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ABSTRACT

THE ROLE OF ECOLOGICAL AND PHYLOGENETIC CONDITIONS IN THE OCCURRENCE AND FREQUENCY OF SEXUAL CANNIBALISM IN SPIDERS

Shawn M. Wilder

Sexual cannibalism, the consumption of a male by a female in the context of mating, is a dramatic form of sexual conflict that occurs in spiders and praying mantids. Among spiders, the frequency of sexual cannibalism is quite variable. However, no general hypotheses have emerged to explain variation in the frequency of sexual cannibalism among taxa. The goal of this dissertation was to explore ecological and phylogenetic factors that may be responsible for variation in the frequency of sexual cannibalism within and among species of spiders. I first review the literature to create a framework to describe how ecological (i.e. food and mate availability) and phylogenetic (i.e. genetic correlations, feeding mode, mating behavior and sexual size dimorphism) influence the frequency of sexual cannibalism. I then conducted three studies to test aspects of the framework that are poorly understood. I first tested how food quality affects female aggression towards males in the wolf spider, *Pardosa milvina*. Females fed nutrient-supplemented prey items were more likely to attack males and engage in sexual cannibalism, which is contrary to the predictions. I also tested the role of mate availability (e.g. exposure or mating) on sexual cannibalism in *Hogna helluo*. While exposure to the opposite sex had few effects, mating status of males and females affected sexual cannibalism. Finally, I examined the role of sexual size dimorphism (SSD) for the frequency of sexual cannibalism within and among species of spiders. In *H. helluo*, females were much more likely to cannibalize the male when the degree of SSD was large. The same pattern held among species, with a higher frequency of sexual cannibalism in species with high degrees of SSD. The results of these studies and evidence in published literature suggest that female hunger and male vulnerability to female attacks (e.g. SSD) are major determinants of the occurrence of sexual cannibalism. Hence, while previous studies have suggested a polyphyletic origin of sexual cannibalism through several different hypotheses, my results suggest that female foraging (i.e. viewing sexual cannibalism as a predator/prey interaction) may be a more parsimonious explanation for the evolution of this behavior among taxa.

THE ROLE OF ECOLOGICAL AND PHYLOGENETIC CONDITIONS IN THE OCCURRENCE AND FREQUENCY OF SEXUAL CANNIBALISM IN SPIDERS

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DEDICATION

This thesis is dedicated to my parents, Michael and Joanne Wilder, who introduced me to nature through camping, hiking, biking, tidal pool searching and boating. I would not have been able to do this without their tremendous support and encouragement.

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GENERAL INTRODUCTION

Traditional views of mating systems suggest that females maximize reproductive success by being selective and only mating with the highest quality males while males maximize reproductive success by mating with as many females as possible (Bateman 1948, Trivers 1972, Andersson 1994). These sex roles can result in a conflict of interest during mating interactions (Arnqvist and Rowe 2005). Sexual conflict is manifest in many forms among animals, including: extra-pair copulations in birds (Petrie and Kempenaers 1998), coevolutionary arms race in grasping and antigrasping structures in water striders (Rowe and Arnqvist 2002), and toxic male seminal proteins in fruit flies (Wolfner 1997, 2002). One relatively dramatic form of sexual conflict is sexual cannibalism, the consumption of a male by a female in the context of mating (Elgar 1992, Elgar and Schneider 2004). Females may gain parental investment from the male, in terms of nutrients in the male body, while males lose all future reproductive success (Elgar 1992). While females often benefit from cannibalism at a cost to males, the exact nature of the balance of costs and benefits for males and females can depend upon a number of circumstances (e.g. timing of cannibalism, future expected reproductive success and competition for mates) and in rare cases males can even solicit cannibalism by females (Andrade 1996).

While sexual cannibalism has been reported in a number of species of invertebrates, this behavior is especially prevalent in praying mantids and spiders (Elgar 1992). In some species of spiders, sexual cannibalism can occur during most mating encounters (Elgar 1992). However, the frequency of sexual cannibalism is quite variable and can range from 0 to 100 % of mating encounters among species in the same family (e.g. Araneae, Theridiidae; Andrade 1996, Knoflach and van Harten 2000, 2001, Knoflach and Benjamin 2003). Efforts to understand the evolution of sexual cannibalism have focused on in-depth studies of the adaptive benefits of engaging in this behavior in a limited number of taxa (e.g. *Latrodectus hasselti* Andrade 1996, 1998; *Nephila* spp. Elgar and Fahey 1996, Schneider and Elgar 2001, 2002; *Argiope* spp. Elgar et al. 2000, Fromhage et al. 2003, Foellmer and Fairbairn 2003, 2004). These efforts have produced a number of hypotheses to explain the evolution of sexual cannibalism. Some of these hypotheses can provide insight into variation in the frequency of sexual cannibalism among species. For example, species in which male sacrifice has been documented are likely to engage in sexual cannibalism more frequently than species in which males struggle to avoid being cannibalized by females (Elgar 1992, Miller 2007). However, there is no general framework available to understand variation in the frequency of sexual cannibalism within and among species.

For simplicity, sexual cannibalism can be thought of as a predator / prey interaction. As with most predator / prey interactions, the occurrence of sexual cannibalism may depend upon the motivation of the female to capture the male and the vulnerability of the male to the female attack (Polis 1981, Polis et al. 1989, Brose et al. 2006, Wise 2006). A number of factors that vary among species could impact either female motivation to attack or male vulnerability to the attack. There can be variation both within and among species in ecological conditions such as food or mate availability, which can affect the selective benefit of cannibalism for females. For example, cannibalism could be very costly to a virgin female if she consumes a male before mating and there are few other males available with which to mate. Species also differ in their phylogenetic history, which could affect the ability of females to capture males. For example, females of species with predatory feeding modes may be able to more easily capture males than females of herbivorous species and males may be easier to capture if they are very small compared to females (i.e. a high degree of sexual size dimorphism). Hence, variation in the frequency of sexual cannibalism within and among species could be related to variation in ecological and phylogenetic conditions experienced by these species.

The goal of this dissertation was to explore some of the ecological and phylogenetic factors that may be responsible for variation in the frequency of sexual cannibalism within and among species of spiders. Certain ecological (i.e. food and mate availability) and phylogenetic (i.e. genetic correlations, feeding mode, mating behavior and sexual size dimorphism) factors can influence the occurrence of sexual cannibalism by affecting the selective benefit for the female to kill and consume the male or by affecting male vulnerability to female attacks. In the first chapter, I review the literature on sexual cannibalism to create a framework to describe how ecological and phylogenetic factors influence the frequency of this behavior within and among species. I then conducted three studies to test aspects of the framework that are poorly understood. In the second chapter, I tested how food quality affects female aggression towards males in the wolf spider *Pardosa milvina*. Most studies of the effects of food availability on the occurrence of sexual cannibalism have focused on food quantity (Elgar and Schneider 2004). However, recent evidence suggests that spiders may be nutrient-limited in the field (Denno and Fagan 2003, Fagan and Denno 2004). Nutrient-limited females could be more likely to engage in sexual cannibalism because consuming the male body could remediate a nutrient deficiency.

In the third chapter, I manipulated exposure to the opposite sex and mating status of both male and female wolf spiders, *Hogna helluo*, to test if mate availability affected mating behaviors and the occurrence of sexual cannibalism. There is a lower cost of precopulatory cannibalism for females if males are abundant and a higher cost of cannibalism for males if females are abundant in the population. In the final chapter, I examined the role of sexual size dimorphism (SSD) for the frequency of sexual cannibalism within and among species of spiders. I randomly paired male and female *H. helluo* to test if sexual cannibalism was more likely to occur if the size difference between males and females was large. I then collected data on the frequency of sexual cannibalism and mean SSD for a wide range of spiders from the literature to test if SSD predicted the phylogenetic distribution of sexual cannibalism. I conclude by discussing the implications of these results for the evolution of sexual cannibalism in spiders.

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CHAPTER 1: A REVIEW OF THE ROLES OF ECOLOGICAL AND PHYLOGENETIC FACTORS IN THE OCCURRENCE AND FREQUENCY OF SEXUAL CANNIBALISM

Abstract

Sexual cannibalism, the consumption of the male by the female before, during or after mating, can be a striking example of sexual conflict with potentially large fitness consequences for males and females. Predominantly observed in praying mantids and spiders, sexual cannibalism varies widely in frequency among species from absent to nearly obligatory. In this review, I examine how ecological and phylogenetic factors may affect the occurrence and frequency of sexual cannibalism within and among species. Certain factors may facilitate the evolution of sexual cannibalism if they affect the selective benefit of cannibalism for the female or the vulnerability of the male to the female's attack. Ecological factors such as food and mate availability may primarily influence cannibalism by affecting the benefit of cannibalism for females. For females, the benefit of cannibalism may be higher when the availability of prey items is low. Hence, there may be selection for plasticity in cannibalistic behavior based on hunger level and this plasticity may occur on a range of time scales. Similar effects are also expected for food quality (e.g. the concentration or ratio of nutrients), although it has yet to be investigated. Mate availability can affect the propensity of virgin females to engage in precopulatory cannibalism. If males are rare and females consume a potential mate before copulation, then they risk remaining unmated and, hence, not producing any offspring. Mate availability can also affect the benefits of cannibalism for males. If male competition for females is high and males can gain a paternity advantage from being cannibalized, then males may sacrifice themselves to females. Phylogenetic factors such as feeding mode, sexual size dimorphism, certain mating behaviors and genetic constraints may influence the vulnerability of the male to the female or the propensity of females to attack males. Selection for high levels of sexual cannibalism may be more likely for species in which females have a predatory feeding mode, especially if they can rapidly subdue large prey items. Cannibalism is also likely to evolve in species where males are vulnerable to female attacks because they are much smaller than females (i.e. high female-biased sexual size dimorphism) or if they use a mating behavior where the male body is positioned close to the female mouthparts. Finally, if genetic constraints prevent plasticity in female aggression among life stages or among contexts (e.g. foraging, antipredator behavior and mating) then females with high levels of aggression may be more likely to cannibalize even if it is not the optimal behavioral decision. For many species, there may be several ecological and phylogenetic factors that could act synergistically or antagonistically to facilitate or hinder the

evolution of sexual cannibalism. While in some cases it may be difficult to separate the effects of co-occurring factors, in other cases comparative and other phylogenetically-based approaches may aid in determining the influence of ecological and phylogenetic factors for the evolution of sexual cannibalism.

Introduction

Over the past 30 years, there has been increased attention on the role of sexual conflict in mating systems (Parker 1979, Choe and Crespi 1997, Arnqvist and Rowe 2005). Males and females often have different optimal outcomes during a mating encounter (Choe and Crespi 1997). In many species, males attempt to mate with as many females as possible and to invest as few resources as possible in each mating while females attempt to mate with only the highest quality males and to acquire as many resources from the male as possible (Andersson 1994). Sexual cannibalism, the consumption of a male by a female before, during or after mating, is considered one of the most dramatic manifestations of sexual conflict, especially in cases where the female consumes the male body as a “nuptial gift” when the male would instead benefit more by finding other mates (Bateman 1948, Elgar 1992, 1998, Elgar and Schneider 2004).

The costs and benefits of sexual cannibalism to males and females may exert strong selective pressures influencing its occurrence and frequency. These selective pressures may have an important influence on adaptations that affect either a) the motivation of females to capture males, b) the motivation of males to escape from female attacks or c) the vulnerability of males to capture by females. It is important to recognize that sexual cannibalism is a two stage event that includes a female attack and successful capture. Most research on sexual cannibalism has focused on female motivation to attack or male motivation to escape from a female attack. Factors affecting male vulnerability to these attacks have been rarely studied but may be important in determining if sexual cannibalism occurs.

The timing of sexual cannibalism in relation to copulation affects the benefits to males and females. Females may gain benefits in both pre- and postcopulatory sexual cannibalism while males can only benefit in postcopulatory cannibalism. In the case of precopulatory sexual cannibalism, females may be able to reject unpreferred males and gain nutrients from the male’s body. This behavior may be costly to the female if encounters with males are rare and they risk remaining unfertilized (Newman and Elgar 1991). For males, precopulatory sexual cannibalism is always costly because they do not copulate and forfeit any future reproductive success. In postcopulatory sexual cannibalism, females again benefits by gaining male nutrients, which in this case may be considered a form of paternal investment. This paternal investment may benefit a male if it increases fertilization success or female fecundity, but it comes at a cost to future reproductive success (Buskirk et al. 1984, Elgar 1992, Andrade 1996).

Past reviews and studies of sexual cannibalism have focused directly on the costs and benefits of sexual cannibalism (Elgar 1992, Morse 2004, Elgar and Schneider 2004). However, the strength of these selection pressures may depend on the conditions in which selection is taking place. For example, the value of males as prey items may depend upon local ecological conditions such as food availability or quality, population density and sex ratio. In addition, selection in other contexts may have important implications for the frequency of sexual cannibalism. The ability of females to capture males or for males to escape may depend upon the phylogenetic context, which includes factors such as the types of courtship and mating behaviors that are utilized by a species, genetic correlations between males and females or between social or environmental circumstances (e.g. foraging, predator avoidance and mating) and the degree of sexual size dimorphism.

The purpose of this review is to examine how ecological and phylogenetic conditions may affect the occurrence and frequency of sexual cannibalism (Figure 1). To accomplish this goal, I: 1) discuss how several ecological and phylogenetic conditions may affect selection pressures involved with sexual cannibalism, 2) review the evidence for the impact of these conditions on sexual cannibalism and 3) propose future avenues of research to explore the role of ecological and phylogenetic conditions for sexual cannibalism. Examining ecological and phylogenetic conditions may provide insight into the taxonomic distribution of sexual cannibalism and may aid in identifying factors related to intra and interspecific variation in the frequency of sexual cannibalism.

Explanations for the Evolution of Sexual Cannibalism

Sexual cannibalism occurs in a wide range of species but is most prevalent in praying mantids (Insecta, Mantodea) and spiders (Arachnida, Araneae) (reviewed in Elgar 1992). The frequency of sexual cannibalism among these taxa varies considerably and frequencies of sexual cannibalism from 0 to nearly 100% of all mating encounters can occur within the same family (e.g. Araneae, Theridiidae; Andrade 1996, Knoflach and van Harten 2000, 2001, Knoflach and Benjamin 2003). Several explanations have been proposed for the evolution of sexual cannibalism including: female foraging, mate rejection, male sacrifice and genetic constraints (Elgar 1992, Andrade 1998). I briefly summarize the major explanations below to provide a background for understanding the selective pressures involved with sexual cannibalism. A more detailed review of these explanations and their predictions is available in Elgar (1992), Andrade (1998), Morse (2004) and Elgar and Schneider (2004).

One of the most frequently studied explanations is that sexual cannibalism is adaptive for females because it provides a fecundity benefit from consuming the male body (Elgar 1992). Cannibalizing a male either before or after mating may allow a female to avoid starvation or to produce a larger clutch of young. Males may also be higher quality food than other prey items because the ratio of nutrients in their bodies may be closer to the ratio of nutrients that females need to grow and produce young (Fagan and Denno 2004, Matsumura et al. 2004). Some support for this hypothesis is provided by feeding experiments in which food-limited females are more likely to cannibalize males than well-fed females (Andrade 1998, Johnson 2001, Schneider and Elgar 2001, Herberstein et al. 2002). Additional support is provided by studies that show benefits to females that are allowed to cannibalize their mate (Birkhead et al. 1988, Elgar and Nash 1988). However, nine of ten studies have failed to detect a significant fecundity benefit of sexual cannibalism (Andrade 1996, Spence et al. 1996, Arnqvist and Henriksson 1997, Fahey and Elgar 1997, Maxwell 2000, Elgar et al. 2000, Johnson 2001, Stalhandske 2001, Fromhage et al. 2003, reviewed in Elgar and Schneider 2004). Although it has received a great deal of study, there have been few comprehensive tests of the food-limitation hypothesis for sexual cannibalism and, hence, the applicability of this explanation is largely unknown.

Mate rejection is another way that females may benefit from sexual cannibalism. Courtship by unpreferred males may be costly to females by increasing visibility to predators and reducing prey capture (Pruden and Uetz 2004). However, precopulatory sexual cannibalism would allow the female to eliminate the disturbance caused by unwanted males and also gain a meal. In the garden spider (*Araneus diadematus*), larger males are more likely to mate with females while smaller males are more likely to be cannibalized before getting a chance to mate (Elgar and Nash 1988). Interestingly, there was no difference in the lunge rate of females towards males of different sizes, which suggests that precopulatory sexual cannibalism in this species may act as a screen to allow females to reject small males that are not strong enough to repel female attacks (Elgar and Nash 1988). Hebets (2003) also provides some evidence for the mate rejection hypothesis by observing that female wolf spiders (*Schizocosa uetzi*) are more likely to mate with a familiar male phenotype and more likely to cannibalize an unpreferred and unfamiliar phenotype. A recent review suggests that while mate choice is a plausible explanation for precopulatory sexual cannibalism there is very little evidence available to evaluate this explanation (Prenter et al. 2006).

Under certain circumstances the fitness benefits of sexual cannibalism for males may exceed the benefits of future matings and select for male sacrifice (Andrade 1996, 2003, Schneider and Elgar 2001, Fromhage et al. 2005). Males can increase the probability of sexual cannibalism by decreasing their resistance to female attacks either during or after mating. In the most dramatic cases of reduced resistance, males die in copula (Foellmer and Fairbairn 2003) or perform a "copulatory somersault" that places the male body directly against the female mouthparts (Forster 1992). Males may benefit from sexual cannibalism by providing females with nutrition to enhance the females ability to produce young (Birkhead et al. 1988), or by increasing fertilization success through longer copulation duration (Andrade 1996, Schneider and Elgar 2001) or use of their body as a mating plug (Knoflach and Van Harten 2001, Foellmer and Fairbairn 2003).

In cases where there is no apparent net benefit of sexual cannibalism to either sex, this behavior has been hypothesized to be nonadaptive ("genetic constraints hypothesis" sensu Arnqvist and Henriksson 1997). Some females may actually lose mass by consuming prey as small as males and some aggressive females may attack all males that are encountered before mating and remained unmated despite several mating attempts (Morse 1979, Arnqvist and Henriksson 1997, Morse 2004). However, this overt aggression may be selected for if the benefits it creates in earlier life stages outweigh the costs during adulthood. This may be the case for some species of spiders in which indiscriminate predation as a juvenile may allow individuals to reach a large adult size and have higher fecundity. Due to genetic constraints, this indiscriminate predation may carry over into adulthood and result in cannibalism of some suitable mates, thus, delaying the production of young (Arnqvist and Henriksson 1997, Johnson and Sih 2005). Hence, sexual cannibalism may not be adaptive for some species but may be maintained as a byproduct of selection for high levels of aggression that result in large adult size.

