/0593/bj3890593f12.htm[5]

9.3.2 Observed Sex Differences:

Males and females of most sexually reproductive species learn and retain information differently throughout their lives. These differences have been observed in many species, from invertebrates to humans. As discussed earlier, rats are a common test animal that we believe to exhibit behavior similar to humans. Thus, many of the assumptions we have about learning processes are based on experiments using rat models.

As discussed in the introduction and in Box 9.9 (Hippocampal Activity), males typically perform better on spatial learning tasks. Sex-differences in learning also occur in a variety of other learning paradigms. Dalla (2009b) focuses on classical and operant conditioning paradigms, including classical eyeblink conditioning, fear-conditioning, active avoidance and conditioned taste aversion. This chapter will explain each paradigm in detail and outline some of the more influential work done in the field. These sex-differences have been explained in terms of physiological, hormonal, and role differences between male and female rats.

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[5] http://www.biochemj.org/bj/389/0593/bj3890593f12.htm

9.3.2.1 Sex Differences in Classical Eyeblink Conditioning (CEC):

The **Classical Eyeblink Conditioning paradigm** is a task which employs the **denominated taxon**strategy, and requires the learning of arbitrary associations between a set of stimuli and a set of responses. In most set-ups, animals are conditioned to blink following a sound, or conditioned stimulus. To teach this behavior, stimulation of the eyelid is given immediately following the noise and causes the animal to blink (unconditioned, automatic response). Over time, the subject learns to blink as soon as he hears the noise, regardless of whether the stimulation occurs. This is the conditioned response (Dalla, 2009b).

A variation of this procedure is *trace conditioning* in which the stimulus and response are separated by a longer interval of time. Trace conditioning is directly related to hippocampus activity (discussed later). Sex differences can also be observed through *delay conditioning* in which the conditioned stimulus and the conditioned response overlap and the response does not depend on the hippocampus (Dalla, 2009b).

During both trace and delay conditioning, females performed better than males. Females learn to blink with less training and, on average, blink more quickly after the conditioned stimulus than males. After a few days of training, however, both sexes reached the the same level of performance, suggesting that the sex difference is present in the learning process and not in the ultimate performance ability. Perhaps the most convincing evidence for female performance superiority in the CEC paradigm is that females that were trained and then re-exposed to the stimulus weeks later responded with the correct conditioned response more often than males did. Thus, females were able to retain information longer than their male counterparts (Dalla, 2009a).

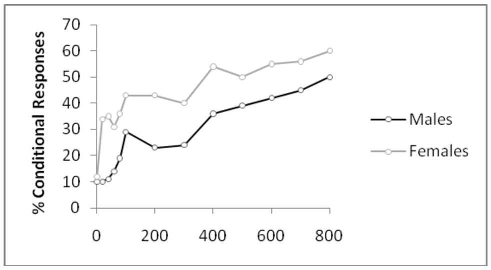

Figure 9.18: Females outperform males in classical eyeblink conditioning (CEC) in which a conditioned stimulus (CS) of white noise is paired with an unconditioned stimulus (US) to cause an eyeblink response. Females emit more conditioned responses than males during trace CEC. In this experiment, rats were trained with 200 trials/day of trace CEC for 4 days. The sex difference is significant during the first two days of training.
(reproduced from data in Dalla, 2009a)

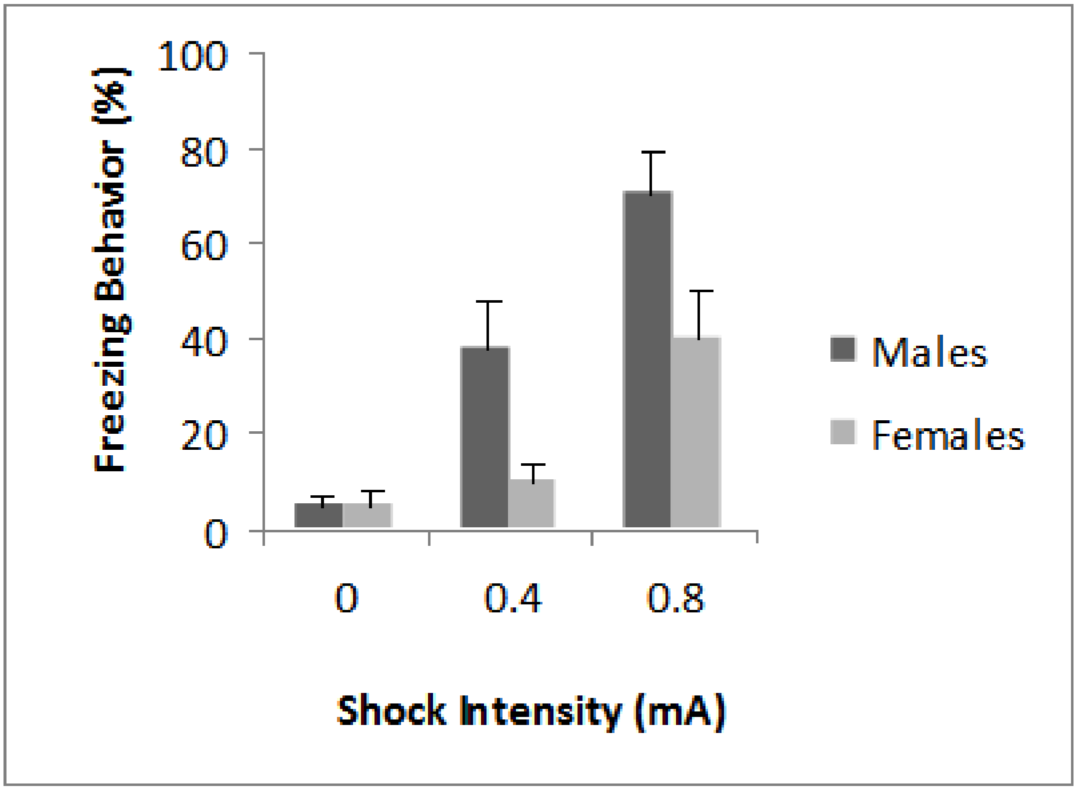

Figure 9.19: This graph shows the mean percent freezing behavior in adult male and female rats in each of three foot-shock conditions during an 8-min test. Males showed significantly more freezing than females in both the high (.8mA) and low (.4mA) shock groups. There was no significant difference for the un-shocked group.
(Reproduced from data in Maren, 1994)

9.3.2.2 Sex Differences in Fear Conditioning:

Fear conditioning resembles CEC in that during both paradigms learning occurs in response to an aversive stimulus. During fear conditioning, however, the animal learns to associate a particular contextual cue with the aversive stimulus, usually a foot-shock, and when they receive the cue they remember and prepare for the stimulus. This preparation typically consists of freezing in place (Dalla, 2009b). This type of experiment is carried out in a set up similar to the one shown in Photo 2 which is sound and light-proof to avoid environmental distractions. Generally, male rats demonstrate more spontaneous anxiety/fear in situations that are innately aversive, for example, males defecate more and move less in open fields, tend to enter and explore novel environments less frequently, and freeze more in response to unfamiliar sounds than females (Pryce, 1999).

Pryce (1999) studied the sex differences in responses to the fear-conditioning paradigm. He studied three different strains of rats; Wistar, Fischer, and Lewis. Males and females of each strain were trained to recognize an auditory cue that signaled foot shock. Freezing time was recorded for the initial training day, for a second day of cue and shock, and a third day in which the cue was given without shock. He found that female rats responded to the cues less frequently, in other words they froze less when they received contextual cues. On day one, all strains showed no sex-difference in percent of freezing. In later trials, male Fisher and Lewis rats exhibited significantly more freezing behavior , and Wistar males approached significance on the last trial (auditory only) (Pryce, 1999). This study showed some variation among different rat strains in fear conditioning and learning retention, but the general idea that males freeze more often holds true.

Several studies have concluded that the limbic structures, the amygdale and hippocampus, are important in fear conditioning (See Box 9.10 (Age Impairment)). Associative long-term potentiation (LTP) has been proposed as the synaptic mechanism responsible for acquisition of fear conditioning in adult rats (Maren, 1994). This study, and others, shows that males have a higher magnitude of hippocampal LTP than females (Pryce, 1999).

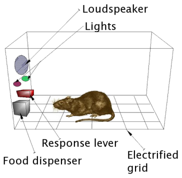

Figure 9.20: *The Skinner Box* is sometimes used in experiments dealing with fear conditioning or operant conditioning. In this picture, the loudspeaker or the lights can provide a cue, which alerts the rat that the aversive stimulus is coming during fear conditioning. During operant conditioning, the response lever can be used to avoid the foot shock.
Photo courtesy of Wikimedia and Andreas1.

Box 9.9: Hippocampal Activity

Although the exact mechanisms are unknown, it is thought that the synaptic flexibility during formation of the hippocampus contributes to the formation and retention of memories (Leurner, 2006). Hippocampal activity has been shown to differ between males and females, particularly in rodent species.

In a wide range of mammals, the dentate gyrus in the adult hippocampus produces a large number of new neurons in a process called **neurogenesis** (Leurner, 2006). This production is reduced by stressful experiences such as predator scents, social dominance, maternal deprivation, and mild foot-shocks (Shors, 2007).

Because treatment with antidepressants, such as Prozac (fluoxetine), increases neurogenesis in the hippocampus (Shors, 2007) and the volume of the hippocampus is less in depressed patients relative to normal patients (Neumeister, 2005) it is believed that the hippocampus is directly related to depression and learned helplessness.

Learned helplessness is one way animals express depression. Shors et al (2007) studied the connection between neurogenesis and learned helplessness in the rat model. They found that in males, but not females, the ability to control the stress increased hippocampal activity and thus reduced helplessness behavior.

9.3.2.3 Sex Differences in Operant Conditioning:

Operant conditioning occurs when an animal must make a deliberate response in order to learn. Usually, they learn to avoid a stimulus such as the foot shock discussed in the previous section. Dalla and colleagues (2008) used a one-way avoidance task where rats had to pass through a doorway once to avoid shock. Although rats are able to learn this task on the first day of training, females learned to escape sooner than males (Dalla, 2008).

Shores *et al* (2007) used the same one-way avoidance task to test hippocampal activity (see Box 9.10 (Age Impairment)) and learned helplessness in rats. Two groups of rats were placed in shock-chambers in which one group could escape and avoid the foot-shock (controllable stress group) and one group could escape but could not avoid the foot-shock (uncontrollable stress group). Both groups were then put in new chambers where escape was possible. In this new learning situation, male and female rats that were previously in the controllable stress group were able to learn to avoid the foot-shock quickly. For those previously in the uncontrollable stress group, however, male rats expressed **learned helplessness** more frequently than females (Shores, 2007). Learned helplessness is a behavior that occurs when an individual is places under uncontrollable stress and learns that escape is not possible. Thus in new learning tasks they move less and either take longer to learn to escape or cannot learn to escape at all (Shores, 2006). This type of behavior, then, is associated with an inability to learn future tasks that require movement.

Even larger sex-differences tend to emerge when facing more difficult operant conditioning tasks. A two–way avoidance task was used in Dalla's study (2008) in which rats had to pass though the doorway twice to avoid shock (controlled stress). During training, rats were coupled to another rat that was shocked regardless of completion of the task (uncontrolled stress). When males were exposed to the new, more difficult task, most males trained under uncontrollable stress took longer to learn to escape, and thus exhibited learned helplessness. In some cases, males would not return to the place they received their first shock and thus could not pass through the doorway twice and never learned to avoid the shock. In contrast, females were able to learn to escape the novel task relatively quickly, regardless of the prior type of stress they were exposed to (Dalla, 2008).

Studies have also shown that females will retain escape information longer than males. Van Haaren (1990) showed that females placed in the shock chamber without any shock presentation escape sooner than males. This suggests that extinction of the learned behavior is slower to occur in females.

Sex differences in operant conditioning are at least partially related to differences in performance. Averse stimulation caused female rats to respond actively while male rats typically froze in place which inhibited escape (Dalla, 2009). Females also are generally more active (Hyde, 1983) and more sensitive to shock (Van Haaren, 1990) than males, which may result in their passing through the doorway before males and an increased incentive to figure out how to escape the shock.

Box 9.10: Age Impairment

Barret *et. al.* (2009) examined the effect of age on spatial learning for female Sprague-Dawley (an outbred strain) and male and female Dark Agouti (an inbred strain) rats. Rats at 6, 11, 14, 17, 20, and 26 months of age were tested for performance. The trials consisted of 3 trials/day for 10 days and performance was based on the ability to reach criterion, which was classified as less than 2.5 errors/trial average on any single day of testing.

Barnes maze vs. MWM:

The MWM has been criticized because rats are submerged in water causing high stress levels and it requires a high level of physical fitness, which is detrimental to aging rat performance.

Instead, the Barnes maze places subjects on an open, unprotected circular platform where they have to find the correct escape hole on the edge of the platform (see photo below). Since the hole is relatively easy to find, it is important that un-trained subjects cannot see previous trials and that the platform is thoroughly cleaned after each trial to avoid visual cues on the platform that would alert the subject to the correct escape hole.

Age and Performance:

At six months, all rats reached the learning criterion. For AD males, performance impairment began at 11 months. DA females experienced performance impairment at 14 months, and SD females experienced impairment at 17 months. The oldest groups was tested at 26 months, and at this age only 70% of SD females, 33% of DA females, and 57% of DA males reached criterion.

In all groups, the percentage of non-learners increased with age, but substantial strain and gender differences were present, highlighting the potential error of comparing age data for different groups (Barret, 2009).

Figure 9.21: Photo courtesy of Wikimedia and Bd008

9.3.2.4 Sex Differences in Conditioned Taste Aversion:

In conditioned taste aversion, animals are fed a novel sweet solution which either contains an aversive compound which makes the animal ill or an aversive compound is administered immediately after the animal consumes the solution. Eventually, animals learn to associate the solution with illness and avoid it (Dalla, 2009).