Ecological Conditions

Organisms face a variety of ecological conditions that can have important impacts on growth, survival and reproduction. Many ecological conditions such as food availability, population density and sex ratio can be variable within and among species and this variation can affect the selective benefits of sexual cannibalism for females and males. Hence, ecological conditions should primarily affect the occurrence or frequency of sexual cannibalism by affecting female motivation to engage in cannibalism or male motivation to escape from cannibalism (Figure 1). Below I discuss how food and mate availability affect the selective benefit of cannibalism for females and males. For food availability, I discuss how low food quantity has been demonstrated to affect cannibalism by females and how food quality, which has rarely been studied in the context of sexual cannibalism, may have similar effects on cannibalistic attacks by females. For mate availability, a high abundance of males may decrease the costs of precopulatory cannibalism by virgin females and may increase the tendency of males to sacrifice themselves after mating if there is a paternity advantage.

Food Availability

Food-limitation is likely to be an important prerequisite for the fecundity advantage of sexual cannibalism (Newman and Elgar 1991). For females, the nutritional benefit of consuming a male must be balanced against the risk of remaining unfertilized from precopulatory sexual cannibalism or the potential for injury from postcopulatory sexual cannibalism (Newman and Elgar 1991). When food availability or quality is low the benefit of consuming a male becomes high and, thus, there may be stronger selective pressure for a female to cannibalize a male. For many species in which sexual cannibalism is common, there is likely to be some benefit of consuming a mate given that predatory invertebrates are frequently food-limited in nature (Wise 1993, Denno and Fagan 2003, Wise 2006).

In many species, there may be plasticity in cannibalistic behavior in response to current feeding conditions. Many studies have examined the relationship between hunger and sexual cannibalism (Table 1). In 5 species of spiders (Jackson 1980, Breene and Sweet 1985, Elgar and Nash 1988, Arnqvist and Henriksson 1997, Fromhage et al. 2003) there is no relationship, while in 10 other species, including spiders (Andrade 1998, Johnson 2001, Schneider and Elgar 2001, Herberstein et al. 2002, Persons and Uetz 2005, Wilder and Rypstra unpublished data), praying mantids (Kynaston et al. 1994, Liske and Davis 1987, Maxwell 2000) and parasitic isopods (Tsai and Dai 2003), there is a positive relationship between hunger and sexual cannibalism. For species with positive relationships between hunger and sexual cannibalism, it seems clear that food availability plays a role in this behavior (i.e. females that experience lower food availability will be more likely to cannibalize their mate). For virgin females engaging in precopulatory cannibalism, a positive relationship between hunger and cannibalism may be beneficial for species that experience fluctuations in food availability because it will allow females to make a tradeoff between acquiring sperm and acquiring food. For postcopulatory cannibalism or mated females engaging in precopulatory cannibalism, a positive relationship between hunger and cannibalism allows females to balance the risk of injury from male retaliation with the need to acquire food. It is important to note, however, that lack of a relationship between food availability and sexual cannibalism does not preclude the role of food limitation for sexual cannibalism because consistently low food availability could select for fixed, high levels of aggression towards all potential prey, including males (e.g. Sih et al. 2004, Johnson and Sih 2005).

In other species, there may be developmental plasticity in adult levels of aggression based on juvenile feeding history. For example, individuals that experience low food levels as a juvenile may become more aggressive towards potential food items as an adult. Consistently low food levels as a juvenile may indicate that food levels during adulthood may also be low and, hence, females may need to become more aggressive or cannibalistic to acquire sufficient food. Several species appear to show developmental plasticity in cannibalistic behavior. Female Mediterranean tarantulas, *Lycosa tarantula*, that were not provided with supplemented food as juveniles gained more mass than previously supplemented females as adults, which may be due to a higher tendency of unsupplemented females to cannibalize the relatively large males of this species (Moya-Larano et al. 2003). More direct evidence for the influence of juvenile feeding history is provided by studies of the orb-weaving spider, *Nephila plumipes* (Schneider and Elgar 2002), and the fishing spider, *Dolomedes triton* (Johnson 2005b). Laboratory studies of these species show that females that mature at a smaller adult size, which could be due to poor feeding conditions as a juvenile, are more likely to cannibalize their mate regardless of their current feeding condition (Schneider and Elgar 2002, Johnson 2005b). Thus, these small females may be able to respond to poor prior feeding history as juveniles by increasing their rate of foraging and sexual cannibalism as adults to ensure adequate food resources for reproduction.

In order for selection to favor sexual cannibalism under food limitation, females must gain some fitness benefit from consuming the male body such as higher survival, egg sac mass, number of eggs, hatching success of eggs or time to produce an egg sac. Most studies of the fitness effects of sexual cannibalism for females have examined the effects of the consumption of a single male on fecundity measures such as clutch size (reviewed in Elgar and Schneider 2004). However, to date, there is little empirical support for a fecundity benefit of sexual cannibalism. Of the 10 studies that have examined the effect of consumption of a male on female fecundity, only one (Birkhead et al. 1988) has reported higher fecundity of cannibalistic females (Andrade 1996, Spence et al. 1996, Arnqvist and Henriksson 1997, Fahey and Elgar 1997, Maxwell 2000, Elgar et al. 2000, Johnson 2001, Stalhandske 2001, Fromhage et al. 2003).

The only study to detect a fecundity benefit of sexual cannibalism is unique relative to the other nine studies in that the investigators studied a species with a relatively low degree of sexual size dimorphism (the praying mantis, *Hierodula membranacea*, in which males are about 2/3 the size of females, Birkhead et al. 1988). In species with high degrees of sexual size dimorphism, the male body may be an inconsequential meal. For example, in *Latrodectus hasselti* males weigh less than 2 % of the mass of adult females (Andrade 1996). In addition to the absolute size of the male, the size of the male relative to the amount of food that a female needs to consume before egg production may be important. In *Nephila plumipes*, the male body may represent only 1 % of the mass of food that a female typically consumes before producing an egg sac (Schneider and Elgar 2002), whereas in the wolf spider *Hogna helluo* males may represent 8 % of the food consumed by a female before she produces an egg sac (Wilder and Rypstra unpublished data). The mass of a male relative to the amount of food consumed before female egg production may prove to be a useful measure in predicting the relative benefit of sexual cannibalism for female fecundity.

Few studies have utilized a food-limited feeding regime when testing for a fecundity benefit of sexual cannibalism (Birkhead et al. 1988, Andrade 1996, Spence et al. 1996, Arnqvist and Henriksson 1997, Fahey and Elgar 1997, Maxwell 2000, Elgar et al. 2000, Johnson 2001, Stalhandske 2001, Fromhage et al. 2003). However, in addition to a low degree of sexual size dimorphism, Birkhead et al. (1988) used a fairly food-limited feeding regime for females, which may be another reason why they detected a significant fecundity benefit. Tests for a fecundity benefit of sexual cannibalism using well-fed females are inconsistent with the conditions of the hypothesis and less likely to detect a significant benefit of cannibalism.

Studies of the reproductive benefit of nuptial feeding (not including sexual cannibalism) provide evidence that a fecundity benefit may be more likely, or more detectable, for food-limited than well-fed females (Boucher and Huignard 1987, Butlin et al. 1987, Gwynne 1988, Simmons and Bailey 1990, reviewed in Vahed 1998). For example, Boucher and Huignard (1987) simultaneously manipulated female feeding regime and nuptial gift presence in the insect *Caryedon serratus* and observed that only food-limited females gained a fecundity benefit from consuming male gifts. Similar studies are needed on species that engage in sexual cannibalism to test if female feeding history influences the fecundity benefit that females gain from consuming the male.

To date, studies of the role of food availability for sexual cannibalism have only considered food quantity. However, in addition to quantity, prey quality could have important effects on sexual cannibalism. Even if there is a high abundance of food, females may be nutrient limited if that food is of low quality. Females require food with elemental compositions very similar to their own body or with certain ratios of carbohydrate to protein in order to grow and reproduce (Urabe and Watanabe 1992, Simpson and Raubenheimer 1995, Raubenheimer and Simpson 1997, 1999, Sterner and Elser 2002, Matsumura et al. 2004). However, in nature, predatory insects often have greater nitrogen content and a higher ratio of nitrogen to carbon than do herbivorous prey (Fagan et al. 2002, Denno and Fagan 2003, Fagan and Denno 2004). In addition, certain required amino acids may not be present in all prey and are not likely to be present in the same ratios in predaceous and herbivorous arthopods (Slansky and Rodriguez 1986). The absence or insufficient abundances of certain amino acids can result in reduced growth and higher mortality (Mayntz and Toft 2001). Higher quality prey and prey with higher nitrogen content have important impacts on the growth and survival of many predaceous arthopods (Uetz et al. 1992, Li and Jackson 1997, Toft 1999, Toft and Wise 1999, Snyder et al. 2000).

Recent evidence suggests that predaceous arthopods can select food items that optimize essential nutrients and amino acids and are more likely to kill and consume prey that contain nutrients that are limited in their diet (Greenstone 1979, Mayntz et al. 2005). This could have important implications for sexual cannibalism because males of the same species are more likely to have nutrients and amino acids in ratios equal to, or at least closer to, those required by females than other prey items (Snyder et al. 2000, Denno and Fagan 2003). Hence, even if females have a high availability of prey they may still attempt to cannibalize males if their diet is lacking in certain nutrients.

In summary, while food availability and the associated fecundity benefits hypothesis for the evolution of sexual cannibalism have been well studied compared to other aspects of sexual cannibalism, there are still considerable gaps in our understanding of how food and feeding history influence the frequency of sexual cannibalism. One of the most considerable gaps is in the area of food quality. Ecologists are just beginning to realize the importance of the amounts and ratios of nutrients in food for foraging animals and incorporate these ideas into foraging theory, which in the past has been dominated by energetic concerns (Stephens and Krebs 1986, Sterner and Elser 2002). Ambient food quality may prove to be an important factor affecting the frequency of sexual cannibalism in the field, especially given the uncanny ability of predaceous arthopods to select food items that contain nutrients they lack (Greenstone 1979, Mayntz et al. 2005). In addition, most studies of the effects of food availability have been conducted in the laboratory. More data are needed on sexual cannibalism, hunger levels and food consumption in the field to ensure that laboratory conditions are comparable to those experienced in nature. For example, while most studies of the effects of hunger on sexual cannibalism utilize short starvation periods of approximately a week for the female, data for a species of wolf spider suggests that the body condition of females collected in the field is similar to the condition of females that have been starved for 3 months or more in the laboratory (Wilder and Rypstra in review).

Mate Availability

A number of ecological conditions may affect mate availability including: high predation, habitat patchiness, and sex-biased predation or parasitism. These conditions can affect mate availability by reducing the overall density of a species or affecting the sex ratio. Mate availability, in turn, can be a critical factor affecting the decision of a female to engage in precopulatory sexual cannibalism or the decision of a male to avoid postcopulatory sexual cannibalism (Figure 1).

For females, precopulatory sexual cannibalism is risky because the female does not mate with the current suitor and risks remaining unmated if she cannot locate another male. Hence, any decrease in the availability of males through low population density or highly female-biased sex ratio should increase the risk of not finding another mate and, therefore, decrease the propensity of a female to engage in precopulatory cannibalism (Newman and Elgar 1991). It is important to note that this primarily applies to virgin females engaging in precopulatory cannibalism or to systems where maximum female reproductive output requires several matings (Newman and Elgar 1991). This hypothesis was supported in a model by Newman and Elgar (1991) in which females balanced mating and precopulatory cannibalism depending on relative food and mate availability. In one of the few empirical studies to test the role of mate availability on precopulatory cannibalism, Johnson (2005a) manipulated the perception of mate availability for juvenile female fishing spiders, *Dolomedes triton*. Females that were allowed to cohabit with a caged male for at least 10 days prior to maturation were more likely to engage in a precopulatory attack on a male during a mating trial (Johnson 2005a). However, more research is needed on the effects of timing of exposure, number of exposures and length of exposure on precopulatory attacks in a wide variety of species to test the role of prior exposure on female cannibalistic behavior.

In addition to overall availability of males, there can also be variation in male quality such that, even if males are overall abundant, high quality males may be rare. The model of Newman and Elgar (1991) suggests that when male availability is high females should cannibalize males. If male quality is variable, then at high male availability females have the ability to be selective in mating and could bias their precopulatory sexual cannibalism towards lower quality mates. Hebets (2003) provides some preliminary evidence to support this hypothesis. In her experiment, juvenile females were each exposed to several males all of which belonged to one of two phenotypes and, hence, all females had a relatively high perception of mate availability (Hebets 2003). Interestingly, in this experiment, preference and sexual cannibalism were inversely related (Hebets 2003). Females preferred to mate with males of a familiar phenotype and were more likely to cannibalize males of the unfamiliar phenotype (Hebets 2003). Hence, when mate availability is high and females have the ability to engage in precopulatory cannibalism with relatively little risk, they may bias their cannibalism towards unpreferred mates, a hypothesis that deserves further study.

The availability of females could also influence the propensity of a male to avoid postcopulatory sexual cannibalism. If competition for mates is fierce and males can gain a paternity advantage through sexual cannibalism, then there may be selection for males to sacrifice themselves to females during or after mating (Andrade and Kasumovic 2005, Fromhage et al. 2005). Fromhage et al. (2005) demonstrated in a model that a monogamous male phenotype that can increase fertilization success through terminal investment can prevail over a polygamous male phenotype that has lower fertilization success if the male sex ratio is biased and, even more so, if males also experience high search costs. These conditions seem to be met in many of the species of spiders in which males engage in terminal investment and allow themselves to be consumed by females (Andrade and Kasumovic 2005). In the eight species for which there are enough data, species with terminally investing males often have fierce competition between males on the female web and males experience very high mortality during the search for females (Andrade and Kasumovic 2005). For example, in the redback spider *Latrodectus hasselti*, in which males somersault into the female jaws during mating, up to six males may be found on a female web at one time and there is an 86 % probability of male mortality during mate search (Forster 1992, Andrade and Kasumovic 2005). This copulatory somersault is not in vain, as males that are cannibalized gain higher paternity over their uncannibalized competitors (Andrade 1996). Hence, while the traditional Bateman paradigm suggests that promiscuity is a favorable tactic for males, when males face intense competition and little access to additional females there may be selection for male monogamy through self sacrifice (Bateman 1948, Andrade and Kasumovic 2005, Fromhage et al. 2005).

While population density and sex ratio are known to vary within and among species, relatively few studies have examined the role of these factors for sexual cannibalism. From the female perspective, evidence suggests that females may be more likely to engage in precopulatory cannibalism when males are more abundant (Newman and Elgar 1991, Hebets 2003, Johnson 2005a). Further research is needed to examine how females assess male abundance, if that assessment is based on absolute male abundance or sex ratio and how fine-tuned female responses are to variation in male availability. Interestingly, in some species male overtly sacrifice themselves to females when there is high male competition over females and when sacrifice provides a paternity benefit (Andrade and Kasumovic 2005, Fromhage et al. 2005). However, nearly all cases of male sacrifice that have been identified thus far are obligatory and it is not known if other species show male sacrifice in less dramatic manifestations. For example, males could influence the probability of sexual cannibalism by changing their resistance to female attacks or rate of escape following mating. Such flexibility in male sacrifice could be possible in systems where male competition and access to females is variable. Future efforts in modeling and experimental manipulations of the density and sex ratio both in the lab and field should provide tremendous insight into the role of mate availability for sexual cannibalism.

Phylogenetic Conditions

Selection pressures from a number of different sources have acted on morphological and behavioral traits of organisms to produce characteristics that allow individuals to attempt to maximize their reproductive success. Sometimes these adaptations can have important consequences for sexual cannibalism by increasing the ability of a female to capture a male or decrease the ability of a male to escape from a female. In the following sections, I will discuss the importance of feeding mode, sexual size dimorphism, mating behaviors and genetic correlations for the frequency of sexual cannibalism. Characteristics such as predatory feeding mode, high degrees of sexual size dimorphism with females larger than males, mating positions in which male body parts are close to female mouthparts or genetic tendencies towards high levels of aggression may predispose species to higher frequencies of sexual cannibalism. Hence, once there has been selection for females to attack males, some phylogenetic factors may affect whether that attack is successful and sexual cannibalism occurs.

Feeding Mode

Feeding mode may be a major factor determining the phylogenetic distribution of sexual cannibalism. Among the many feeding modes used by animals, predators may be predisposed to have a higher frequency of sexual cannibalism. Sexual cannibalism has been reported for over 90 species of animals and over 90 % of these species are predatory (Elgar 1992, Elgar and Schneider 2004).

Quite simply, predatory species may be more likely to engage in sexual cannibalism because females have evolved morphological characteristics that allow them to capture and consume other animals. Due to the morphology of their mouthparts, it may be impossible or improbable for females in herbivorous (e.g. plant mining, sap sucking and gall forming), detritivorous, nectarivorous and filter feeding species to inflict enough damage to kill a male before the male had a chance to escape. Even if the female has the physical ability to kill a male (e.g. strong sharp mouthparts of some herbivores), she may not attempt to do so because it would take a significant amount of time and expose the female to the risk of damage from retaliation by the male. Nonpredatory species with mouthparts that can kill and consume conspecifics do sometimes exercise cannibalism; however, it is usually asymmetrical and involves an adult cannibalizing a juvenile or adults and juveniles cannibalizing eggs (reviewed in Elgar and Crespi 1992). When individuals are more similar in size, such as adult females and males, cannibalism may not be a viable option unless females are predatory. In addition, for some nonpredatory species, females may not possess enzymes capable or efficient enough to extract nutrients from conspecific flesh and, hence, there would be little or no selection for females to attempt to cannibalize males.