Randall-Thomson (2003) performed conditioned taste aversion on rats using morphine and lithium chloride (LiCl) as the aversive compound. Each day, liquid-deprived subjects were given a 20 minute access period to a saccharine solution and every four days were injected with either morphine or LiCl, for a total of four trials (16 days). Acquisition of the aversive behavior did not differ by sex, and both males and females typically learned to avoid the solution by the fifth day. Memory extinction rates were then measured for this learned behavior. Although the rates did not differ between males and females for morphine, the female LiCl-induced rats went back to the saccharin solution sooner than males. This suggests that females forget learned taste aversion before males (Randall-Thompson, 2003).

Male Rats Perform Better:	Female Rats Perform Better:
In the Classic Fear-Conditioning Paradigm	During Classic Eyeblink Conditioning(in both trace and delay conditioning)
In certain lever-pressing paradigms (positive stimuli operant conditioning)	In fear-potentiated startle
In Conditioned Taste Aversion	On most operant conditioning tasks (including Active Avoidance)
On Spatial Learning Tasks (MWM)	In Spatial Memory Tasks

Table 9.2

9.3.3 Hormonal Differences

Although the non-reproductive effects of gonadal hormones have been given significantly less attention than the reproductive effects, the magnitude of sex-differences in some learned responses seems to be heavily influenced by sex hormones. It appears that testosterone, typically present in higher levels in males, has little effect on sex-differences. Estrogen, a typically feminine hormone, does play some role. For example, the difference in performance between male and females in CEC is greater when females begin training in **proestrus**, when estrogen levels are high (Dalla, 2009).

In both CEC and fear conditioning, although castration of adult male rats does not alter the conditioned response, removing the ovaries of adult females did. Research suggests that removal of the ovarian tubes, and thus of female-specific hormones, can reduce the learning bias, causing ovariectomized females to perform at the same level as males (Gupta, 2000, Wood, 1998). The differences could not be re-established by administering normal doses of estrogen to females who had the ovaries removed, although very high doses did increase performance (Gupta, 2000, Leuner, 2004). However, some studies show that removal of the ovaries in females and castration in males has no effect on the learning differences (Dalla, 2008). It is only fair to note that it is highly unlikely that there can be a total dependence of basic learning processes on one or even a few hormones. The adaptive value of learning is too great. Because males and females of all species undergo drastic changes in sex hormone availability throughout their lifetime, learning cannot be exclusively influenced by hormone levels.

Box 9.11: Hormonal-Based Learning Differences in Humans

As in rodents, early androgens appear to masculinize spatial ability in humans (Puts, 2007).

In one study, second-trimester testosterone levels correctly predicted spatial abilities when girls were 7 years old (Grimshaw, 1995). And another study showed that girls with male twins had better spatial ability, presumably because she was exposed to her male twin's androgens during development (Cole-Harding, 1988).

Further evidence for the hormonal role of sex-differences in humans comes from analysis of sex-atypical hormone conditions. Patients with Turner syndrome are phenotypically female, but lack part of their X chromosome. These girls have undifferentiated gonads which lead to extremely low androgen and estrogen levels. Patients with TS express impaired visual-spatial and perceptual abilities, attention, working memory with normal verbal function. Pubertal androgen and estrogen replacement hasn't been shown to successfully restore these deficits, so it is believed that early androgens are necessary to later organizational effects (Ross, 2006).

Patients with congenital adrenal hyperplasia (CAH) over-produce androgens from the adrenal glands. Studies have found that girls with CAH tend to exhibit masculinized spatial abilities (Hines, 2003).

9.3.4 Evolutionary Explanation

In the study of sex differences in learning ability, functional, phylogenetic, developmental, and proximate explanations have made complementary contributions to our understanding of a behavioral sex difference. But, it wasn't until 1986 that the first paper that attempted to explain why sex differences in the hippocampus have evolved (Puts, 2007). The idea of non reproductive sex-differences causes problems with Darwin's theory of natural selection, because males and females of the same species should theoretically be sharing the same environments, eating the same foods, being preyed upon by the same predators and risking the same diseases. Where skewed sex-ratios or different maximum reproductive potential between the sexes can explain the emergence of sexually-selected, within-species, traits such as bright plumage or antlers to attract a mate, spatial learning differences aren't as easily explained.

An evolutionary model of spatial learning sex-differences must include two assumptions. First spatial ability is fundamentally a navigational adaptation; animals will be able to navigate better if they can acquire and manipulate data on the location or risks and rewards in an environment. Sex-differences will only occur in species in which males and females exploit the environment differently, for example if only one sex leaves to forage, hunt, or reproduce while the other remains in a smaller home range. The second assumption is that an increase in spatial learning ability comes with some cost to its recipient. Energy is required to travel further and the risk of predation is greater. Without costs, there would be no reason that both sexes wouldn't acquire the same trait (Gaulin, 1992b).

Gaulin (1992b) explains that to discuss this evolutionary theory, we must first recognize that spatial ability effects reproductive success. Currently, the 'mating system hypothesis' is the most widely-accepted explanation for these sex differences. Because the spatial organization of animal populations depends on the mating system of that species, differences in mating systems lead to differences in spatial learning. In monogamous species, pairs situate themselves apart from other pairs and both sexes experience similar environmental risks and rewards. In polygamous species, one sex orients itself apart from other same-sex individuals, similar to monogamous pairs, while the opposite sex travels from mate to mate. Therefore, in species where one sex has a much larger range to forage, hunt, or mate than the opposite sex, that sex should acquire some navigation advantage (Gaulin, 1992b).

In the rodent model, it is fairly clear that laboratory rats and polygynous species of wild rodents show a distinct male advantage on various types of maze tasks. This increased male spatial ability contrasts the absence of sex-differences in monogamous laboratory mice and monogamous wild rodent species (Puts, 2007).The hippocampus, a brain structure important for spatial processing, shows similar sex-differences that support this mating system hypothesis(see Box 9.10 (Age Impairment)). The hippocampus of male and female monogamous rodent species are typically the same size while in polygynous species, males have been found to have a significantly lager hippocampi (Puts, 2007).

9.3.5 Conclusion

When looking at non-reproductive sex differences in any species, behavior is normally quantified as the frequency of the behavior or the level of performance and not the ways the actions are performed by different test groups or individuals. Trying to record differences in the physical actions performed would lead to subjective data collection based on the researcher's observations and make it nearly impossible to standardize results between experimenters. It must also be noted that in learning experiments even a small amount of methodological variety can exaggerate or weaken the results. This makes reproduction of experiments difficult and weakens the validity of claims made in many of the articles I have discussed. Because of these methodological difficulties, there have been many debates over the legitimacy of rat-learning experiments and the learning processes involved.