While most cases of sexual cannibalism occur in predatory species, this behavior does occur in some non-predatory species. One notable example is the sagebrush cricket, *Cyphoderris strepitans* (Eggert and Sakaluk 1994). Males of this species have abnormally fleshy hindwings on which females feed during mating. This does not fit the classic definition of sexual cannibalism because the male is not killed but is sometimes considered sexual cannibalism because part of the male is consumed by the female (Eggert and Sakaluk 1994, Johnson et al. 1999, Sakaluk et al. 2004). One explanation for why the male is not killed in this species, despite the female's desire to consume him, may be that the female jaws cannot effectively subdue the male. Hence, when a species is not predatory, if sexual cannibalism occurs, then the extent of sexual cannibalism or conditions under which it occurs may be limited.

Despite the fact that most sexually cannibalistic species are predators, not all predatory species are sexually cannibalistic. Among predatory species, the frequency of sexual cannibalism may vary depending upon the predatory ability of the species. Sexual cannibalism may be especially likely in predators that have evolved the ability to catch large prey. At the very least, predatory females must be able to kill prey as large as males in order for sexual cannibalism to occur. However, sexual cannibalism is more likely in species that can kill prey much larger than males because this ability decreases the chance that the female will become damaged by retaliation by the male. For example, female *Hogna helluo* can kill prey items (including conspecifics) that are larger in proportion to their body size than can *Pardosa milvina* (Rypstra and Samu 2005). As predicted, the frequency of sexual cannibalism in the more voracious *H. helluo* (> 30 % of mating interactions, Wilder and Rypstra in review) is much higher than that of *P. milvina* (~ 1 % of mating interactions, Schlosser and Rypstra unpublished data). Special adaptations for capturing large prey, such as raptorial forelegs and venom, may be one reason why sexual cannibalism is so prevalent in praying mantids and spiders. Hence, while being a predator is an important condition affecting the frequency of sexual cannibalism, there may be variation in sexual cannibalism among predators depending upon their voracity.

Sexual Size Dimorphism

In many animal taxa males and females differ in size. In birds and mammals, males tend to be the larger sex likely because there has been selection for larger male size due to the importance of male-male competition (Andersson 1994). However, in invertebrates, females tend to be the larger sex, which may result from selection for both larger female size and smaller male size (Head 1995, Hormiga et al. 2000). A phylogenetic study of orb-weaving spiders suggested that increases in the size of females has contributed to sexual size dimorphism in 22 genera and that decreases in male size have contributed to sexual size dimorphism in 2 genera (Hormiga et al. 2000). Females may become larger in invertebrates because clutch size it closely related to adult female size (i.e. fecundity selection: Head 1995). Males may become smaller because small male size decreases juvenile mortality, allows rapid reproduction and increases climbing speed to locate females (Vollrath and Parker 1992, Moya-Larano et al. 2002). Variation in the strength of these selective factors among species has contributed to a wide range of sexual size dimorphism in some invertebrates such as spiders where dimorphism may range from females slightly smaller than males to females greater than 10 times the size of males (Kaston 1981).

Selection for a greater degree of sexual size dimorphism may create a condition where males are more vulnerable to female attacks. This is important in cases where females attempt cannibalism and males struggle to avoid being eaten either before, during or after mating. For example, size dimorphism is known to be an important factor affecting the occurrence of predation and of cannibalism of juveniles (Polis 1981, Polis et al. 1989, Elgar and Crespi 1992, Balfour et al. 2003, Rypstra and Samu 2005, Wise 2006). For sexual cannibalism to be maintained, females must be able to capture and kill males without risking retaliation. If males were able to damage females during an attack, then there may be selection against sexual cannibalism because any benefit of this behavior (e.g. gaining a meal or removing an unwanted suitor) may be counteracted by lost future reproductive success. If damage could occur, then selection against cannibalism may take place in a manner analogous to selection for "limited war" in conflicts modeled by Maynard-Smith and Price (1973). Thus, low degrees of sexual size dimorphism may discourage sexual cannibalism and high degrees of sexual size dimorphism (e.g. through fecundity selection on females or mortality selection on males) may create a condition where females are better able to capture and kill males without risk of damage and, hence, create favorable conditions for the evolution of sexual cannibalism.

Support for the hypothesis that high degrees of sexual size dimorphism result in higher frequencies of sexual cannibalism is provided by mating experiments that examine if the probability of female attacks or the probability of sexual cannibalism is related to male size or sexual size dimorphism within a species (Table 2). While there is little data available on attack rates of females on males of different sizes, in *Schizocosa ocreata* females are more likely to attack smaller males (Persons and Uetz 2005). In terms of successful cannibalisms, there are eight species in which females are more likely to cannibalize males if the degree of sexual size dimorphism of the pair is large (Table 2). In the wolf spider *Hogna helluo*, random selection of males and females can result in pairings that range in sexual size dimorphism with females 0 to 53 % larger than males (Wilder and Rypstra unpublished data). This range in dimorphism can have a large impact on the occurrence of sexual cannibalism as the frequency of cannibalism is 4 % for pairings in the lowest quartile of SSD (i.e. females 13 % larger than males) and 68 % for pairings in the highest quartiles of SSD (i.e. females 41 % larger than males). As with predation and cannibalism of juveniles, it seems that when there is a greater size disparity between males and females, then there is a higher likelihood that the male will become a meal (Polis 1981, Polis et al. 1989, Elgar and Crespi 1992, Balfour et al. 2003, Rypstra and Samu 2005, Wise 2006).

However, within some species there may be not relationship between male size and sexual cannibalism or the relationship between may be reversed (Elgar and Nash 1988, Arnqvist and Henriksson 1997, Schneider et al. 2000, Johnson 2005b). In *Nephila plumipes* and *Argiope aurantia*, females more frequently attack larger males (Elgar and Fahey 1996, Foellmer and Fairbairn 2004). In *Nephila plumipes*, this results in a higher probability of sexual cannibalism for larger males (Elgar and Fahey 1996, Schneider and Elgar 2001). This interesting positive relationship between sexual size dimorphism and sexual cannibalism in this species may be related to the fact that this species has a greater mean degree of sexual size dimorphism than most other species studied thus far (Table 2). The extremely small size of some males in *N. plumipes* may allow them to approach the female undetected. Elgar and Fahey (1996) observed that females responded with more leg movements and web tugs to larger males. In fact, females did not respond at all to the presence of small males (Elgar and Fahey 1996). In addition to reduced conspicuousness, extremely small males may be less frequently attacked by females because they provide few nutrients (Elgar and Fahey 1996, Morse 2004). In *Nephila plumipes*, males are only 2% of the mass of females (Elgar and Fahey 1996). Thus, while small males are more vulnerable to sexual cannibalism in many species, there may be a point where small size reduces vulnerability to cannibalism by decreasing conspicuousness and value as a meal.

In addition to affecting the probability of sexual cannibalism within a species, sexual size dimorphism may be related to the frequency of sexual cannibalism among species. Elgar (1992) conducted a broad taxonomic study and failed to detect a relationship between sexual size dimorphism and an index of cannibalism (i.e. none, low or high). More recently, Wilder and Rypstra (in review) compiled quantitative data on sexual size dimorphism and the frequency of sexual cannibalism for 27 species of spiders representing 21 genera and 12 families, 74 % of which were unavailable in the original study by Elgar (1992). The data set included frequencies of sexual cannibalism ranging from 0 to 100 % and sexual size dimorphism (measured as female size/male size) ranging from 1.17 to 4.89. Using species as data points, there was a relatively strong positive relationship between sexual size dimorphism and the frequency of sexual cannibalism. This positive relationship remained significant after controlling for phylogeny using comparative analysis by independent contrasts (Purvis and Rambaut 1995). The strength of the relationship ($r^2 > 0.47$) was surprising given the inclusion of species with apparent adaptations to reduce the frequency of sexual cannibalism. These results provide support for the hypothesis that females are more successful at cannibalizing males in species with higher degrees of sexual size dimorphism.

If smaller males are generally more vulnerable, then why is there not selection for males to become larger to decrease the degree of sexual size dimorphism? Tradeoffs between time to maturity, mate searching ability or juvenile mortality and adult male size may explain why selection has maintained high degrees of sexual size dimorphism in some species. In seasonal environments, males that tradeoff adult size to mature early may have greater access to or less competition for virgin females. These smaller males can also have a higher average speed during climbing which may allow them to reach females more quickly and reduce time spent vulnerable to predators during mate-searching (Moya-Larano et al. 2002). In addition, in species with high degrees of sexual size dimorphism, many cases of sexual cannibalism are postcopulatory and males have few opportunities for finding additional mates, which reduces the cost of sexual cannibalism in terms of future mating opportunities. Thus, the benefits of early maturation and the low cost of sexual cannibalism in terms of lost mating opportunities may prevent sexual cannibalism from selecting for larger male size.

Mating Behavior

Once a male and female decide to mate with each other, sperm must be transferred. In many arthopods, fertilization is internal, which means that male and female genitalia must come into contact during copulation. Among species, copulation can occur in a variety of arrangements. However, for a given species, the location of genitalia, body form and lifestyle may create conditions that predispose that species to mate in a certain position. Certain mating behaviors or positions may have important implications for sexual cannibalism by affecting the vulnerability of the male to female attacks before, during or after mating. Hence, a mating position where the male is more vulnerable to attack may create a condition favorable for the evolution of sexual cannibalism.

In spiders, the male copulatory organs are located on the pedipalps, which are modified appendages by the mouthparts that are also used to manipulate food. After molting to adulthood, males typically transfer droplets of sperm from their genital opening, which is on the underside of their abdomen, to a specialized web and then induct these droplets into the pedipalps (Foelix 1996). The female genitalia, the epigynum, is located on the ventral surface of her abdomen near the connection between the abdomen and carapace. The locations of male and female genitalia and the varied lifestyles of spiders (i.e. tangle webs, sheet webs, orb webs, wanding, etc.) have allowed spiders to evolve several copulatory positions, some of which may provide the female with a greater chance of successfully capturing the male during or after mating.

In many web-building spiders, the male climbs onto the ventral surface of a female while she is hanging from the web. When on the ventral surface of the female, the direction that the male faces may determine whether or not the female is able to kill and consume the male during mating. In some species, males and females face opposite directions. This often places the male abdomen very close to the female mouthparts and allows the female to cannibalize the male during mating (i.e. *Latrodectus hasselti*, Andrade 1998). Even when the male faces the same direction as the female he may still face a high risk of sexual cannibalism because his body is very close to the female spinnerets and the fourth pair of legs which are often used to wrap prey in silk (i.e. *Argiope aurantia*, Foellmer and Fairbairn 2004). Hence, high rates of sexual cannibalism may be more likely to evolve in species where males copulate on the ventral surface of the female.

In many wandering spiders, including wolf, fishing and jumping spiders (families: Lycosidae, Pisauridae and Salticidae, respectively), male copulate while on the dorsal surface of the female. Unlike the ventral surface, mating on the dorsal surface places the male body away from the female mouthparts and, thus, precludes the possibility of sexual cannibalism during copulation in these spiders. However, males mounting on the dorsal position of females is not always safe, as evidenced by some praying mantids in which females can bend at the junction of the pronotum and abdomen to kill and consume males in copula (Liske and Davis 1987, S. M. Wilder personal observation).

In addition to mating position, the location of copulation may have an important effect on the probability of sexual cannibalism. In some species, mating takes place in confined spaces. In the parasitic isopod, *Ichthyoxenus fushanensis*, pairs live in a small cavity within the host species (Tsai and Dai 2003). Females sometimes cannibalize males and males sometimes cannibalize females and then change sex to become females (Tsai and Dai 2003). In several species of spiders, a male will guard a penultimate female within a cavity or retreat and mate with the female once she molts to adulthood (Fahey and Elgar 1997, Moya-Larano et al. 2003). When the male and female are confined to a small area, the probability of sexual cannibalism may be higher because males have less of a chance to escape following mating, although if an area is too small it may physically constrain the ability of females to cannibalize males. However, experiments and field observations are necessary to test if sexual cohabitation or mating in confined spaces (e.g. burrow or retreat) results in a higher risk of cannibalism.

In other species, copulation takes place in the open. For praying mantids, copulation often takes place on exposed vegetation and males can jump or fly off of the females back following mating (Lawrence 1992, Maxwell 1998). Similarly, many wolf spiders (Araneae, Lycosidae) and fishing spiders (Araneae, Pisauridae) mate on the soil surface and the male is able to freely run away from the female following copulation. In some other species of fishing spiders, mating can take place while the male and female hang from a thread of silk and males can escape after copulation by climbing up the thread of silk or descending on their own line of silk (Bruce and Carico 1988). Many species of web-building spiders also mate in the open, either in the center or periphery of the female web. If attacked before or after mating males of these species may escape by jumping off of the female web or descending on a silk line. Hence, when mating occurs in the open males may be at a lower risk of sexual cannibalism because they have more opportunities for escape.

Finally, the number of copulations required for a full insemination may also affect the probability of sexual cannibalism. In spiders, both males and females have paired reproductive organs. While some males can use both pedipalps to inseminate both sides of the female epigynum in a single mounting, some males only inseminate a single side of the female reproductive tract while mounted and must remount the female to inseminate the other side. For example, in *Latrodectus hasselti*, 87 % of males survive the first mounting and insertion whereas only 52 % of males survive 2 mountings and insertions (Andrade 1998). However, while it may be costly for males to attempt to fertilize both spermathecae of the female, there may be selection for this risky behavior because males can lose a significant amount of paternity (e.g. up to 30 %) if a rival male is able to inseminate an empty spermatheca (Snow and Andrade 2005).

Genetic Correlations

Behavioral plasticity allows individuals to respond to multiple situations with optimal behaviors. However, behavioral plasticity may be constrained if a species has not evolved adaptations to uncouple behavior among contexts. Recent evidence suggests that behavioral plasticity may be constrained to be similar among situations in some organisms, a phenomenon referred to as a behavioral syndrome (Sih et al. 2004). For example, aggression is part of a behavioral syndrome in the funnel-web spider, *Agelenopsis aperta* (Riechert 1993). In this species, individuals in grassland habitat, where food is limited, have faced selection for higher levels of aggression than spiders in riparian habitat, where food is abundant (Hedrick and Riechert 1989, Riechert 1993). High levels of aggression towards prey are genetically-based and correlated with levels of aggression in other contexts such as territoriality and antipredator behavior (Hedrick and Riechert 1989, Riechert and Hedrick 1993, Riechert and Johns 2003). While sexual cannibalism does not appear to be frequent in this species, possibly due to female catalepsis during mating (Becker et al. 2005), behavioral syndromes of aggression could predispose some species to higher levels of sexual cannibalism.

Arnqvist and Henriksson (1997) first proposed that behavioral syndromes may be important for sexual cannibalism in the fishing spider, *Dolomedes fimbriatus*. While testing the role of food availability for sexual cannibalism, Arnqvist and Henriksson (1997) observed that there was no relationship between female hunger and the occurrence of sexual cannibalism in *D. fimbriatus*. Furthermore, some female fishing spiders were cannibalistic or aggressive towards all males that they encountered and remained unmated at the end of the trial period while other females were able to mate and produce egg sacs in the same time period (Arnqvist and Henriksson 1997). For those females that produced egg sacs, fecundity was strongly related to fixed adult size, which is a function of juvenile feeding. Hence, Arnqvist and Henriksson (1997) hypothesized that there was strong selection for indiscriminate aggression during the juvenile stage, due to fecundity benefits of large adult size, and that genetic constraints resulted in a spillover of that aggression into the adult stage where aggression towards food also affected aggression towards mates.

The only experimental test of the role of behavioral syndromes for sexual cannibalism was conducted on the fishing spider, *D. triton* (Johnson and Sih 2005). In this study, female *D. triton* that were more likely to cannibalize a male were also more voracious towards prey items and more bold when exposed to simulated predation threats (Johnson and Sih 2005). In addition, Johnson and Sih (2005) found support for the genetic constraints hypothesis of Arnqvist and Henriksson (1997) by documenting that juvenile and adult levels of aggression were correlated. Hence, sexual cannibalism seemed to be associated with an overall higher level of aggression in multiple contexts and did not appear to be an adaptive choice made by females in response to hunger. However, while there is support for the hypothesis that behavioral syndromes of aggression may contribute to sexual cannibalism in fishing spiders (Araneae, Pisauridae), it is not yet known how well this hypothesis applies to other taxa.

Discussion

Ecological and phylogenetic factors may have important impacts on the occurrence and frequency of sexual cannibalism. Ecological and phylogenetic conditions can affect the frequency of sexual cannibalism by affecting motivation of females to cannibalize or males to escape capture or by affecting vulnerability of males to female attacks. In terms of ecological conditions, the environment (i.e. local food availability, population density and sex ratio) can affect the strength of selective pressures acting on females and males and affect the motivation of females to kill and consume males or the motivation of males to escape from females. For example, low food availability may increase the potential contribution of a male body to the female diet and select for higher levels of sexual cannibalism. In terms of phylogenetic conditions, selection in other contexts can result in morphological or behavioral traits that affect the ability of females to capture males or of males to escape from females. For example, fecundity selection for larger female size can create a condition (i.e. high female-biased sexual size dimorphism) where females are much larger than males and, hence, better able to capture and consume males.

For many species, several ecological and phylogenetic factors may occur together. The confluence of several factors may explain why sexual cannibalism is prevalent in some taxa and not others. For example, a combination of food-limitation, predatory feeding mode and female-biased sexual size dimorphism may explain why sexual cannibalism is especially prevalent in praying mantids and spiders (Wise 1993, Foelix 1996, Prete et al. 1999). Furthermore, within spiders, a combination of factors may explain possible differences in sexual cannibalism between wandering and web-building spiders. Wandering spiders, which tend to have relatively low frequencies of sexual cannibalism, have relatively low sexual size dimorphism and a mating position where males are safe, whereas web-building spiders, which tend to have higher frequencies of sexual cannibalism, have the opposite characteristics (Christenson and Goist 1979, Arnqvist 1992, Andrade 1996, Hebets et al. 1996, Elgar et al. 2000, Knoflach and VanHarten 2001, Schneider and Elgar 2001, Stalhandske 2001, Fromhage et al. 2003, Persons and Uetz 2005). However, while a combination of factors may aid in determining gross distributions of sexual cannibalism among taxa, such combinations may make it difficult to tease apart the role of each individual factor for the frequency of sexual cannibalism.

In some species, observed frequencies of sexual cannibalism may not match those predicted based on ecological and phylogenetic conditions because males have evolved adaptations to avoid sexual cannibalism. In terms of morphological adaptations, males of *Tetragnatha* spp. have extremely large chelicerae that they use to lock open the female chelicerae during mating (Bristowe 1958). Rather than lengthening their jaws, males in the family Araneidae have proportionately longer legs for their body size than males in the families

Tetragnathidae and Gasteracanthidae (Elgar et al. 1990). The relatively longer legs in the family Araneidae, in which sexual cannibalism is fairly common, may allow males to assess female receptivity from a distance (Elgar et al. 1990). Behavioral adaptations, although not quite as striking, can also be effective at reducing the frequency of sexual cannibalism. Males may avoid precopulatory cannibalism by feigning death, approaching females cautiously, approaching females from behind and approaching females while they are feeding on prey (Lawrence 1992, Prenter et al. 1994, Elgar and Fahey 1996, Maxwell 1999, Bilde et al. 2006, Fromhage and Schneider 2005). Males may also decrease the probability of sexual cannibalism by mating on a specially constructed mating thread or tying the female with silk (Bristowe 1958, Bruce and Carico 1988, Elgar 1991). These morphological and behavioral adaptations may prove to be a further difficulty in testing the role of ecological and phylogenetic conditions for sexual cannibalism.

Multiple approaches are necessary to test the hypotheses proposed in this review. For the ecological conditions, field and laboratory studies may prove useful. For example, Andrade (1998) provided convincing evidence for the role of food availability for sexual cannibalism in *L. hasselti* by conducting a food supplementation experiment and observations in the field. Johnson (2005a) provided preliminary evidence for the role of mate availability for sexual cannibalism in *D. triton* in laboratory experiments in which females previously exposed to males attacked potential mates more frequently. Phylogenetic conditions, however, may be somewhat more difficult to test and may require the use of a comparative approach. One of the only examples of a comparative approach to test for the role of phylogenetic conditions is that of Wilder and Rypstra (unpublished data). This study utilized a phylogenetically-controlled analysis on data from a range of species of spiders and found that sexual cannibalism was more frequent in species in which there was a greater difference in size between males and females (Wilder and Rypstra in review). Similar phylogenetic or comparative approaches could be taken to examine the role of other phylogenetic factors for the occurrence and frequency of sexual cannibalism.

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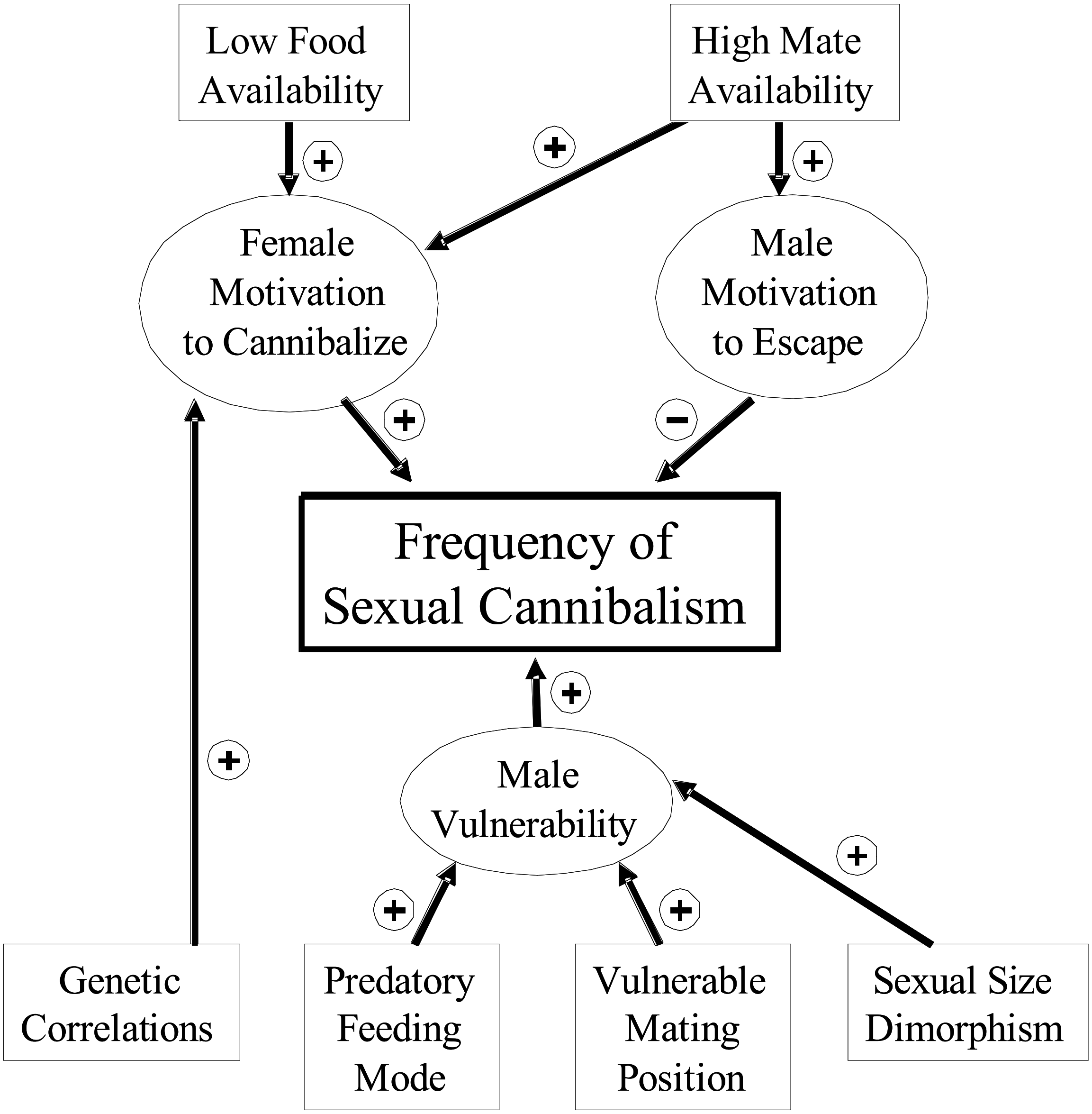
Table 1. Summary of studies investigating a relationship between female hunger and the probability of sexual cannibalism for a range of invertebrate species.

Taxa	**Species**	**Relationship Between Hunger and Sexual Cannibalism**	**Citation**
Spiders	*Dolomedes fimbriatus*	none	Arnqvist and Henriksson (1997)
	Latrodectus mactans	none	Breene and Sweet (1985)
	Araneus diadematus	none	Elgar and Nash (1988)
	Argiope bruennichi	none	Fromhage et al. (2003)
	Phidippus johnsoni	none	Jackson (1980)
	Latrodectus hasselti	positive	Andrade (1998)
	Dolomedes triton	positive	Johnson (2001)
	Schizocosa ocreata	positive	Persons and Uetz (2005)
	Hogna helluo	positive	Wilder and Rypstra (unpublished)
	Argiope keyserlingi	Virgin: no Mated: positive	Herberstein et al. (2002)
	Nephila plumipes	Virgin: positive Mated: no	Schneider and Elgar (2001)
Praying Mantids	*Sphodromantis lineola*	positive	Kynaston et al. (1994)
	Tenodera aridifolia sinensis	positive	Liske and Davis (1987)
	Iris oratoria	positive	Maxwell (2000)
Isopods	*Ichthyoxenus fushanensis*	positive	Tsai and Dai (2003)

Table 2. Summary of studies investigating a relationship between sexual size dimorphism (SSD) and female attacks and successful cannibalisms for a range of spider species. "NA" indicates that data were not available

		Relationship Between SSD and		Average SSD in Body Length (Female / Male)	
Family	Species	Female Attacks	Sexual Cannibalism		Citation
Araneidae	*Argiope keyserlingi*	NA	positive	2.80	Elgar et al. (2000)
	Argiope aurantia	negative	none	4.00	Foellmer and Fairbairn (2004)
	Araneus diadematus	none	positive	1.89	Elgar and Nash (1988)
	Argiope bruennichi	NA	none	3.33	Fromhage et al. (2003)
Lycosidae	*Schizocosa ocreata*	positive	positive	1.26	Persons and Uetz (2005)
	Hogna helluo	NA	positive	1.73	Wilder and Rypstra (this study)
Pisauridae	*Dolomedes fimbriatus*	none	positive	1.91	Arnqvist and Henriksson (1997)
	Dolomedes triton	none	positive	1.75	Johnson (2005)
Tetragnathidae	*Nephila plumipes*	negative	negative	4.20	Elgar and Fahey (1996), Schneider and Elgar (2001)
	Nephila edulis	none	positive	3.83	Schneider et al. (2000), Elgar et al. (2003)
	Nephila fenestrata	NA	none	NA	Fromhage and Schneider (2005)
Theridiidae	*Latrodectus hasselti*	NA	none	4.00	Andrade (1998)

Figure 1. Diagrammatic representation of the effects of ecological (top rectangles) and phylogenetic (bottom rectangles) factors on the frequency of sexual cannibalism. Circles represent the mechanisms through which these factors affect the frequency of sexual cannibalism.



CHAPTER 2: DIET QUALITY AFFECTS MATING BEHAVIOR AND EGG PRODUCTION IN A WOLF SPIDER

Abstract

Recent evidence suggests that the quality (i.e. nutritional content) of food can have important impacts on life history and behavior. I tested the effects of diet quality of prey fed to males and females on mating behaviors, sexual cannibalism and egg production in the wolf spider, *Pardosa milvina*. There was no effect of diet quality on the occurrence of mating or the timing of copulatory behaviors. Contrary to my predictions, females on the high quality diet engaged in a greater number of attacks on males before and after mating and were more likely to cannibalize males following mating. Egg production of females that matured and mated in the lab was not affected by diet quality. However, field-caught adult females produced egg sacs more quickly when raised on the high quality diet. My results suggest that the quality of prey can limit the latency to female egg production. However, females do not compensate for low quality diets by increasing attack rates or cannibalism on males. Rather, as has been seen in a couple of foraging studies, females on the high quality diet appear to be more voracious predators. Few studies have considered the role of food quality for mating. These results highlight the need for more research on the role of food quality for mating interactions and the mechanisms responsible for more voracious feeding by females on high quality diets.

Introduction

Food availability is a fundamental factor that can influence the life history and behavior of a variety of organisms (Wilbur et al. 1974, Pyke et al. 1977). Animals require certain amounts of energy and nutrients for metabolism, growth, and reproduction (Raubenheimer and Simpson 1997, Sterner and Elser 2002, Simpson et al. 2004). Yet, both the quantity and quality (e.g. carbon, nitrogen, phosphorus, lipid, protein, or vitamin content) of food can vary in nature and have important impacts on fitness (Sterner and Elser 2002). To satisfy nutritional requirements and avoid nutrient limitation, animals have evolved a variety of adaptations including increased consumption rate, selective consumption of certain food types or parts of food items, and dietary mixing (Slansky and Rodriguez 1987, Yang and Joern 1994, Simpson et al. 2004, Mayntz et al. 2005, Simpson et al. 2006). However, despite these adaptations, animals can still experience nutrient limitation in nature if the overall quantity of food is limited and precludes increased consumption or selectivity. Hence, it is important to understand the consequences of feeding on low quality diets for life history and behavior.

Diet quality may be particularly important for terrestrial predatory arthropods, which are frequently food and nutrient limited in nature (Wise 1993, Fagan et al. 2002, Denno and Fagan 2003, Fagan and Denno 2004, Wise 2006). For example, extensive observations of wolf spiders in the field have revealed that rates of prey capture are very low (Nyffeler and Benz 1988, Nyffeler and Breene 1990). In addition, many prey items, especially herbivorous prey, have lower concentrations of nitrogen in their tissues than that presumably required for optimal growth (Urabe and Watanabe 1992, Fagan et al. 2002, Denno and Fagan 2003, Fagan and Denno 2004, Matsumura et al. 2004). Feeding on low quality prey can have dramatic consequences for the development of predatory arthropods including reductions in survival, growth and energy reserves (Toft and Wise 1999, Mayntz and Toft 2001, Oelbermann and Scheu 2002, Jespersen and Toft 2003, Mayntz et al. 2003, Mayntz and Toft 2006, Raubenheimer et al. in press). However, not all effects of food quality are predictable. Mayntz and Toft (2006) observed greater foraging by spiders maintained on high quality diets despite the prediction that spiders on low quality diets should increase consumption to compensate for the low nutrient content of their food. Hence, it is important to experimentally test the effects of diet quality on the life history and behavior of predatory arthropods.

The recent feeding history of males and females can affect many aspects of reproduction including mate choice (Bonduriansky 2001, Cotton et al. 2006), sexual ornament size (Andersson 1994), courtship display rate (Kotiaho et al. 1998), and fecundity (Kreiter and Wise 2001, Kotiaho 2001). While most studies of the effects of feeding on reproduction have examined food quantity, several recent studies have provided evidence that diet quality or nutritional status of invertebrates may also be important for reproductive behaviors (Wagner and Hoback 1999, Holzer et al. 2003, Hunt et al. 2004, Bertram et al. 2006). For example, male crickets with low concentrations of nutrients in their bodies or those provided low quality food court females less intensely and are less attractive as mates (Wagner and Hoback 1999, Holzer et al. 2003, Hunt et al. 2004, Bertram et al. 2006). However, not much is known about how the mating behavior of predatory species responds to food quality and if there are interactive effects of male and female diet quality on mating behavior and egg production.

The purpose of this study was to test the effects of diet quality of males and females on mating behavior, sexual cannibalism and egg production in the wolf spider, *Pardosa milvina* (Hentz 1844) (Araneae, Lycosidae). In spiders, low quantities of food have been reported to result in a lower frequency of mating, higher frequency of aggression and sexual cannibalism, and lower female fecundity (e.g. Kessler 1971, Wise 1979, Andrade 1998, Kotiaho 2000, Uetz et al. 2002, Persons and Uetz 2005). Hence, I expected parallel effects for low food quality. I manipulated the media on which *Drosophila melanogaster* were raised to produce low and high quality prey of the same species (e.g. Mayntz and Toft 2001). I predicted that there would be significant effects of male and female diets on mating, with higher frequencies of mating in trials in which males, females or both were fed high quality diets. I also predicted that levels of aggression towards males and sexual cannibalism would be higher for females on the low quality diet since females could potentially remediate a nutrient deficiency in their diet by consuming males. Finally, I predicted that females would produce egg sacs more quickly and would produce larger egg sacs when raised on the high quality diet.

Methods

Pardosa milvina is a relatively small species of wolf spider (adult males: 10 - 15 mg; adult females: 15 - 25 mg) that occurs at high densities in agricultural fields in the Midwestern US (Marshall and Rypstra 1999, Marshall et al. 2002). All spiders used in these experiments were collected from agricultural fields at the Miami University Ecology Research Center

(Oxford, Butler County, Ohio) from March - May 2006. Spiders were maintained in the laboratory in translucent plastic cups (5 cm high x 8 cm wide) with a moist peat moss substrate on a 13:11 light:dark cycle at approximately 25 °C and 70% humidity. Animals used in mating trials were collected as penultimates (i.e. one molt from adulthood) and raised to maturity in the laboratory. Individuals were fed a diet of two appropriately sized domestic cricket nymphs (*Acheta domesticus*) twice per week until maturity. A second group of mature females with egg sacs were collected from the field and used to further explore the effects of diet on egg sac production.

Experimental Diet Treatments

All spiders were fed adult vestigial-winged *D. melanogaster*. I manipulated the quality of *D. melanogaster* as prey by raising them on two different types of media (e.g. Mayntz and Toft 2001). For the low quality prey, *D. melanogaster* were raised on potato flake medium (Ward's™ Instant *Drosophila* Medium). For the high quality prey, *D. melanogaster* were raised on potato flake medium (Ward's™ Instant *Drosophila* Medium) supplemented with 40 % crushed dog food (Ol' Roy™ Dog Food; 21 % protein) by mass. There is no difference in dry mass of *D. melanogaster* raised on the two types of media (Wilder and Rypstra in prep.). Feeding spiders with *D. melanogaster* raised on media supplemented with dog food has significant effects on spider growth and foraging (Mayntz and Toft 2001, Mayntz et al. 2003, Jespersen and Toft 2003, Mayntz et al. 2005, Mayntz and Toft 2006).

Experiments

I conducted a full-factorial experiment in which I manipulated the prior diet (either low or high quality prey) of both males and females and paired them in all four possible combinations (n = 17 or 18 per treatment). For the experimental feeding regimes, males and females were fed either low or high quality flies for several weeks before the mating trials. Males were fed two flies twice per week for four weeks and females were fed four flies twice per week for three weeks. Following the end of the feeding period, males and females were randomly paired for mating trials.

Trials were conducted in plastic containers 14 cm in diameter with smooth acetate walls. The bottom of the arena was covered with a layer of plaster of paris. Between trials, I sprayed the arenas with 70 % ethanol and rubbed the bottom of the arena to remove the top layer of plaster and any chemical cues left from the previous trial. I videotaped three trials at a time. Each arena was visually and seismically isolated from the others using partitions and foamboard. Females were introduced into the arenas and allowed to deposit pheromones and chemical cues for 10 minutes before the male was introduced. Trials began when the male was introduced and ended after 20 minutes or, if mating extended beyond 20 minutes, 2 minutes after the end of mating. If sexual cannibalism occurred, I removed the male's body so that the female could not consume it.

Immediately following the trials, I measured carapace width to the nearest 0.01 mm and mass to the nearest 0.1 mg for both males and females. I tested the effects of diet treatment on body condition using analysis of covariance on spider mass with carapace width as a covariate (Garcia-Berthou 2001). Condition was analyzed separately for males and females. I used two-factor analysis of variance (ANOVA) to test for effects of male and female diet treatment on number of attacks before and after mating, latency to male courtship, courtship duration, latency to mating, and copulation duration. Separate log-linear analyses were used to test the effects of male and female diet treatment on categorical responses including: the occurrence of mating, and attacks before and after mating. The frequencies of sexual cannibalism were too low to use log-linear analysis; hence, I tested the effects of female diet on sexual cannibalism with a Fisher Exact Test. T-tests and ANOVAs were conducted using Minitab software (release 14.2). Log-linear analyses and Fisher Exact Tests were conducted using Vassarstats (R. Lowry, website: faculty.vassar.edu/lowry/vassarstats.html).