Sex differences have been reported during acquisition, retention and loss of information in most of these paradigms. In general, female rats perform better than males in the classical eyeblink conditioning, in fear-potentiated startle and in most operant conditioning tasks, such as the active avoidance test. However, in the classical fear-conditioning paradigm, in certain lever-pressing paradigms and in conditioned taste aversion, males outperform females or are more resistant to memory extinction (Dalla, 2009). Although females expressed less learned helplessness, females may respond more negatively to stressful situations. A type of wall hugging behavior, called **thigmotaxis**, is often seen when an animal is introduced to a new (and potentially risky) environment. Perot-Sinal *et. al (*1996) showed that during water-maze tasks, female rats displayed more thigmotaxis, thus took longer to find the hidden platform (which is usually not near a wall) and performed less successfully. This sex difference was more pronounced at the beginning of training (Perrot-Sinal, 1996).

According to evolutionary theory, the development of sex-differences in spatial ability can be predicted in species in which one sex's range is different from the other sex's range. This model holds for polygynous rodent species (including the laboratory rat), primates, and humans, to name a few. In such ancestrally polygynous species such as our own, males evolved to have higher working memory in order to find and remember the moving and depleting resources over larger ranges that are associated with hunting while females evolved to have a higher reference memory that allowed them to find static resources associated with gathering.

9.3.6 Discussion Questions

1) Why do scientists believe that spatial learning is more developed in males than females? How can we test this?

2) Can you think of some selective reasons why females perform better in the CEC memory retention, most operant tasks, and spatial memory tasks?

9.3.7 Glossary

- **classical eyeblink conditioning (CEC) paradigm** – a procedure in which an animal is exposed to a noise which is immediately followed by an aversive stimulation to the eyelid which causes the animal to blink; the animal eventually becomes conditioned to blink when it hears the noise, with or without the aversive stimulation (Dalla, 2009)
- **denominated taxon** – a learning strategy that involves repetition, animals remember and repeat the same set of movements to reach a goal
- **estrus**- The periodic state of sexual excitement in the female of most mammals, excluding humans, that immediately precedes ovulation and during which the female is most receptive to mating; heat.
- **learned helplessness** – this occurs when a subject learns that escape from an negative stimulus is impossible; the subject will move less and will have difficulty learning new escape strategies in new tasks
- **local strategies** – a learning strategy in which animals learn how to reach a goal through environmental, visual cues that surround the test site (for example the MWM)
- **Morris water-maze (MWM)** – most commonly used method to study spatial behavior, subjects are put into a pool of water and learn to find a non-visible platform using spatial cues around the platform; the water is typically made opaque with dye or beads so the animal cannot see the escape platform
- **neurogenesis**–the production of new neurons
- **operant conditioning** – a task in which an animal must make a response to learn; often they learn how to avoid or escape an aversive stimulus, such as a mild foot shock
- **polygynous**- a mating pattern in which a male mates with more than one female in a single breeding season
- **proestrus-** The period immediately before estrus in most female mammals, characterized by development of the endometrial and ovarian follicles
- **thigmotaxis** – a behavioral response when introduced to a new, possibly dangerous, environment that is best described as "wall-hugging"

9.3.8 References

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9.3.9 About the Author

Figure 9.22

Vanessa Lippay was born on March 23, 1988 in Shamokin, Pennsylvania. There, she lives with her two parents, her younger brother, and three dogs. She received her undergraduate degree in 2010 from Rice University in Houston, Texas where she studied Ecology and Evolutionary biology and earned a B.A. in Biosciences. She plans on attending graduate school in the fall to obtain a Masters Degree in either Biology or Biomedical Sciences and eventually plans on going to medical school to become a physician. Her interests include film, her dog Bruce, dance, and travel.

Chapter 10

Foraging

10.1 Foraging in the Domestic Pig, Sus Scrofa[1]

Author: Arielle Layman

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[1] This content is available online at <http://cnx.org/content/m34730/1.3/>.

10.1.1 Introduction

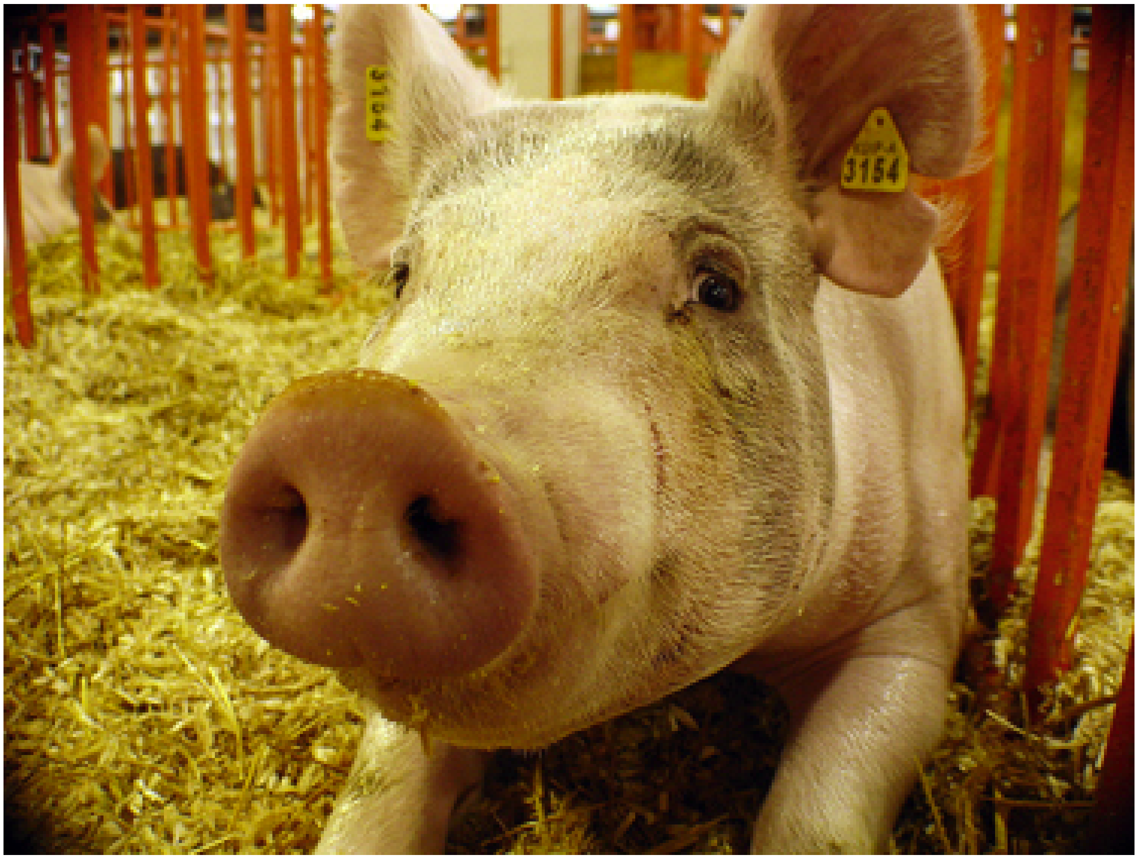

Figure 10.1: A domestic pig, *Sus scrofa*. Creative Commons-Licensed <http://www.flickr.com/photos/fleur-design/428341583>

Optimal foraging theory uses theories of natural selection to interpret organisms' feeding strategies. It predicts that animals that maximize caloric intake while minimizing costs will increase their fitness (Stephens, 2007). When applying the theory to an organism, three factors, which are called assumptions, must be considered:

1. Decision Assumptions
    a. What is the organism's goal in foraging? For example, is it looking to maximize nutrient intake or prevent starvation?
2. Currency Assumptions
    a. How will the organism compare choices?

3. Constraint Assumptions
    a. What limits does the organism face? For instance, what is available and what is safe to eat? (Stephens, 1986)

The predictions of optimal foraging theory vary greatly depending on the organism studied. An herbivore may have to weigh the risk of being preyed upon while against the nutritional benefit of the food. A carnivore may have to choose between a high-risk high-gain scenario, such as attacking large but difficult to subdue prey, and a low-risk low-gain scenario, such as consuming easy to attack but less substantial prey. Optimal foraging theory can therefore be divided into two main questions: how long should an herbivore stay in a food patch and which prey should a carnivore consume? (Stephens, 1986).

Often, a forager's decisions are dependent on those of another forager, and **social foraging** theories apply. For example, a bee may perform a dance to show its hive the location of nectar (Kamil, 1987) or predators may hunt in packs (Giraldeau, 2000)

The domestic pig, *Sus scrofa domestica*, is an interesting organism to study in the light of optimal foraging theory. It is an omnivore that faces few constraints—it is preyed upon by few predators and has a varied diet— so it has many foraging options (Watson, 2004). Comparing its behavior to its undomesticated predecessor, the wild boar (*Sus scrofa*), provides a unique perspective on the evolution of foraging.

Box 10.1: What are some criticisms of optimal foraging theory?

When optimal foraging theory emerged in 1966, it was highly controversial and stayed that way for years. Many criticisms of the theory centered on use of the word "optimal". Opponents of the theory claimed that as a result of trade offs in natural selection, behavior can never truly be optimal (Gould, 1979). Others asserted that optimal behavior would require animals to achieve a high level of intelligence to determine the consequences of their foraging actions (Stephens et al., 2007). Early on, the most damaging criticisms were that optimal foraging theory either had not been tested sufficiently, or that it had been tested and failed (Perry and Pianka, 1997).

Proponents of optimal foraging theory responded in several ways. When the theory was most controversial, researchers continued studying it but did not use the word "optimal" in their work (Perry and Pianka, 1997). Stephens et al. explain that an animal does not need to understand its own foraging behavior for it to be optimal, just as a baseball player does not have to understand physics (2007). Most importantly, numerous studies, including some mentioned in this chapter, have upheld the predictions of optimal foraging theory.

10.1.2 How have natural and artificial selection shaped pigs' foraging strategies?

Humans domesticated pigs over 8,000 years ago (Mignon-Grasteau et al., 2005). Although the domestic pig and its ancestor the wild boar are vastly different in appearance (Figure 10.2 and Figure 10.3), few behavioral differences between the subspecies have been found (Gustafsson, 1999b). For more about domestication, see Box 10.2 (What is the relationship between domestication and natural selection?).

Gustafsson et al. examined foraging differences between domestic pigs and crossbred pigs, which had one domestic parent and one wild parent. The pigs foraged in a maze containing buckets with a limited amount of food to model gradually depleting patches. In some conditions, the researchers put barriers between patches in order to induce a cost of moving from one patch to another. They made three predictions based on optimal foraging theory: that pigs would adjust their foraging strategy as food in a patch was depleted by spending less time in that patch; that pigs would spend more time in each patch when there was a cost associated with moving between patches, and that wild boar hybrids would move between patches more frequently and spend less time in each patch, using a costlier strategy. (Gustafsson, 1999a)

Figure 10.2: Top: A female domestic pig and her piglets. Creative Commons- Licensed <http://commons.wikimedia.org/wiki/File:Sow_and_five_piglets.jpg>.
Bottom: A female wild boar and her piglets. Creative Commons- Licensed <http://www.flickr.com/photos/j-pocztarski/3456321271>

Each prediction is based on the main tenet of optimal foraging theory: that animals minimize costs and maximize food intake while foraging. Domestic pigs were expected to use a less costly strategy because through the process of domestication, costly strategies are selected against (Jensen and Gustafsson, 1997). A costly strategy that involves moving frequently between patches may be beneficial in the wild because it reduces the chance of being caught by predators. Under the protection of humans, this strategy would not be advantageous because it would cause the pigs to expend energy moving when they were not in danger of being caught by predators.

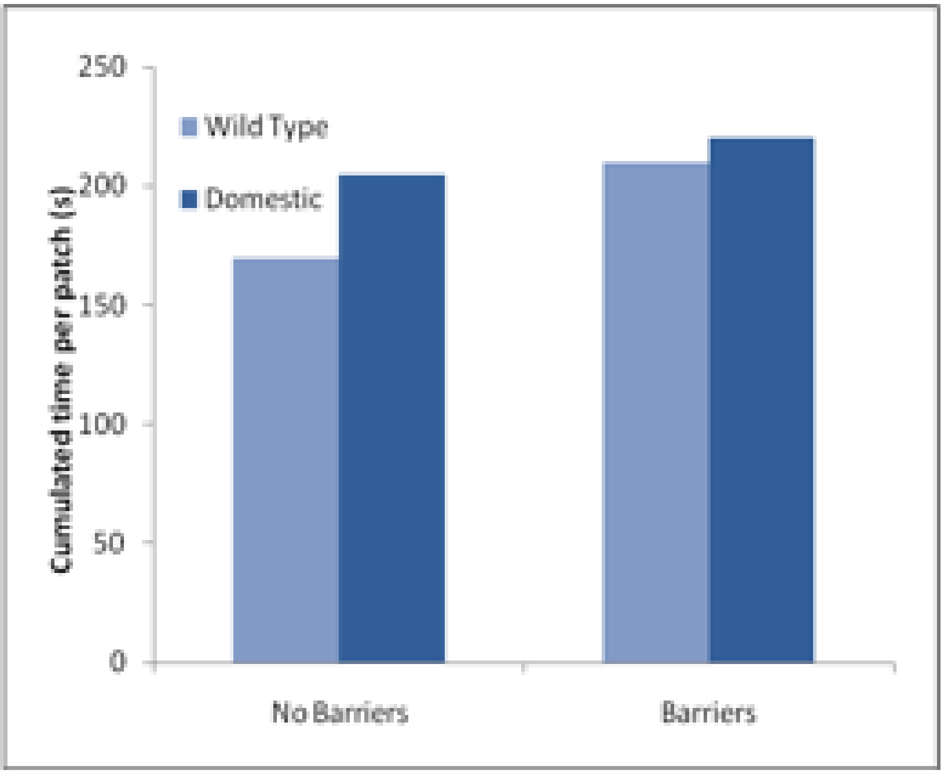

Figure 10.3: After Gustafsson et al., 1999.

Gustafsson et al.'s data support their hypotheses. Domestic and crossbred pigs' behavior followed optimal foraging theory. Both groups spent less time in patches with less food and visited fewer patches when there was a cost to move to a different patch. As predicted, the crossbred pigs used a costlier foraging strategy by moving between patches more frequently than the domestic pigs (Figure 10.3).