Following mating trials, all females were returned to their original containers and maintained on their respective diet for 14 days or until they produced an egg sac. I recorded the day that the egg sac was produced and the mass of the egg sac to the nearest 0.1 mg. I tested for effects of female diet treatment on time to produce an egg sac using Kaplan-Meier survival analysis, which incorporates data on both latency to produce and percent of females that produced egg sacs. I tested for effects of male and female diet on egg sac mass using a two-factor ANOVA.

To further explore the effects of diet quality on egg production I conducted a second experiment. On 3 May 2006, I collected 36 females with egg sacs. The egg sacs were removed and the spiders were randomly assigned to low or high quality feeding regimes. Females were fed four *D. melanogaster* from their respective diet treatment (low or high quality) twice per week and monitored daily for egg sac production. I recorded the date of egg sac production and the mass of the egg sac to the nearest 0.1 mg. The experiment was terminated after 21 days. I tested for effects of female diet treatment on time to produce an egg sac using Kaplan-Meier survival analysis. I tested for effects of female diet on egg sac mass using an independent samples t-test.

Results

Mating Behavior

There were no effects of male or female diet treatment on body condition (Male Diet: $F_{1,62} = 0.02$, $p = 0.89$; Female Diet: $F_{1,67} = 0.05$, $p = 0.82$). Overall, mating occurred in 62 percent (44 of 71) of the experimental trials and there were no effects of male or female diet treatment on the frequency of mating (Table 1, Table 2). In a typical mating trial, males began courtship after 74 ± 9 s (mean ± 1 SE), there were 132 ± 21 s from the start of male courtship until mating and pairs spent 610 ± 51 s in copula. There were no significant effects of male or female diet treatment on the latency to male courtship, courtship duration, latency to mating, and copulation duration (Table 3).

Aggression and Sexual Cannibalism

Before mating, females were more likely to attack males on the high quality diet than males on the low quality diet (Table 1, Table 2). However, there was no effect of male diet treatment on the mean number of attacks ($F_{1,40} = 0.84$, $p = 0.36$). Females on the high quality diet tended to engage in a greater mean number of attacks on males before mating than females on the low quality diet (Figure 1a; $F_{1,40} = 3.83$, $p = 0.057$). After mating, females on the high quality diet tended to be more likely to attack males than females on the low quality diet (Table 1, Table 2). In addition, females on the high quality diet engaged in a higher mean number of attacks on males than females on the low quality diet (Figure 1b; $F_{1,40} = 6.22$, $p = 0.017$). Females on the high quality diet treatment engaged in postcopulatory sexual cannibalism (14 %, 5 of 36) significantly more frequently than females on the low quality treatment (0 %, 0 of 35; Fisher Exact Test: $p = 0.05$).

Egg Production

In the mating experiment, there was no effect of female diet treatment on latency to produce an egg sac (Figure 2a; Wilcoxon: $\square^2_1 = 0.16$, $p = 0.69$). There was also no significant effect of male diet ($F_{1,22} = 0.01$, $p = 0.96$), female diet ($F_{1,22} = 0.02$, $p = 0.90$) or the interaction ($F_{1,22} = 0.03$, $p = 0.87$) on egg sac mass (Figure 3a).

However, field-caught adult females maintained on the high quality diet produced egg sacs significantly more quickly than females on the low quality diet (Figure 2b; Wilcoxon: $\square^2_1 = 3.90$, $p = 0.048$). There was no significant effect of female diet treatment on egg sac mass (high quality = 5.92 ± 0.13, low quality = 5.99 ± 0.20; $t_{20} = 0.29$, $p = 0.78$).

Discussion

Diet quality had significant and unexpected effects on mating behavior and egg production in the wolf spider, *P. milvina*. There was no effect of diet quality on the occurrence of mating or the timing of copulatory behaviors. However, contrary to my predictions, females on the high quality diet engaged in more attacks on males both before and after mating and engaged in a higher frequency of sexual cannibalism than females on the low quality diet. The only results that supported my predictions were those on egg sac production in which females captured as adults in the field produced egg sacs more quickly on the high quality diet. These data suggest that diet quality of prey can limit the timing of egg production. Yet females do not compensate for low diet quality by increasing their attacks on males. Instead, females on the high quality diet engaged in more attacks and more cannibalism.

Studies of the effects of food quality on mating in crickets have shown that males fed high protein diets call more intensely and are more attractive to females (Wagner and Hoback 1999, Holzer et al. 2003, Hunt et al. 2004). In spiders, experiments manipulating the quantity of food (e.g. number of prey items) fed to males have demonstrated larger sexual ornament size and higher courtship intensity of males on high quantity diets (Kotiaho 2000, Uetz et al. 2002). Hence, I predicted that male *P. milvina* on high quality diets would begin courtship earlier, court longer and be more attractive to females. However, there were no effects of male diet treatment on latency to courtship, courtship duration or the probability of mating. Similarly, there is also evidence that diet quality does not affect courtship behavior in male *Schizocosa* spp. (E. A. Hebets pers. comm.). But, a recent study of *P. prativaga* did detect some effects of diet quality on male courtship behavior (S. Toft pers. comm.). One potential explanation for a lack of an effect of diet quality on male courtship in the current study is that food quality may be more important when food quantity is limited and males in my study may have been relatively well-fed. Another explanation is that males may have different nutritional requirements than females. Males may require prey items with high carbon or lipid content to provide the energy needed for energetically expensive courtship displays (Kotiaho et al. 1998). Further experiments that manipulate both the energy and nutrient content of prey items are needed to test if energy, nutrients or both have an effect on male courtship behavior.

Contrary to my predictions, females on the high quality diet attacked males and engaged in sexual cannibalism more than females on the low quality diet. Additionally, the frequency of sexual cannibalism was surprisingly high (14 % on the high quality diet), especially since previous experiments with *P. milvina* involving hundreds of trials and food quantity manipulations have failed to detect a frequency of sexual cannibalism higher than 2% (Rypstra et al. 2003, Schlosser 2005). Using similar diet treatments, foraging experiments have shown that female *Pardosa* spp. fed high quality diets (flies raised on dog food-supplemented media) consume a greater biomass of food (*P. prativaga*; Mayntz and Toft 2006) and kill a greater number of prey items (*P. milvina*; P. Sebastian and A.L. Rypstra unpublished data) than females fed lower quality diets (flies raised on unsupplemented media). Hence, high quality diets may increase female voracity or predatory ability both towards heterospecific prey and males, although the mechanism responsible is unknown (Mayntz and Toft 2006).

Morphological measures of body condition (e.g. abdomen size or weight relative to body size, Jakob et al. 1996) are typically used to assess female hunger level. However, in my experiment, the standard measure of body condition failed to predict female aggression and sexual cannibalism. Body condition alone may not be an accurate measure of hunger level or aggression towards potential prey items because females can have the same body condition but differ in their nutritional history and level of aggression towards prey (Mayntz and Toft 2006, P. Sebastian and A.L. Rypstra unpublished data) and conspecifics. Further research on the relationship between body nutrient content of predators and foraging behavior is needed to examine if predator nutrient composition may be another measure, in addition to body condition, of hunger level or foraging motivation.

I observed significant effects of diet on the latency to egg sac production using field caught adult females but not with virgin females that were mated in the laboratory. When individuals were mated in the laboratory, females on both treatments may have had sufficient time prior to mating (i.e. three weeks on their experimental feeding regime) to accumulate enough nutrients to produce an egg sac, which would decrease the probability of detecting a treatment effect. This is supported by the fact that when I used field caught adult females, which had presumably already mated in the field, females were able to produce egg sacs after only 14 days on their feeding regimes and over 80 % of females produced eggs sacs within 21 days. Mate availability does not appear limited in populations of *P. milvina* and females likely do not have to wait several weeks to mate in the field (Marshall and Rypstra 1999, Marshall et al. 2002). Hence, the experiment with field caught adult females is likely more representative of conditions experienced in nature.

My experimental manipulations affected the quality of prey for *P. milvina* but it is not clear what aspects of food quality were manipulated. There is a higher percent nitrogen and a lower C:N ratio in dog food supplemented flies relative to control flies, which may be due to the high protein content of dog food (Wilder and Rypstra unpublished data). However, nitrogen (or protein) is likely not the only factor affecting the quality of flies raised on dog food supplemented media. For example, Mayntz and Toft (2001) observed that *P. amentata* grew larger when raised on flies supplemented with dog food than flies supplemented with only amino acids. Dog food contains a number of other ingredients that could affect fly quality including bone meal, which could elevate phosphorus content, and various vitamins and minerals. Further studies using manipulations of single and combined factors (e.g. lipid, protein, phosphorus, vitamins and minerals) are needed to determine which aspects of food quality are important for the life history and behavior of predatory arthropods.

The current study provided a general manipulation of food quality (i.e. low vs. high). However, further studies are needed to determine which aspects of food quality (e.g. C, N, P, lipid, protein) impact reproductive behaviors and egg production. Ecological stoichiometry (ES; Sterner and Elser 2002) and geometric feeding (GM; Raubenheimer and Simpson 1999) are two frameworks that may prove useful for studying the role of the ratio of multiple limiting compounds (e.g. energy and nutrients) for evolution, life history, and behavior. Both frameworks have the potential to provide mechanistic connections between the composition of food items, physiology and organismal performance (Elser et al. 1996, Raubenheimer and Simpson 1997, 1999, Elser et al. 2000, Sterner and Elser 2002, Simpson et al. 2004). The main differences between the frameworks are in their measurements of food contents (ES: carbon, nitrogen and phosphorus; GM: carbohydrate, lipid and protein), their primary connections between individual performance and other fields (ES: population and ecosystem ecology; GM: physiology and animal behavior), and the taxa in which they have been most frequently studied (ES: algae and aquatic crustaceans; GM: terrestrial herbivorous arthropods) (Simpson and Raubenheimer 1995, Elser et al. 1996, Raubenheimer and Simpson 1997, 1999, Elser et al. 2000, Sterner and Elser 2002, Simpson et al. 2004). However, despite these differences, these frameworks have tremendous potential, both separately and combined, for guiding future research and providing a comprehensive view of the role of food quality for the ecology and evolution of animals.

I provide evidence that food quality had significant effects on mating interactions in the wolf spider *P. milvina*. Surprisingly, despite strong, uni-directional predictions, I observed opposite effects of food quality on aggression, with females on the high quality diet engaging in more attacks and more cannibalism of males. Diet quality is an important parameter that can vary in nature. Yet, few studies have examined the role of food quality for animal behavior. Further research examining the effects of explicit manipulations of energy and nutrient content of diets on life history, behavior and physiology will provide great insight into the importance of food quality for invertebrates and the mechanisms by which it affects organismal performance.

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Table 1. Results of log-linear analyses testing the effects of male and female diet treatment (low or high quality prey) on the occurrence of mating, attacks before mating, and attacks after mating.

		Mating		Attacks Before Mating		Attacks After Mating	
Effect	df	G^2	p	G^2	p	G^2	p
Male Diet	1	0.04	0.84	4.68	0.03	0.34	0.56
Female Diet	1	0.42	0.52	0.62	0.43	3.32	0.07
Male * Female Diet	4	3.20	0.52	6.66	0.16	4.24	0.37

Table 2. Frequencies of mating, attacks before mating, and attacks after mating by male and female diet treatment.

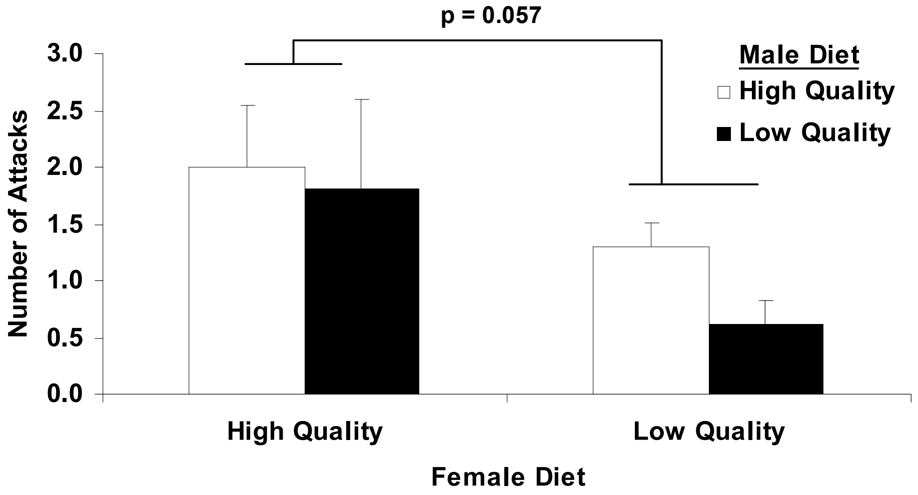
Male Diet	Female Diet	Mating	Attacks Before Mating	Attacks After Mating	Sexual Cannibalism
High Quality	High Quality	67 % (12 of 18)	82 % (9 of 11)	75 % (9 of 12)	11 % (2 of 18)
	Low Quality	56 % (10 of 18)	90 % (9 of 10)	40 % (4 of 10)	0 % (0 of 18)
Low Quality	High Quality	50 % (9 of 18)	70 % (7 of 10)	60 % (6 of 10)	17 % (3 of 18)
	Low Quality	76% (13 of 17)	46 % (6 of 13)	42 % (5 of 12)	0 % (0 of 17)

Table 3. Results of 2-factor analysis of variance testing the effects of male and female diet treatment (low or high quality) on copulatory behaviors.

	Latency to Courtship		Courtship Duration		Latency to Mating		Copulation Duration	
Effect	$F_{1,61}$	p	$F_{1,40}$	p	$F_{1,40}$	p	$F_{1,40}$	p
Male Diet	0.25	0.62	0.01	0.96	0.02	0.90	0.01	0.99
Female Diet	0.70	0.41	1.89	0.18	0.01	0.54	0.02	0.89
Male * Female Diet	0.11	0.74	0.02	0.88	0.39	0.95	0.02	0.90

Figure 1. Comparison of the effects of male and female diet treatment (low or high quality) on the mean number of attacks by females on males: A) in the two minutes before mating and B) in the two minutes after mating. Bars and p-values indicate a comparison of the female diet effect

A) Before Mating



B) After Mating

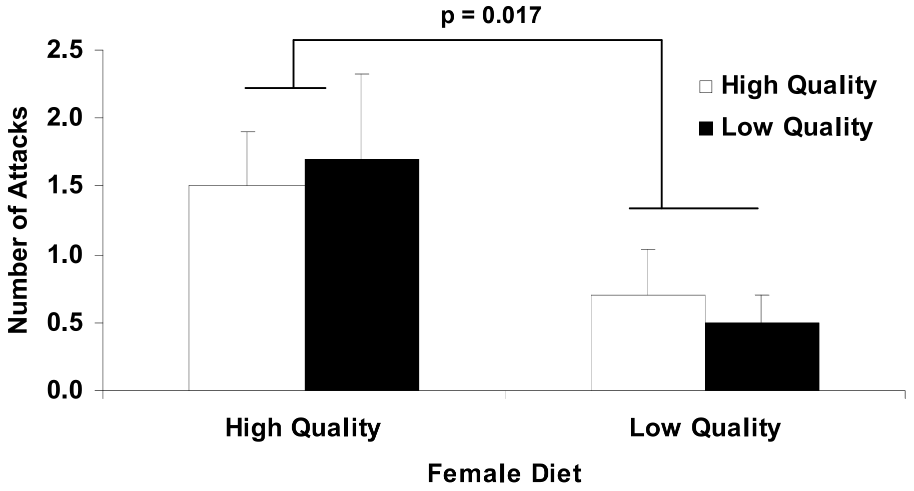
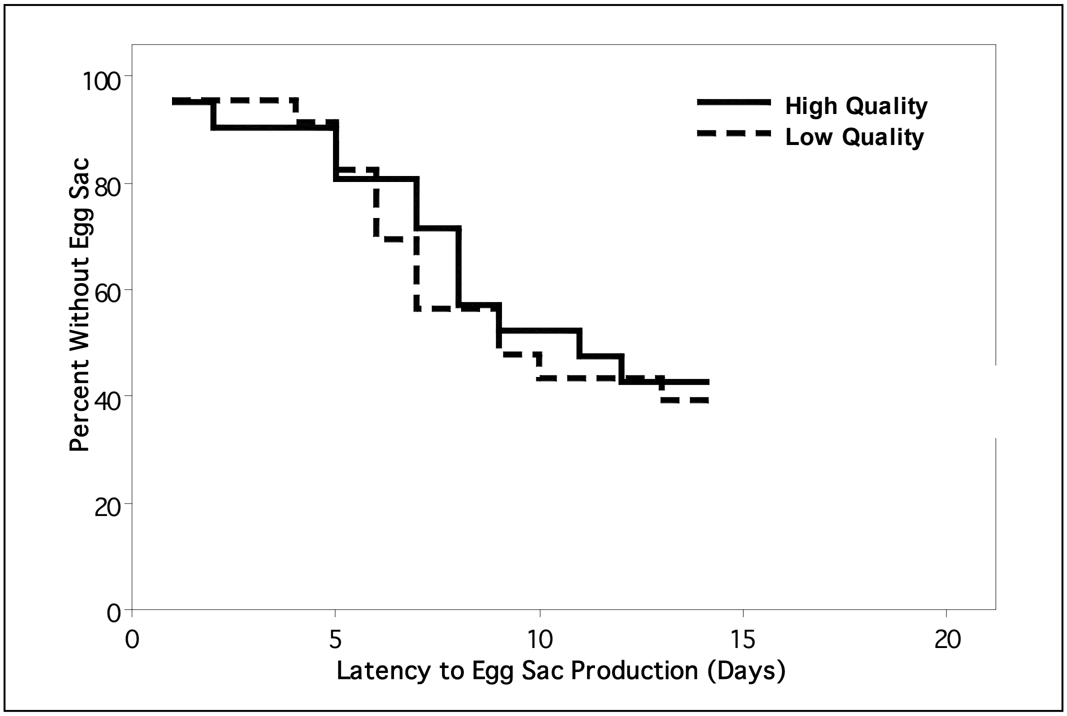


Figure 2. Survival plots displaying the effect of female diet treatment (low or high quality) on the time until egg sac production in: A) the first experiment with females mated in the laboratory (p = 0.69) and B) the second experiment with females collected as adults from the field (p = 0.048).