The finding that domesticated animals use a less costly foraging strategy than wild ones is not limited to pigs—for example, it has been found in comparisons of domesticated and crossbred chickens (Andersson, 2001; Schutz, 2000)—and may be characteristic of the domestication process (Jensen and Gustafsson, 1997).

Box 10.2: What is the relationship between domestication and natural selection?

Domestication is the process by which animals adapt to humans and their environment (Price, 1984). The main feature of domestication that separates it from tamingis that for domestication to occur, humans must control which individuals reproduce (Mignon-Grasteau et al., 2005). This process, in which humans select for desired traits and may produce new breeds, is called artificial selection.

Resource allocation theory argues that an animal's resources are balanced between traits for breeding and production (Mignon-Grasteau et al., 2005). Thus, when humans select for a particular trait, there will be a decrease in another trait unless the animal's resources increase. As a consequence of this, humans selecting for one trait may unintentionally change an unrelated trait.

For some traits, the pressures of artificial selection and natural selection may bring about the same result. For example, both natural and artificial pressures favor large pigs. Traits for self-defense or predatory behavior are not selected by humans, and often decrease or are lost in the process of domestication (Mignon-Grasteau et al., 2005). For instance, natural selection has resulted in wild boars with long, sharp tusks while selective breeding has resulted in domestic pigs with less conspicuous tusks.

10.1.3 How do pigs interact when foraging?

Wild and domestic pigs are highly social animals (Grandin, 2009, Graves 1984). As piglets, they fight viciously over their mother's teats before setting up a hierarchy that determines which sibling receives the most milk (Fraser, 1991; Fig. 4).. Even after they are weaned, pigs' feeding behavior is complex and rarely solitary. **Social foraging theory** is used to study these types of interactions, in which one forager's actions affect another's (Giraldeau and Caraco, 2000). Social foraging theory and optimal foraging theory are not competing theories. Optimal foraging theory predicts the behavior of individual foragers while social foraging theory predicts the behavior of foragers in groups.

Adult pigs also establish dominance hierarchies that help quell competition for food (Nielsen, 1996), but this does not mean that aggression motivated by food resources disappears entirely. Wild boars fight more often in the winter when food is scarce than in the summer when it is more plentiful (Graves, 1984). Thomsen et al. hypothesized that this may be due to the spatial distribution of food as well as its availability (Thomsen et al., 2010). They predicted that the number of aggressive interactions between domestic pigs would increase when buckets of food were clustered together versus spread out to a medium or far distance from each other, even if the total amount of food were the same in each condition. As shown in Figure 10.5, this hypothesis was supported.

Figure 10.4: Piglets suckling. Creative Commons-Licensed. <http://commons.wikimedia.org/wiki/File:Sau_mit_ihren_Ferkeln.jpg>

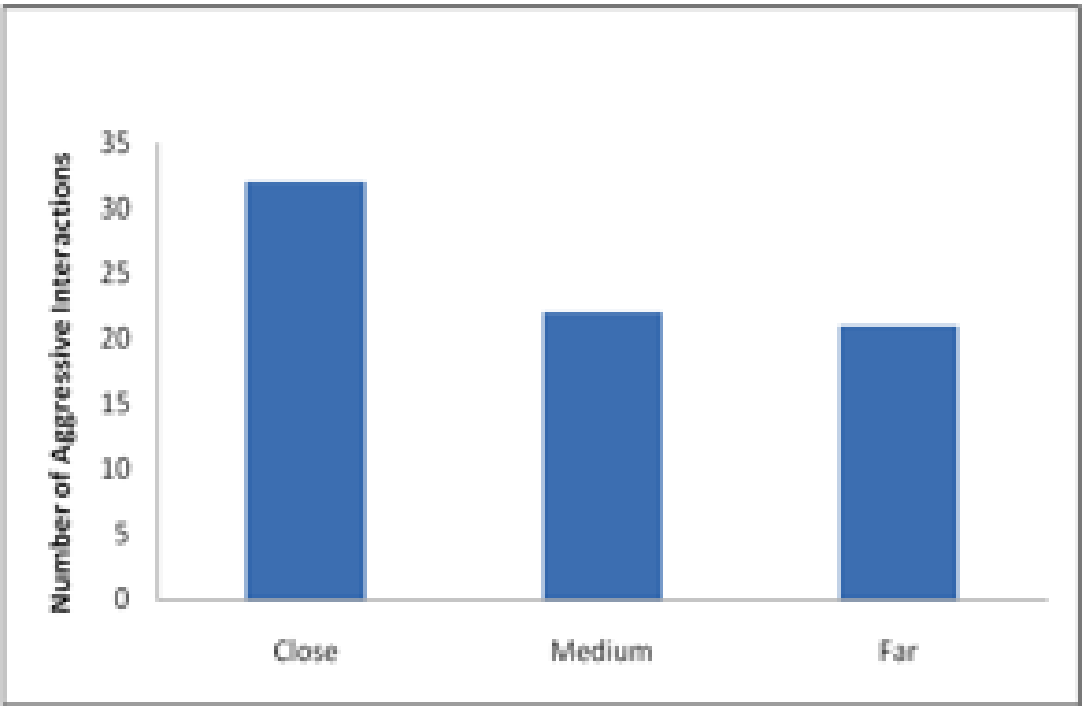

Figure 10.5: After Thomsen, et al., 2010

Thomsen et al. explain that this is because when pigs are foraging at a medium or far distance from each other, a subordinate pig has more time to react between the time a dominant pig chooses to feed from the subordinate pig's bucket and the time it gets to that bucket. The subordinate pig can quickly abandon its bucket, avoiding a confrontation. When buckets are close together, a dominant pig can choose to feed from a subordinate pig's bucket and get there before the subordinate pig can move.