A)



B)

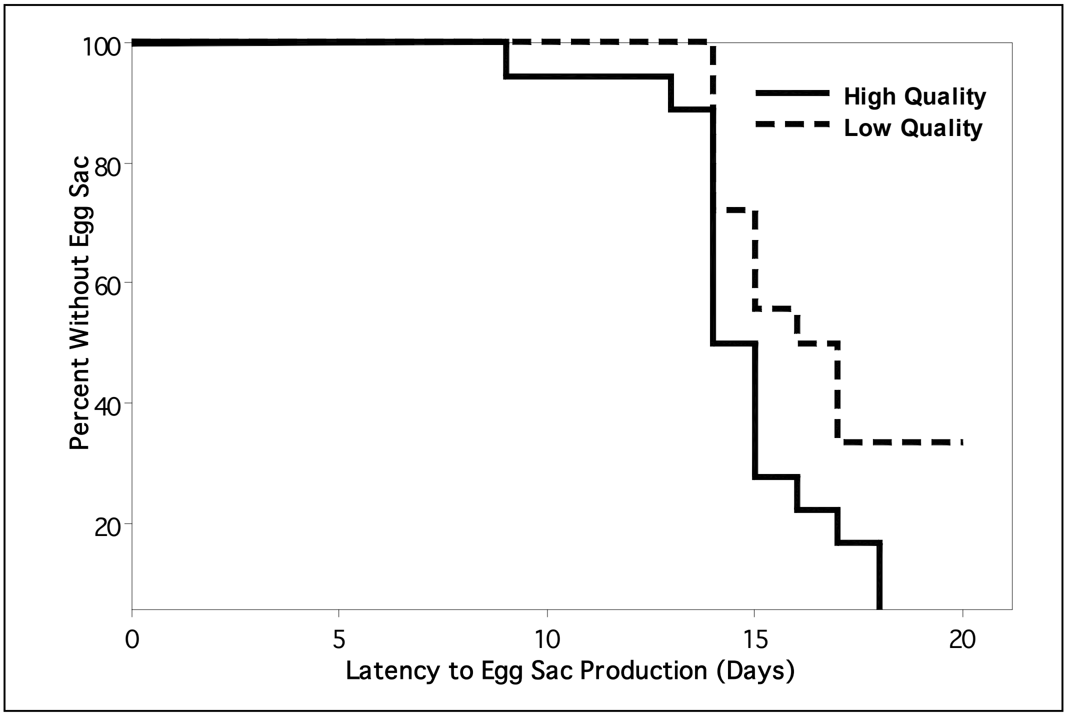
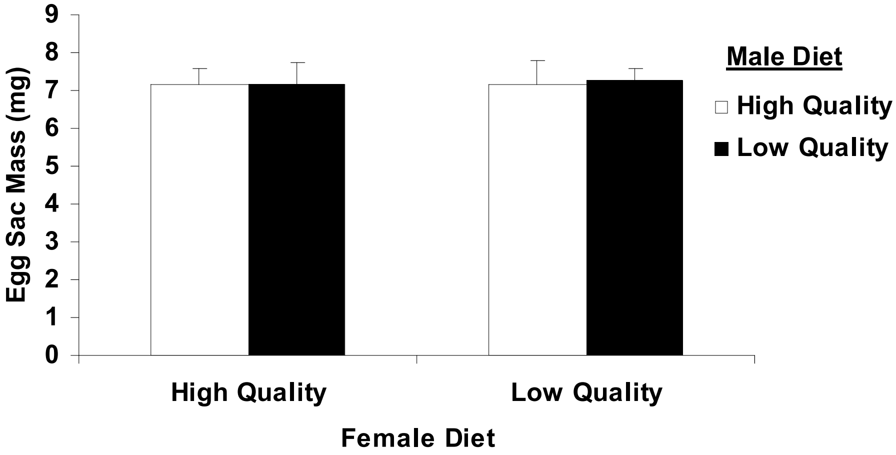


Figure 3. Comparisons of the mass of egg sacs produced by females: in relation to male ($p = 0.96$) and female ($p = 90$) diet treatment in the first experiment

A)



CHAPTER 3: PRIOR ENCOUNTERS WITH THE OPPOSITE SEX AFFECT MALE AND FEMALE MATING BEHAVIORS IN A WOLF SPIDER

Abstract

Mate availability can vary widely in nature depending upon population density and sex ratio and can affect the ability of individuals to be selective in mate choice. I tested the effects of prior encounters with mates (i.e. exposure to the opposite sex either with or without mating) on subsequent mating behavior in two experiments that manipulated mate availability for both males and females in the wolf spider, *Hogna helluo*. The probability of mating in the experimental trial depending upon whether the prior encounter involved mating or not and males and females responded in opposite directions. Exposure without mating resulted in a higher frequency of mating for females and a lower frequency of mating for males, while prior mating experience resulted in a lower frequency of female remating and a higher frequency of male remating. Prior exposure without mating did not affect female aggression. However, mated females engaged in precopulatory cannibalism more frequently than virgins. Mated males escaped postcopulatory cannibalism more frequently than virgins. My results show that males respond to exposure without mating in the expected manner. However, prior mating had unexpected effects on males, which may be due to mated males being of higher quality. There were little or no effects of the size of the prior exposure or mate on subsequent mating behaviors despite exhaustive statistical analysis. Given that population densities of *H. helluo* are frequently low in nature, there may not have been selection pressure for the adaptations required to remember the phenotypes of previous potential mates.

Introduction

Mate availability can have important consequences for sexual selection (Trivers 1972; Emlen and Oring 1977; Kokko and Rankin 2006). High mate availability can decrease intrasexual competition for access to the opposite sex and can increase selectivity in mate choice (Halliday 1983; Bonduriansky 2001; Kokko and Rankin 2006). Males and females can respond to variation in mate availability through genetically-distinct alternative mating strategies (Shuster 1989; Shuster and Wade 1991), or through behavioral plasticity (mating tactics: Perrill 1978; Thornhill 1981; Brockmann and Penn 1992, or copulatory behaviors Gabor and Halliday 1997; Bateman and Fleming 2006; Kokko and Rankin 2006). Of these responses, plasticity is more flexible and can allow individuals to respond adaptively to variation in mate availability on a short time scale.

In order for behavioral plasticity to be effective, individuals must have reliable cues of mate availability. A number of studies have shown that mating status of females affects their receptivity towards or selection criteria for subsequent mates (Jackson 1981; Gabor and Halliday 1997; Herberstein et al. 2002; Norton and Uetz 2005). In some species, females will mate indiscriminately as virgins to avoid sperm limitation and subsequently become selective in mate choice (Gabor and Halliday 1997; Bateman et al. 2001; Pitcher et al. 2003). Evidence also suggests that exposure to members of the opposite sex without copulation can influence subsequent receptivity or mate selectivity in some species (Milinski 2001; Hebets 2003; Johnson 2005). For example, female fishing spiders that cohabited with males as juveniles are more aggressive towards males as adults (Johnson 2005). Most studies of the effects of mate availability on mating behavior have manipulated male availability for females (Shelly 1993; Souroukis and Murray 1995; Gabor and Halliday 1997; Bateman et al. 2001; Milinski 2001; Wagner et al. 2001; Pitcher et al. 2003; Johnson 2005). However, theory and recent evidence suggest that female availability may also affect male behavior (Bonduriansky 2001; Mathews 2002; Bateman and Fleming 2006).

Interestingly, not only can a prior encounter with a potential mate affect receptivity and mate choice, but the phenotype of the prior exposure or mate can be important and affect acceptance of a subsequent mate (Gabor and Halliday 1997; Bateman et al. 2001; Milinski 2001; Pitcher et al. 2003). Individuals often encounter mates sequentially in nature and may use information on the quality of mates encountered to form a mate acceptance threshold

(Dombrovsky and Perrin 1994). For example, in sticklebacks, females are more likely to display receptivity to a low quality male if they had previously been exposed to a low quality male than if they had been previously exposed to a high quality male (Milinski and Bakker 1992). However, most studies of the effects of the phenotype of a prior encounter on subsequent mating have been conducted on species that occur at moderate to high densities in the field and it is not known if species that occur at low densities in nature display similar effects (Gabor and Halliday 1997; Bateman et al. 2001; Milinski 2001; Hebets 2003; Pitcher et al. 2003).

The wolf spider *Hogna helluo* (Araneae, Lycosidae) is an ideal species with which to examine the effects of mate availability on mating behavior. Populations usually occur at relatively low densities in the field and females do not appear to emit an airborne mate attraction pheromone (A. Schlosser and A. L. Rypstra unpublished data), which suggests that encounters between males and females may be relatively infrequent (Marshall and Rypstra 1999; Marshall et al. 2002). However, under certain circumstances (e.g. high habitat structure or prey availability) population density can increase dramatically (Marshall et al. 2000). Hence, mate availability can vary over relatively short spatial and temporal time scales for male and female *H. helluo*. Behavioral plasticity would allow individuals to adjust their mating behavior appropriately to current conditions.

The purpose of this study was to examine if male and female *H. helluo* display plasticity in mating behaviors in response to information about the availability of the opposite sex. I manipulated the perception of mate availability of focal individuals either by exposing them to visual and chemical information from the opposite sex without the opportunity to mate (Experiment 1) or through mating experience (Experiment 2). I then tested focal individuals in subsequent trials to examine if their mating behavior depended upon their prior experience, or lack thereof, with the opposite sex.

Since most studies of sequential exposure and mating status have only manipulated females, the first goal of my study was to test if males and females respond similarly to encounters with the opposite sex. I predicted that both exposure without copulation and mating of males and females would result in reductions in the frequency of subsequent mating because both males and females would perceive a higher density of the opposite sex and, hence, the chance to be more selective in mate choice. The second goal of my study was to test if prior exposure had similar effects on subsequent mating behavior as a prior mating. For females, I predicted that the response to prior mating would be stronger than the response to prior exposure because sperm transfer can cause physiological changes in females (Aisenberg and Costa 2005). But, for males, I predicted that they would respond similarly whether the prior encounter was an exposure or a mating. Finally, I tested if males and females exhibit sequential mate choice by testing the effects of the size of the stimulus animal from the exposure or prior mate on subsequent mating behaviors. I predicted that if individuals discriminate between mates based on size, then information about the size of previously encountered stimulus animals or mates might affect subsequent mating behavior.

Methods

Study Species: The wolf spider *H. helluo* (females, ca. 300-800 mg; males, ca. 150-300 mg) is present in agricultural fields in the Midwestern United States (Marshall et al. 2002). All individuals used in this study were lab-reared offspring of females collected in and around the agricultural fields at the Miami University Ecology Research Center (Oxford, Butler County, OH). Upon hatching and dispersal from the mother, individual spiderlings were placed in translucent plastic containers (8 cm diameter x 5 cm high) with 1 cm of moist peat moss, a slice of potato and an active culture of *Sinella curviseta* (Collembola, Entomobryidae). Spiders were maintained in an environmental chamber at 25^{o}C and a 13:11 light:dark cycle. Spiderlings were switched to a diet of two appropriately sized crickets (*Acheta domesticus*) once or twice per week after approximately one month on the collembola diet. Upon reaching approximately one cm body length, individuals were transferred to larger containers (11 cm diameter x 8 cm high). All spiders were checked for maturity after molting and, when mature, were labeled with the date of maturity.

Mating Trials: Mating trials for both experiments were conducted in circular plastic containers (19 cm diameter x 6 cm high) lined with clean filter paper. Males and females were randomly paired. Females were allowed to acclimate and deposit silk (which induces male courtship upon contact) for 30 minutes before a male was introduced under a clear plastic vial opposite the female. Following a 15 minute acclimation period for the male, the vial was removed and individuals were able to interact. Trials were videotaped for 90 minutes in isolated booths, which contained 6 fluorescent lights and a video camera mounted one meter above the arena.

Prior to running trials, I recorded the carapace width (to the nearest 0.01 mm) and mass (to the nearest 0.1 mg) of males and females. Carapace width was used as a measure of size because this structure is fixed at maturity. The ratio of mass to carapace width was used as a measure of body condition because energy reserves and consumed food cause the abdomen of spiders to increase in size relative to the fixed carapace size (Jakob et al. 1996). During review of the videotapes, I recorded the occurrence of copulation, occurrence of sexual cannibalism, time of first contact between male and female, time of female receptivity posture, time of male mounting, and time of male dismounting.

Experiment 1: Exposure without Mating: All males and females were maintained on a constant feeding regime upon reaching adulthood. Males were maintained on one juvenile domestic cricket twice each week and were fed two days prior to mating trials. Females were fed once per week for three weeks before the start of trials. For the first two feedings, females were fed one cricket that was approximately the same volume as the female carapace. For the third feeding, females were allowed up to six hours to feed on five crickets that were each approximately the same volume as the female carapace. Females began the exposure regime two days after the third feeding.

This experiment utilized a full-factorial design of exposing males and females either to a member of the opposite sex (i.e. stimulus animal) or to a blank control (neither sex exposed, n = 13; only female exposed, n = 14; only male exposed, n = 12; and both sexes exposed, n = 14). Given that female *H. helluo* build burrows and that males appear to search for females, exposures were conducted by introducing a male into a female's container. When individuals were exposed to the opposite sex, a clear plexiglass divider containing 18 holes (2 mm in diameter each) was placed in the female container and the male was introduced on the opposite side of the divider from the female for a 15 minute exposure period. The divider allowed both visual and chemical communication between males and females. Individuals used as the "cue" animal for exposures were taken from a separate pool of animals and never used in mating trials. Control trials involved no exposure to the opposite sex. For control trials for males, a clear plexiglass divider was placed in a clean container with one cm of a peat/soil mixture and the male was placed on an arbitrary side of the divider for 15 minutes. For control trials for females, a clear plexiglass divider was placed in the female's container for 15 minutes. The exposure regime for both males and females followed a four day schedule. Individuals were exposed to a different member of the opposite sex or to a blank control on day one and day three and mating trials (as described above) occurred on day four.

Experiment 2: Prior Mating: In this experiment, I randomly paired males and females for mating trials. Males were fed one, and females two, juvenile crickets per week and both sexes were fed one cricket two to four days prior to the trial. All individuals were tested in one trial as a virgin and all females that mated and a random subset of males that mated were tested again in a second trial. Hence, I had a full factorial combination of males and females that were virgin and mated (i.e. both sexes virgin, n = 101; female virgin and male mated, n = 16; male virgin and female mated, n = 68; and both sexes mated, n = 9).

Statistical Analyses:

I tested the effects of encounters with the opposite sex on frequencies of mating using log-linear analysis. I tested the effects of male and female exposure to visual and chemical cues of the opposite sex on time to mating, time to female receptivity, time from female receptivity to mating and copulation duration using a two factor analysis of variance (ANOVA). Female receptivity was measured as the time the female assumed the stereotypical posture that allows the male to climb onto the dorsal surface of the female. However, for the mating status experiment, the number of trials in which mating occurred were low in two of the categories; so, I conducted separate independent samples t-tests for males (virgin trials: n = 68; mated trials: n = 16) and females (virgin trials: n = 78; mated trials: n = 6) to test the effects of mating status on the timing of copulatory behaviors.

Since the overall frequency of sexual cannibalism was low in Experiment 1, I compared the frequency of aggression among treatments with log-linear analysis. Attacks were defined as rapid movements of the female directly towards the male. The average time between when male and female first encountered each other and when copulation began was 177 ± 35 s. Hence, to provide comparable measures of aggression before and after mating I measured the frequency of aggressive interactions within 180 s prior to mating and within 180 s after the end of mating. In Experiment 2, I compared the effects of male and female mating status for pre- and postcopulatory sexual cannibalism separately using chi-square tests. The frequencies of pre- and postcopulatory cannibalism were too low in some treatments to use a log-linear analysis but were high enough when categories were combined to use chi-square tests.

I tested if male or female size affected mate choice using linear regression on data from the "both virgins" treatment in Experiment 2. I then tested if the size of the prior exposure stimulus animal or prior mate affected the occurrence of mating or the timing of copulatory behaviors in the experimental trial. However, there was no clear *a prior* prediction about whether individuals would discriminate by size based on absolute characteristics (i.e. just the size of the prior exposure individual or mate) or comparative characteristics (i.e. the size of the current mate relative to the prior exposure individual or mate). Hence, several measures of size of stimulus animals (Experiment 1: average size, size of the larger, current mate minus the average size of the prior exposure individuals and current mate minus the size of the larger exposure individual; Experiment 2: size of the previous mate and difference in size between current and previous mate) were used in regressions to test for relationships between the phenotype of the prior stimulus animal and either the occurrence of mating or, if mating occurred, the timing of copulatory behaviors (i.e. time to mating, time to female receptivity, time from female receptivity to mating and copulation duration). I tested for effects of the size of the prior stimulus animal on the occurrence of mating in the test trial using logistic regression. I tested for relationships between copulatory behaviors and the size of the prior stimulus animal using linear regression. For Experiment 1 I conducted 16 linear regression tests (i.e. four predictor and four response variables) for each sex and for Experiment 2 I conducted 8 linear regression tests (i.e. two predictors and four response variables) for each sex. I used a sequential Bonferroni-corrected □ for evaluation of statistical significance for my results because the standard Bonferroni-corrected □ can sometimes become unreasonably low when there are many comparisons (Rice 1989). In the results, I present all p-values calculated by the statistical tests.

Results

Frequency of Mating

Experiment 1. Exposure without Mating: Exposure to the visual and chemical cues of potential mates affected the likelihood that subsequent mating would occur (Figure 1a). Specifically, the likelihood of mating was lower for males that had previously been exposed to cues from a female than control males ($G^2 = 4.38$, $p = 0.04$). There were also nonsignificant trends for a higher frequency of mating if females had been previously exposed to males ($G^2 = 3.06$, $p = 0.08$) and for an interaction with male and female exposure status ($G^2 = 8.88$, $p = 0.06$). There was a reduction in the frequency of mating in the treatment where only males were exposed to females but all other treatments appear higher and relatively similar in the frequency of mating (Figure 1a).

Experiment 2. Prior Mating: Prior mating of males and females also affected the frequency of subsequent mating (i.e. remating) but the patterns were opposite those observed in the prior exposure experiment (Figure 1b). Log-linear analysis revealed a significantly higher frequency of mating for mated relative to virgin males ($G^2 = 4.98$, $p = 0.03$). In contrast, there was a significantly lower probability that females would mate if they had previously mated ($G^2 = 74.34$, $p < 0.001$).