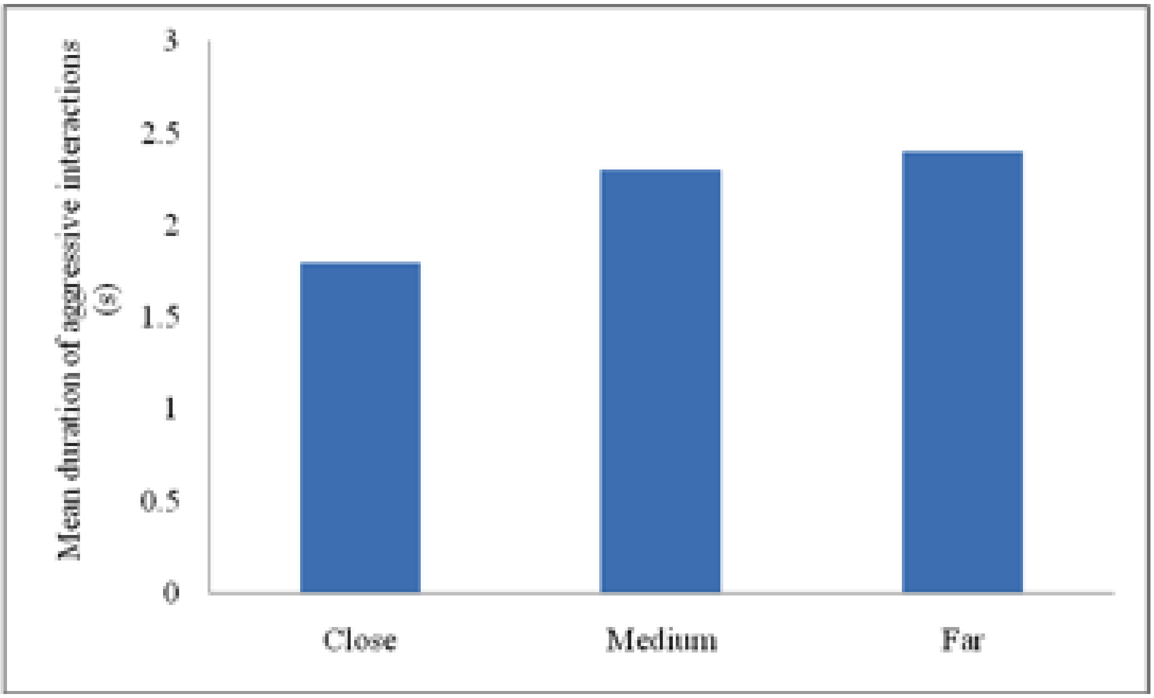

Figure 10.6: After Thomsen, et al.

This was supported by the finding that on average, fights between pigs were shorter when buckets were close together (Figure 10.6). When buckets were close together, a dominant pig would begin a fight and a subordinate pig would back down quickly. When buckets were far apart, there were fewer of these short fights because the subordinate pig had time to leave before the dominant pig could initiate a fight. This suggests another possible reason why wild pigs are more aggressive in the winter- in the winter, the small amount of food available is clumped together so pigs must forage close together. There is a low cost of moving, so dominant pigs may move often and fight with subordinate pigs that do not have time to move out of the way.

The pigs in this study followed optimal foraging theory. Pigs moved between patches (buckets) more frequently when costs were lower (the distance between buckets was smaller). This also explains why there were more aggressive interactions when buckets were closer together; pigs were more likely to move and therefore more likely to have to compete for an occupied bucket.

When food is limited and foragers are in a social hierarchy, social foraging theory predicts that different individuals should play different roles. Dominant animals can seek out food for themselves or take food from their subordinates. Finding food expends more energy than taking it from others, so dominant animals are likely to adopt a "**scrounger**" strategy in which they exploit their subordinates. Since subordinate animals cannot take food from higher-ranked individuals, they have no choice but to use a "**producer**" strategy in which they find food and eat as much as possible before it is taken from them (Giraldeau and Caraco, 2000).

Held, et al. conducted an experiment to test if pigs follow the producer-scrounger model. First, they took pigs to food sources and trained them to relocate them. These sources were buckets full of food in a pen also containing empty buckets. When it was clear that these "informed" pigs were able to remember where the full buckets were, they were paired with heavier "uninformed" pigs that did not know where the food was. The researchers predicted that the larger uninformed pigs would follow a scrounger strategy by following the informed pigs and taking food from them. (Held et al., 2000)

Held et al. found evidence to support their hypothesis. The informed pigs were capable of remembering and relocating buckets of food. When given access to empty buckets and buckets with food that they had been shown previously, they showed a significant preference for the food-filled buckets. When the larger, more dominant pigs were paired with the informed pigs, they inspected food buckets that had just been visited by the informed pigs more often than would be expected by chance. In over half the trials, the dominant pig displaced the informed pig from the bucket it was investigating, which was statistically significant. Non-informed dominant pig spent less time searching for food when paired with an informed subordinate pig than when they foraged alone. Thus, dominant pigs utilized the scrounger strategy, and this strategy was successful. Feral pigs have also been found to use producer and scrounger strategies. Subordinate feral pigs are more likely than dominant pigs to find food sites, which dominant pigs benefit from (Held et al., 2000).

10.1.4 Why do captive pigs exhibit foraging-like behaviors?

Captive domesticated pigs are provided with food and thus do not need to forage. However, they still spend large amounts of their time exhibiting foraging-related behaviors such as rooting, sniffing, biting, and chewing on edible and inedible materials. Often, they are provided with hay so they may carry out these behaviors (Studnitz et al., 2007). When deprived of material suitable for these behaviors, pigs perform **stereotypies**, which are fixed repetitive actions indicative of boredom or frustration (Grandin, 2009). In pigs, stereotypies may include chewing metal bars on their crates, pacing, and chewing with nothing in their mouths.

The importance of foraging behaviors and the relationship between pig stereotypies and inability to forage are well established. When pigs kept on concrete floors were allowed access to soil outdoors, they immediately began to root (Day et al., 1995). Pigs with nose rings do not root, presumably because the pressure of the ring causes pain when rooting (Bornett, 2003). However, when pigs' nose rings were removed, they resumed rooting (Studnitz et al., 2003). Pigs prevented from rooting were found to spend approximately the same amount of time performing stereotypies as other pigs spend rooting (Day et al., 1996).

This suggests that biting and chewing non-edible materials and rooting are related to boredom and the desire to explore surroundings. However, stereotypies and foraging behaviors increase when food is depleted, suggesting that some of these behaviors are hunger related.

Day et al. explored the reasons behind these behaviors by offering domestic pigs three tubes to chew. The first tube released water. Because the pigs were given unlimited access to water, chewing on this first tube indicated exploratory behavior. The second tube released a saccharin solution, which tastes sweet but has no nutritional value. The third tube released a sucrose solution, which provided the pigs with a sweet tasting and nutritious drink. Some pigs were put on a low feeding schedule (restricted access to food) while others were put on a high feeding schedule (unrestricted access to food). The researchers' results are shown in Figure 10.7.