Copulatory Behaviors

Experiment 1. Exposure without Mating: There was no effect of male or female treatment on the time from the start of the trial until the start of mating. Analysis of time until female receptivity and time from receptivity to mating revealed that while previously exposed females (320 ± 43 s) tended to take longer to reach receptivity than unexposed females (194 ± 53 s; $F_{1,31} = 3.11$, $p = 0.088$), once they reached receptivity, previously exposed females (48 ± 22 s) took less time to mate than unexposed females (94 ± 33 s; $F_{1,27} = 4.77$, $p = 0.04$). There were no effects of male or female exposure status on copulation duration.

Experiment 2. Prior Mating: There was a nonsignificant trend for virgin males to copulate longer than mated males ($t = 1.73$, $p = 0.09$). There were no other effects of male or female mating status on time to copulation (male status: $t = 0.69$, $p = 0.50$; female status: $t = 0.11$, $p = 0.92$), time to female receptivity (male status: $t = 1.21$, $p = 0.23$; female status: $t = 0.01$, $p = 0.99$) or time from female receptivity to copulation (male status: $t = 0.25$, $p = 0.81$; female status: $t = 1.36$, $p = 0.22$).

Intersexual Aggression

Experiment 1. Exposure without Mating: Sexual cannibalism occurred in only 15 percent (8 of

53) of the trials. Since the number of cannibalistic events was too small to analyze statistically, I compared aggressive behavior among treatments. The mean number of attacks within the first three minutes after male and female contact was low (overall mean = 0.53 ± 0.14) and was not affected by treatment. There were no effects of female exposure (G^2 = 0.48, p = 0.49), male exposure (G^2 = 2.24, p = 0.13) and no interaction between male and female exposure (G^2 = 3.32, p = 0.51) on the probability of a precopulatory attack (Figure 2a). Similarly, there was no effect of female exposure (G^2 = 0.36, p = 0.55), male exposure (G^2 = 0.04, p = 0.84) or the interaction (G^2 = 4.36, p = 0.36) on the probability of a postcopulatory attack (Figure 2a).

Experiment 2. Prior Mating: Previously mated females were significantly more likely to engage in precopulatory cannibalism than virgin females (Figure 2b; Chi-Square = 6.04, p = 0.01). Too few of the mated females remated (4 of 68) in their second trial to allow for analysis of postcopulatory cannibalism. For males, there was no effect of male mating status on precopulatory cannibalism (Chi-Square = 2.63, p = 0.20). However, previously mated males were less likely to be cannibalized following mating than males that were virgin before the trial (Figure 2b; Chi-Square = 3.87, p = 0.049).

Effects of Size of Prior Exposure or Mate

Females preferred to mate with smaller males (logistic regression: male carapace: z = -1.95, p = 0.05). However, males did not appear to select females on the basis of female size (logistic regression: z = - 0.28, p = 0.78).

Experiment 1. Exposure without Mating: None of the measures of the size of the males used as exposure cues for females (size of average, larger, difference between current male and average or larger) affected the occurrence of mating (all $z \leq 1.29$, all $p \geq 0.17$). Similarly, none of the measures of the size of the females used as exposure cues for males affect the probability of mating using sequential Bonferroni corrected □ levels (all $z \leq 2.03$, all $p \geq 0.04$). For copulatory behaviors, out of 32 regression tests, none were significant using sequential Bonferroni corrected □ levels and only one would have been significant at the traditional □ = 0.05 (Table 1A, B).

Experiment 2. Prior Mating: There were no effects of the size of the previous mate or the difference in size between the previous and current mate on the occurrence of copulation (female: all $z \leq 0.79$, all $p \geq 0.43$; male: all $z \leq 0.74$, all $p \geq 0.46$). There were no significant relationships between the timing of copulatory behaviors and the size of the prior mate (male or female) or difference in size between the current and prior mate using sequential Bonferroni corrected □ levels and only two would have been significant at the traditional □ = 0.05 (Table 2).

Discussion

Both male and female *H. helluo* display plasticity in mating behavior depending upon information on the availability of potential mates. Interestingly, males and females responded in opposite directions within each of the experiments. Males and females also responded differently depending upon the certainty of the information (i.e. whether the exposure involved visual and chemical cues or mating). However, there was no effect of the size of the stimulus animal in the prior encounter on subsequent mating behavior, despite exhaustive analysis. Many studies have only examined the effects of prior experience of females on subsequent mating behavior (e.g. Gabor and Halliday 1997; Bateman et al. 2001; Milinski 2001; Hebets 2003; Pitcher et al. 2003). Yet the response of males to prior experience with females may also be important, especially in systems characterized by mutual mate choice (Bonduriansky 2001, Rypstra et al. 2003). As my results demonstrate, males and females do not necessarily respond in the same manner to cues of mate availability or mating experience. Differences between males and females in the response to prior encounters may be related to differences between the sexes in mating strategies and deserve further study.

Females previously exposed to males without mating were more likely to mate in a subsequent trial. In some mammals, exposure of females to male priming pheromones can accelerate reproductive maturation, oestrus and ovulation (Rekwot et al. 2001); however, it is not known if similar effects occur in spiders. An alternative explanation is that females adjusted their receptivity in response to prior exposures. Population densities of *H. helluo* are often low in the field (Marshall and Rypstra 1999; Marshall et al. 2002) and males may have the potential to exercise mate choice (Rypstra et al. 2003). Hence, females that had been exposed to a male but not mated may have increased their receptivity to the male in the mating trial to ensure mating and avoid delaying reproduction.

In contrast to the exposure without mating results, previously mated females were much less motivated to mate (8 %) than virgin females (67 %). Studies have shown that copulation decreases female receptivity to subsequent mates in several species of spiders (Singer and Riechert 1995; Herberstein et al. 2002; Aisenberg and Costa 2005; Norton and Uetz 2005). Decreased female receptivity in a confamilial spider, *Schizocosa ocreata*, was suggested to be a result of female preference for monogamy (Norton and Uetz 2005), potentially due to the costs of mating (e.g. parasite transfer: Scheffer 1992; male courtship attracting predators: Pruden and Uetz 2004; Roberts et al. 2007). Alternately, decreased receptivity may represent a "trade-up" strategy of sequential choice with females becoming more selective of subsequent mates (Halliday 1983; Gabor and Halliday 1997; Jennions and Petrie 1997; Pitcher et al. 2003). While I did not detect an effect of the size of the previous male on subsequent matings, females could measure male quality through another characteristic that I did not measure (e.g. courtship intensity, body condition, immune function) and only mate if the subsequent male is of higher quality than her previous mate.

Males displayed the opposite pattern of females and their response depended upon whether the previous encounter was an exposure without mating or an exposure with mating. As predicted, males previously exposed to females without mating were less likely to mate with a subsequent female. These males likely perceived that there was a high availability of females and took fewer risks when exposed to a female (i.e. they were more choosy). However, males that had previously mated with a female were more likely to mate with a subsequent female. Interestingly, previously mated males were also less likely to be cannibalized by females following their second mating. One potential explanation for greater mating success and lower cannibalism risk of mated males is that these individuals represent a group of higher quality males. There is little evidence for mate choice by female *H. helluo* and 60 – 100 % of virgin females will mate with the first male with which they are paired (current study; Wilder and Rypstra unpublished data). Yet, there is the possibility that males that mated in the first trial may have had characteristics that made them more attractive to females and allowed greater mating success in the second mating trial. Alternately, there could be a "winner" effect in mating analogous to the winner effect observed in male agonistic encounters in several species of invertebrates (Dugatkin 1997; Hsu and Wolf 1999; 2001). Interestingly, these explanations could be tested in future studies by experimentally manipulating male mating status (e.g. by anesthetizing females; Stratton and Uetz 1981) and examining subsequent mating success of these mated males.

Johnson (2005) found that female fishing spiders that had previously cohabited with males as juveniles were more likely to attack males before mating than females without prior cohabitation with males. In my experiments, female mating status had a similar effect, with mated females engaging in precopulatory sexual cannibalism significantly more often than virgin females. But I observed low levels of sexual cannibalism and no effect of exposure without mating on aggression in my experiment that manipulated prior exposure without mating. One explanation is that exposure without mating may not affect female aggression and cannibalism in *H. helluo*. An alternative explanation for the lack of a treatment effect is that females were relatively well-fed in my exposure experiment compared to the prior mating experiment and, hence, not hungry enough to consume males in the first experiment. Hunger is likely to be an important prerequisite for sexual cannibalism and female hunger has been reported to be a predictor of the occurrence of cannibalism for a number of species of invertebrates (Kynaston et al. 1994; Liske and Davis 1987; Andrade 1998; Maxwell 2000; Schneider and Elgar 2001; Herberstein et al. 2002; Tsai and Dai 2003; Persons and Uetz 2005). The idea that hunger and mate availability could interact to affect the occurrence of sexual cannibalism was first formalized in a model by Newman and Elgar (1991). Further research is needed to experimentally test the interactions of hunger and mate availability for females.

Several studies have shown that individuals are more selective when they have prior experience with mates and can base subsequent mating decisions on the phenotypes of previously encountered mates (Gabor and Halliday 1997; Bateman et al. 2001; Milinski 2001; Hebets 2003; Pitcher et al. 2003). However, the ability to remember the phenotype of prior mates likely requires an investment in specific neural structures, which may be costly, and, hence, is only expected if the benefit of this memory exceeds the costs (Dukas 1999). In my experiments, male and female *H. helluo* appeared to remember that they had been previously exposed to or mated with a member of the opposite sex. While males show no size preference for females, females are significantly more likely to mate with smaller males. However, there appeared to be little or no effect of the size of the prior exposure individual or prior mate on the occurrence of mating or the timing of copulatory behaviors for either males or females. *Hogna helluo* typically occur at low densities in the field (Marshall and Rypstra 1999; Marshall et al.

2002) and, hence, there may be little selective benefit of a memory of the phenotype of individuals previously encountered. These results appear in contrast to a study of the confamilial spider, *S. uetzi*, in which females prefer to mate with males that had leg ornamentation similar to males they were exposed to as juveniles (Hebets 2003). Populations of *S. uetzi* appear to mature fairly synchronously and reproduce in a univoltine pattern, which may make mate availability high for both males and females (Hebets 2003). In species that occur at high densities in the field, there may be selection for memory of phenotypes of previous potential mates because this information could be used to inform mate choice. Taken together, these studies suggest that population parameters could influence adaptations involved in mate choice by individuals. However, future research is needed on the ability of other species to remember the phenotype of prior mates and whether this ability is more prevalent in species that occur at higher densities in nature.

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Table 1. Results of linear regression analyses testing for a relationship between the size of the prior exposure individual and the timing of copulatory behaviors: A) females exposed to cues of males and B) males exposed to cues of females

A.

	Average Male Stimulus		Larger Male Stimulus		Current - Average		Current - Larger	
Behavior	t	p	t	p	t	p	t	p
Time to Female Receptivity	0.62	0.54	0.32	0.75	-0.33	0.74	-0.21	0.84
Time from Receptivity to Mating	-0.01	0.99	-0.18	0.86	0.08	0.93	-0.13	0.90
Time to Mating	0.47	0.64	0.14	0.89	-0.39	0.70	-0.29	0.77
Copulation Duration	-0.82	0.42	-1.36	0.19	-0.41	0.69	0.15	0.89

B.

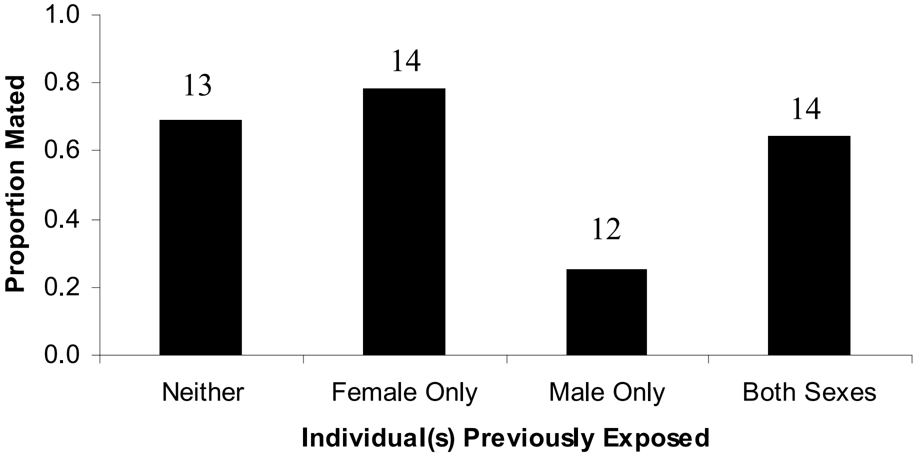
	Average Female Stimulus		Larger Female Stimulus		Current - Average		Current - Larger	
Behavior	t	p	t	p	t	p	t	p
Time to Female Receptivity	0.38	0.71	1.18	0.26	-1.23	0.24	-1.64	0.13
Time from Receptivity to Mating	1.96	0.08	1.29	0.23	-2.00	0.08	-1.88	0.09
Time to Mating	0.98	0.35	1.53	0.16	-1.85	0.09	-2.21	0.05
Copulation Duration	0.76	0.47	0.42	0.68	0.57	0.58	0.58	0.57

Table 2. Results of linear regression analyses testing for a relationship between the size of the prior mate and the timing of copulatory behaviors.

	Prior Male Size		Current - Prior Male		Prior Female Size		Current - Prior Female	
Behavior	t	p	t	p	t	p	t	p
Time to Female Receptivity	1.20	0.30	-1.36	0.25	0.53	0.61	-0.44	0.67
Time from Receptivity to Mating	0.28	0.79	0.16	0.88	-3.06	0.008	1.89	0.08
Time to Mating	1.05	0.36	-1.03	0.36	0.15	0.88	-0.20	0.84
Copulation Duration	-4.81	0.009	1.39	0.24	-1.41	0.18	-0.78	0.45

Figure 1. The effects of prior encounters with the opposite sex on the frequency of mating in the: A) prior exposure (i.e. no copulation) experiment and B) prior mating experiment. Numbers above the bars indicate sample sizes.

A)



B)

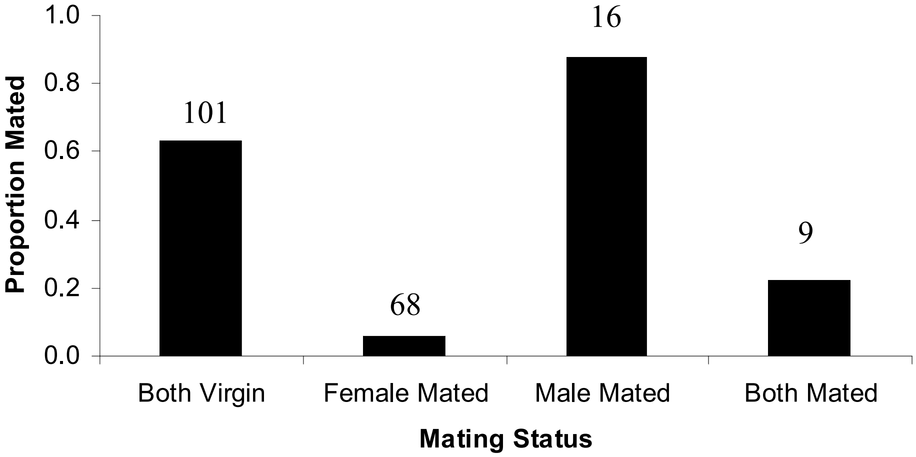
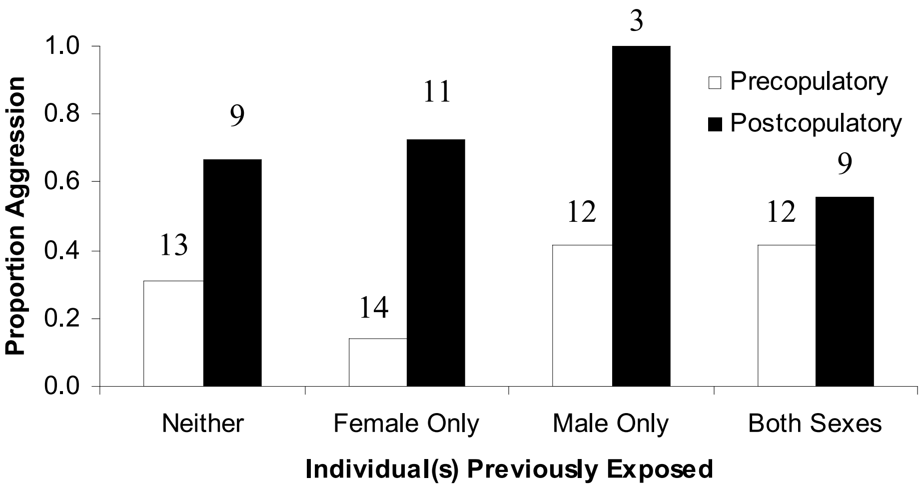
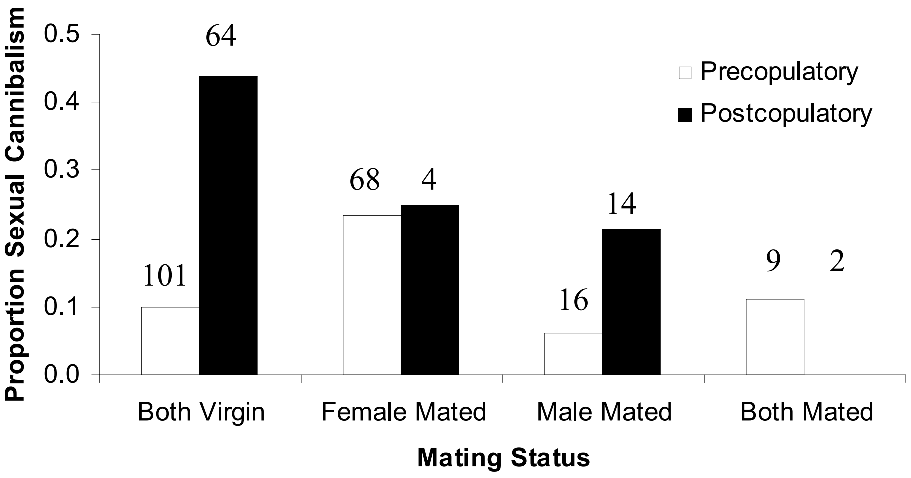


Figure 2. The effects of prior encounters with the opposite sex on: A) aggression of female towards males before and after copulation in the prior exposure experiment and B) pre and postcopulatory sexual cannibalism of males by females in the mating status experiment. Numbers above the bars indicate sample sizes.