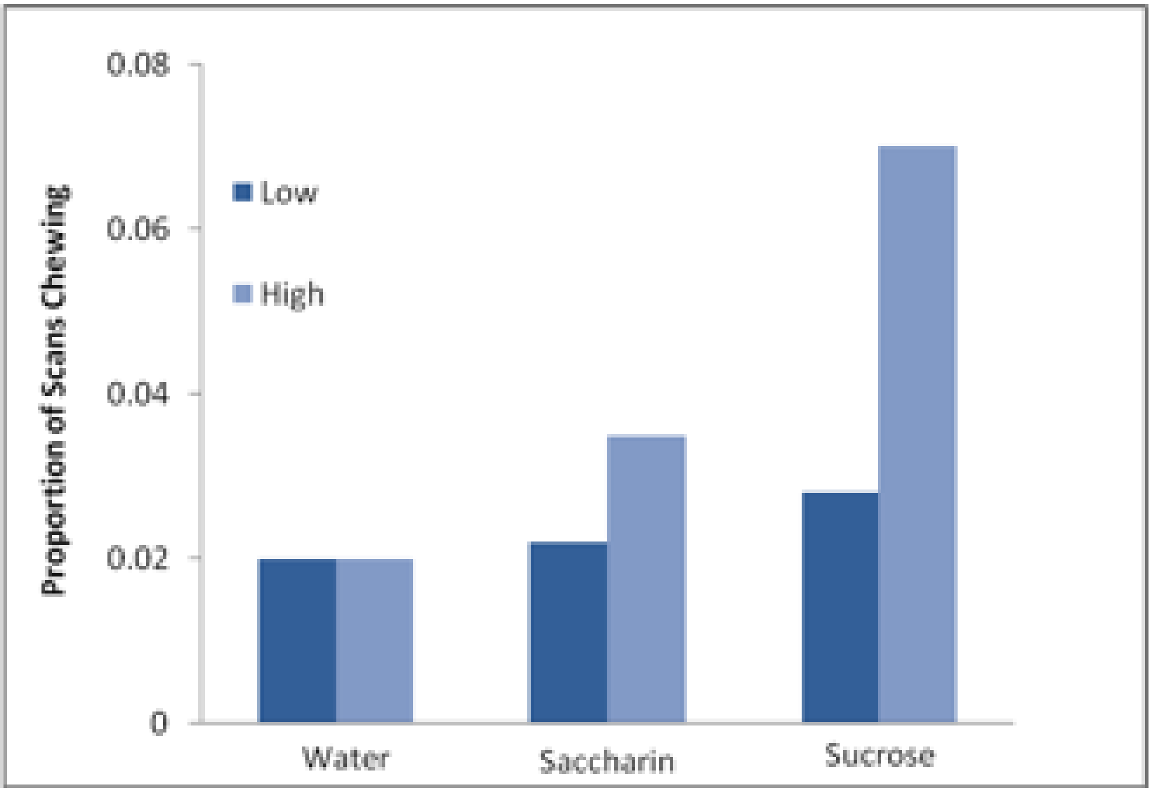

Figure 10.7: After Day et al., 1996.

They found that when pigs were given unlimited food, there was no significant difference in tube preference. However, pigs whose food intake was reduced had a significant preference for saccharin over water and sucrose over saccharin. Pigs whose food intake was limited spent more time chewing the tubes than pigs on the high feeding level schedule. This indicates that some chewing activities were motivated by hunger. However, the substantial amount of time pigs spent chewing the water tube suggests that chewing is also an exploratory behavior. The researchers concluded that young pigs chew to gain information. Taste and nutrition serve as feedback to promote chewing particular materials so that the pig obtains proper nutrition. (Day et al., 1996).

Box 10.3: How can an animal's behavior be explained?

Causes of animal behavior can be divided into two broad categories: proximate causes and ultimate causes. Questions about **proximate causes** ask how a behavior occurs while questions about **ultimate causes** ask why it occurs. Proximate causes involve the immediate condition of an animal that allows it to behave the way it does, including its development and physiology. For example, as noted above, pigs exhibit more stereotypies when they are hungry versus when they are sated. A simple proximate explanation for this might involve low blood sugar triggering the activation of certain genes that code for hormones that make the pig feel hungry and signal the brain to stimulate jaw muscles to bite or chew. Alternatively, ultimate explanations examine how a behavior evolved over time. An ultimate explanation for increased stereotypic behavior in hungry pigs would involve how this would contribute to the pigs' fitness. For instance, hungry pigs chewing nearly anything they can find may have a better chance at finding food than hungry pigs that only exhibit foraging-like behaviors when they are sure they have encountered food. Pigs chewing inedible material would thus be less prone to starvation and more fit. Genes for this behaviors would be selected for, and stereotypies would result.

10.1.5 Summary

Pigs were domesticated from the wild boar over 8,000 years ago, but few behavioral differences between the species have been noted. Both species are called *Sus scrofa*. Domestic pigs are sometimes referred to as *Sus scrofa domesticus*. In the process of domestication, humans control which animals reproduce and animals adapt to their given environment. Artificial selection occurs when humans select for particular traits by allowing animals with those traits to breed.

Optimal foraging theory examines how animals make foraging decisions. It argues that animals forage in such a way as to maximize their caloric intake while minimizing energetic costs. Domestic pigs and wild boars use similar foraging strategies that follow the predictions of optimal foraging theory. For example, they spend more time in one area containing food when energetic costs to move to another area increase. Crossbred pigs use a costlier strategy that involves moving between areas with food more often. That is, they expend more energy when foraging than domestic pigs do. This is likely because vigilance as a means of protection against predators is selected for in wild animals but not domestic ones. Aggression between pigs increases as distance between food sites decreases because pigs move between sites more frequently and subordinate pigs have less time to escape an approaching dominant pig. Domestic and feral pigs follow a producer-scrounger model in which subordinate pigs find food and eat what they can before dominant pigs prevent them from eating more. Foraging is such an important behavior for pigs that even in captivity when unlimited food is available, they will display foraging-like behaviors like rooting in the dirt and biting and chewing inedible materials.

10.1.6 Discussion Questions

- According to Gustafsson, crossbred pigs used a costlier strategy than domestic pigs because they were more vigilant against predators. Present an alternative hypothesis. How would you test it?
- Held et al.'s study found that dominant pigs used a scrounger strategy by exploiting informed subordinate pigs, but it did not test whether subordinate pigs preferentially use a producer strategy. How would you determine if they do? Do you predict that pigs can alternate between strategies?
- Chewing and biting inedible objects expends energy and does not provide nutrition. How do you reconcile this behavior with optimal foraging theory?

10.1.7 Glossary

- **Artificial selection**- human control over animal breeding in order to increase the prevalence of desired traits
- **Conditional strategy**- an inherited mechanism that allows an animal to adapt to various conditions
- **Contrafreeloading**- the phenomenon in which an animal chooses food that requires effort to obtain even though other food is available
- **Domestication**- the process by which humans take care of and breed animals and animals become accustomed to humans
- **Feral**- semi-wild; a feral animal was domesticated but escaped captivity and returned to the wild
- **Optimal foraging theory**- theory that uses natural selection to explain animals' feeding choices

- **Producer**- in social foraging theory, an animal that finds food
- **Proximate cause**- a cause based on immediate reasons for a behavior, such as physiology
- **Resource allocation theory**- theory that argues that in a particular environment, an animal's resources are balanced between traits for breeding and traits for production
- **Scrounger**- in social foraging theory, a dominant animal that takes food from subordinates
- **Social foraging**- foraging in which an individual's decisions are dependent on the actions of another forager
- **tereotypies**- repetitive actions resulting from boredom or frustration
- **Ultimate cause**- an evolutionary reason for a behavior

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10.1.9 About the Author

Figure 10.8

Arielle Layman is a senior majoring in Biochemistry and Cell Biology at Rice University. She is from New Jersey and loves animals, science fiction, and cooking and baking vegan food. Next year she will be moving to rural New Mexico to teach high school science as a Teach For America corps member.

Index of Keywords and Terms

Keywords are listed by the section with that keyword (page numbers are in parentheses). Keywords do not necessarily appear in the text of the page. They are merely associated with that section. *Ex.* apples, § 1.1 (1) **Terms** are referenced by the page they appear on. *Ex.* apples, 1

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