A)



B)



CHAPTER 4: SEXUAL SIZE DIMORPHISM PREDICTS THE FREQUENCY OF SEXUAL CANNIBALISM WITHIN AND AMONG SPECIES OF SPIDERS

Abstract

Sexual cannibalism varies widely among spiders but no general evolutionary hypothesis has emerged to explain its distribution across taxa. Sexual size dimorphism also varies widely among spiders and could affect the vulnerability of males to cannibalistic attacks by females. I tested for a relationship between sexual size dimorphism (SSD) and sexual cannibalism within and among species of spiders using a broad taxonomic data set. For most species, cannibalism was more likely when males were much smaller than females. In addition, using phylogenetically-controlled and uncontrolled analyses, there was a strong positive relationship between average SSD of a species and the frequency of sexual cannibalism. While the degree of size difference has been documented to affect the outcome of predatory interactions, this is the first evidence that the degree of size advantage (e.g. SSD) contributes to the phylogenetic distribution of sexual cannibalism among a broad range of spiders.

Introduction

Sexual cannibalism, the consumption of a male by a female in the context of mating, is an extreme form of sexual conflict in which the female gains material benefits from the male often with little or no apparent benefits to male fitness (Elgar and Schneider 2004). Although present in a variety of taxa including praying mantids (Insecta, Mantodea), beetles (Insecta, Coleoptera) and flies (Insecta, Diptera), sexual cannibalism has been studied most extensively in spiders (Arachnida, Araneae) (Elgar 1992, Elgar and Schneider 2004). Among taxa, the frequency of sexual cannibalism is quite variable (Elgar 1992). This is especially true of spiders where the frequency of sexual cannibalism can range from 0 to nearly 100% of mating encounters even within a single family (e.g. Araneae, Theridiidae; Andrade 1996, Knoflach and van Harten 2000, 2001, Knoflach and Benjamin 2003).

Several hypotheses have been proposed for the occurrence of sexual cannibalism. The foraging hypothesis is one of the most straightforward hypotheses as it simply suggests that a hungry female consumes the male because she needs food (Buskirk et al. 1984, Newman and Elgar 1991, Elgar and Schneider 2004). Alternatively, female consumption of the male could be a result of a "spillover" of aggression from juvenile life stages (Arnqvist and Henriksson 1997). High levels of aggression may be selectively advantageous in juveniles, enabling them capture and consume more prey and grow more quickly. If a high level of aggression persists into adulthood, it can interfere with mating and lead to sexual cannibalism (Arnqvist and Henriksson 1997, Schneider and Elgar 2002, Moya-Laraño et al. 2003, Johnson and Sih 2005). Perhaps the simplest explanation is that sexual cannibalism is a case of mistaken identity where a male is not recognized as a potential mate in enough time, although elaborate courtship in spiders is thought to prevent this in many cases (Elgar 1992, Uetz 2000). Sexual selection has also been invoked to explain the occurrence of sexual cannibalism. For example, females may cannibalize undesirable males as a form of mate rejection (Elgar and Nash 1988, Hebets 2003, Persons and Uetz 2005) or use cannibalism to assert control over the timing of copulation (Fromhage et al. 2003). In some situations, male are actually complicit in sexual cannibalism and can gain paternity benefits by somersaulting into the female's jaws (Andrade 1996). However, most research on sexual cannibalism has focused on the costs and benefits for individual species with the assumption that this behavior is polyphyletic in origin (Elgar and Schneider 2004). Hence, no general evolutionary hypothesis has emerged to explain variation in the frequency of sexual cannibalism across taxa.

In addition to wide variation in the frequency of sexual cannibalism, spiders exhibit broad variation in sexual size dimorphism (SSD) both within and among taxonomic lineages. Variation in SSD among spiders is generally agreed to be due to variation in the strength of fecundity selection (Coddington et al. 1997, Prenter et al. 1999, Hormiga et al. 2000) acting to increase female size coupled with mortality selection and scramble competition (Vollrath and Parker 1992, Moya-Larano et al. 2002) acting to maintain or decrease male size. Evidence from some species of spiders suggests that SSD could affect the occurrence of sexual cannibalism (e.g. Elgar and Nash 1988, Elgar et al. 2000, Schneider and Elgar 2001, Persons and Uetz 2005).

The foraging hypothesis may provide a mechanistic link between SSD and sexual cannibalism. As with any predator/prey interaction, the outcome of females foraging for males should depend upon female motivation to feed and the vulnerability of the male to the female attack (Polis 1981, Polis et al. 1989, Brose et al. 2006). In terms of female motivation, spiders are frequently food or nutrient limited in nature (Wise 1993, Denno and Fagan 2003, Fagan and Denno 2004, Wise 2006) and female hunger is known to affect the occurrence of sexual cannibalism in spiders (Andrade 1998, Schneider and Elgar 2001, Herberstein et al. 2002, Persons and Uetz 2005) and praying mantids (Liske and Davis 1987, Kynaston et al. 1994, Maxwell 2000). If females are motivated to cannibalized males, then a key determinant of whether females are successful at engaging in sexual cannibalism will be male vulnerability to the female attack. Size differences between predator and prey are known to have a large effect on the outcome of predation in a wide range of animals (Polis 1981, Polis et al. 1989, Balfour et al. 2003, Rypstra and Samu 2005, Brose et al. 2006). Hence, the degree of SSD, which varies within and among species of spiders, could affect the occurrence of sexual cannibalism.

I tested the hypothesis that sexual size dimorphism explains variation in the frequency of sexual cannibalism within and among a variety of species of spiders. I first examined how variation in SSD within a common species of wolf spider, *Hogna helluo* (Araneae, Lycosidae), affected the frequency of sexual cannibalism. I predicted that sexual cannibalism would be more likely when the degree of SSD was larger between males and females. I then surveyed the literature to examine if size differences between males and females were a predictor of the occurrence of sexual cannibalism within other species of spiders. Finally, I compiled data on the mean SSD and frequency of sexual cannibalism for a broad taxonomic data set of spiders and tested if species with high degrees of SSD displayed higher frequencies of sexual cannibalism.

Methods

Sexual Cannibalism in *Hogna helluo*. All individuals used in this study were lab-reared offspring of adult *Hogna helluo* (Araneae, Lycosidae,) (females, ca. 300-800 mg; males, ca. 150-300 mg) that were collected in the agricultural fields at the Miami University Ecology Research Center (Oxford, Butler County, OH). Spiderlings were placed in translucent plastic containers (8 cm diameter x 5 cm high) with 1 cm of moist peat moss and an active culture of *Sinella curviseta* (Collembola, Entomobryidae). Spiders were maintained in an environmental chamber at 25^{o}C and a 13:11 light:dark cycle. After 3 to 4 weeks, spiderlings were maintained on a diet of two appropriately sized crickets once or twice per week. Individuals were transferred to larger deli containers (11 cm diameter x 8 cm high) upon reaching approximately 1 cm body length. During feedings, I checked for molts and recorded their date of maturity. Adult females were fed two and males one juvenile crickets (*Acheta domesticus*, ca. 50 mg) twice per week. All males were fed 2 days prior to trials and females were fed 2 - 4 days prior to trials.

Mating trials were run between 0900 and 1900 hours in circular plastic containers (19 cm diameter x 6 cm high) lined with clean filter paper. Females were placed in containers and allowed to acclimate and deposit silk (and pheromones) in the trial arena for 90 minutes. The male was introduced under a clear plastic vial opposite the female for 15 minutes and then the vial was removed and spiders were able to interact. I randomly paired males and females and did not use any spider in more than one trial. Trials were videotaped for 90 minutes in isolated booths, which contained 6 fluorescent lights and a video camera mounted 1 m above the arena.

Prior to trials, I recorded the carapace width of males and females to the nearest 0.01 mm with an ocular micrometer. Carapace width was used as a measure of size because this structure is fixed in size at maturity. Sexual size dimorphism was measured as the ratio of female to male carapace width (female carapace width / male carapace width). Females are larger than males and larger values of the ratio indicate a greater size difference between males and females. I recorded if the female cannibalized the male and the timing of the cannibalism in relation to mating. Binary logistic regression was used to test for a relationship between female size advantage and the occurrence of sexual cannibalism using data from all cannibalisms and from pre- and postcopulatory cannibalism separately.

Relationships between SSD and Sexual Cannibalism Within Species. I surveyed the literature for all studies of spiders in which investigators tested if the size difference between males and females (sexual size dimorphism, SSD) in a pairing affected the probability of sexual cannibalism. I also included the data for *H. helluo* reported in this paper (i.e. see "Methods: Sexual Cannibalism in *Hogna helluo*"). I included studies that tested for a relationship between SSD and sexual cannibalism that either used SSD as a continuous predictor variable or that categorized mating events by the size of the males or females. These data were used to examine how frequently spider species display positive relationships within a species between SSD and the occurrence of sexual cannibalism. I also used these data to test for differences in the mean SSD of species that demonstrated positive, negative or no intraspecific relationship between SSD and sexual cannibalism. This literature search and the search for the data included in the phylogenetic analysis (see below) were conducted using online databases (i.e. Biological Abstracts and Science Citation Index) and by examining the literature cited sections of published papers, including an extensive review on the species in which sexual cannibalism has been observed (Elgar 1992).

Phylogenetic Analysis of SSD and Sexual Cannibalism Among Species. In a second literature search, I compiled data on the frequency of sexual cannibalism (percent of mating encounters ending in cannibalism) in spiders from the literature and by contacting individual researchers. I only included studies that had at least 20 trials to calculate sexual cannibalism. For all the species involved, I estimated body length of males and females, either from that reported in the study or from other publications. I used body length in this case because it is the most commonly reported measure of size. In cases where a range of sizes were given for females or males, I used the midpoint of the range as a measure of size. I calculated sexual size dimorphism as the ratio of average female to male size (Gibbons and Lovich 1990, Prenter et al. 1999). The degree of sexual size dimorphism was logarithmically transformed prior to analysis (Felsenstein 1985, Purvis and Rambaut 1995). Simple linear regression was used to test for a relationship between log sexual size dimorphism and the frequency of sexual cannibalism.

I also used phylogenetically-controlled analyses to examine the relationship between log sexual size dimorphism and the frequency of sexual cannibalism. Moran's *I* spatial autocorrelation statistic was used to test if the frequency of sexual cannibalism and log-transformed sexual size dimorphism were confounded by phylogeny at the family and genus level. Moran's *I* calculations were conducted using the internet-accessible Moran's *I* Eco-Tool (www.eco-tool.net). Phylogenetically-controlled analyses were conducted using Comparative Analysis by Independent Contrasts (CAIC) (Purvis and Rambaut 1995, Pagel and Harvey 1988, Harvey and Pagel 1991, Harvey and Purvis 1991). An updated version of the Coddington and Levi (1991) phylogeny, which is published in Stratton et al. (2004), was used for comparative analyses. In total, 27 species, 20 genera and 11 families were included in the data set. I assumed equal branch lengths when inputting the phylogeny into the CAIC program (Prenter et al. 1999). When branch lengths are unresolved, analyses using equal branch lengths and branch lengths proportional to the number of species they contain provide similar results (Garland et al. 1992). Briefly, CAIC calculates the difference in values (contrasts) for the dependent and independent variables at nodes in the phylogeny. These contrast values are then used in a linear regression forced through the origin (Harvey and Purvis 1991).

Results

In the wolf spider *Hogna helluo*, there is a strong positive relationship between SSD of a randomly selected male and female and the occurrence of sexual cannibalism (logistic regression: $z = 4.63$, $p < 0.001$). This relationship remained when cannibalism was separated into precopulatory ($z = 1.97$, $p = 0.049$) and postcopulatory ($z = 3.94$, $p < 0.001$) cannibalism. The magnitude of the effect in *H. helluo* was large as the frequency of sexual cannibalism varied from 0 to nearly 80 % as female size ranged from 0 to 40 % larger than males (Figure 1).

I compiled data for 12 species of spiders on the relationship between the size dimorphism of male and female in a pairing (female size / male size) and the probability of sexual cannibalism (Table 1). Of these 12 studies, 7 (58 %) found a significant positive relationship between SSD and sexual cannibalism, with cannibalism more likely to occur when there was a greater difference in size between male and female in a pair (Table 1). Four (33 %) studies failed to find a relationship and 1 (8 %) study revealed a negative relationship between SSD and sexual cannibalism. I also compared the mean SSD of a species that demonstrated positive or no relationship between SSD and sexual cannibalism. The mean SSD of species in which there was a positive intraspecific relationship between SSD and sexual cannibalism was significantly lower (mean ± 1 SE; 2.17 ± 0.33) than that of species in which there was no relationship (3.78 ± 0.22; $n = 10$, $t = 4.06$, $p = 0.005$) and the one species with a negative relationship also had the highest mean level of SSD (4.20; *Nephila plumipes*).

Quantitative data on SSD and the frequency of sexual cannibalism were available for 27 species of spiders representing 20 genera and 11 families (app. A). Using species as independent data points, there was a significant positive relationship between log SSD and the frequency of sexual cannibalism (Figure 2a; $p < 0.001$). However, using Moran's I statistic, I detected significant phylogenetic autocorrelation in the data set at the genus level for both log SSD (family level: $z = 0.10$, $p = 0.77$; genus level: $z = 4.38$, $p < 0.001$) and the frequency of sexual cannibalism (family level: $z = 0.38$, $p = 0.56$; genus level: $z = 3.61$, $p < 0.001$). This phylogenetic autocorrelation necessitated the use of comparative analysis by independent contrasts to control for phylogeny (Purvis and Rambaut 1995). After taking into account phylogeny, there was still a significant positive relationship between SSD and the frequency of sexual cannibalism (Figure 2b; $p < 0.001$). Sexual size dimorphism explained a relatively large amount of the variance in the frequency of sexual cannibalism both before ($r^2 = 0.50$) and after controlling for phylogeny ($r^2 = 0.47$).

Discussion

Despite frequent attempts to understand the evolutionary origin of sexual cannibalism, no broad explanations for this behavior have emerged. My results suggest that sexual size dimorphism (SSD) is a major factor explaining the occurrence and phylogenetic distribution of sexual cannibalism in spiders. While size differences are known to affect the outcome of traditional predator/prey interactions (Brose et al. 2006), this is the first evidence that SSD may explain the phylogenetic distribution of sexual cannibalism among a wide range of species. Interestingly, there is no explanation for how sexual cannibalism could have selected for high levels of SSD. The most plausible explanation for the relationship that I observed is that selection pressures (e.g. fecundity selection and differential mortality) have resulted in a given level of SSD for a species and that this level of SSD then predisposes a species to a given level of sexual cannibalism. Hence, the phylogenetic distribution of sexual cannibalism in spiders may be the byproduct of selection for SSD in other contexts.

A previous study failed to detect a relationship between a qualitative measure of sexual cannibalism and SSD among families of spiders (Elgar 1992). However, the power of the previous study may have been compromised by the use of a categorical measure of sexual cannibalism and that fact that comparisons were only done at the family level (Elgar 1992). Interestingly, I observed substantial variation in both SSD and the frequency of sexual cannibalism in some families that would have been obscured by taking the average of the family. In addition, in the 15 years since that study (Elgar 1992), a large number of additional studies (74 % of the data points I included in my analyses) have augmented the existing data on the frequency of sexual cannibalism in spiders.

Prior studies have primarily tested the female foraging hypothesis for sexual cannibalism by testing if females gain a fecundity benefit from consuming the male. Most studies have failed to document a fecundity benefit of sexual cannibalism to females (Andrade 1996, Spence et al. 1996, Arnqvist and Henriksson 1997, Fahey and Elgar 1997, Maxwell 2000, Elgar et al. 2000, Johnson 2001, Stalhandske 2001, Fromhage et al. 2003, reviewed in Elgar and Schneider 2004). However, these studies have tended to examine species with high degrees of SSD in which males represent a small prey item for females. Two tests for a fecundity benefit of sexual cannibalism have been conducted on species with lower levels of SSD and both have documented a fecundity benefit to females (Birkhead et al. 1988, Barry et al. in review). Hence, the degree of SSD for a species may result in a tradeoff between capture ability and nutritional benefit of males. In species with high degrees of SSD, males are easier to capture but they are less beneficial to consume because their bodies are small.

All of the hypotheses for the evolution of sexual cannibalism concern either female motivation to cannibalize or male motivation to escape cannibalism. A critical, yet understudied, factor affecting the occurrence of sexual cannibalism is the success rate of a female attack. In nature, female spiders are frequently food-limited and, thus, should be motivated to cannibalize males, especially if they have already mated (Wise 1993, Wise 2006, Newman and Elgar 1991). Hence, factors affecting the success rate of female cannibalistic attacks may be just as important as female motivation in understanding the occurrence of cannibalism in nature and deserve further attention. Other factors that may affect male vulnerability to female attacks include: male age (Morse and Hu 2004), male nutritional condition, location of the male body relative to female mouthparts during mating, whether one or two copulations are required for full insemination of the female (Schneider et al. 2006) and the location of mating (Elgar 1991).

My results suggest that the relationship between SSD and sexual cannibalism within a species (i.e. positive, negative or none) depends upon the mean level of SSD of that species. For most species, there was a positive relationship between the size difference of males and females and the occurrence of sexual cannibalism. Interestingly, these species had a significantly lower mean level of SSD than species in which there was no relationship between SSD and sexual cannibalism. There was only one species, *Nephila plumipes*, in which there was a negative relationship between SSD of a pair and sexual cannibalism and this species had the highest mean level of SSD (Elgar and Fahey 1996, Schneider and Elgar 2001). In this species, females are also more likely to respond to and attack larger males as they approach females to mate (Elgar and Fahey 1996). Given that males are extremely small compared to females in this species (Table 1), the negative relationship between SSD and sexual cannibalism could be due to either females showing less interest in small males, which would be less of a meal, or females not being able to detect small males (Elgar and Fahey 1996, Schneider and Elgar 2001). Hence, a positive intraspecific relationship between SSD and sexual cannibalism may be most likely in species with low mean levels of SSD. Species with higher levels of SSD may display no relationship between SSD and sexual cannibalism and species with extremely high levels of SSD may display a negative relationship. While I recognize that results that are not statistically significant may be less likely to be published (Koricheva 2003), I do not believe it was a major problem with my data set given that one third (4 of 12) of the studies in my data set did not detect a significant relationship between SSD and sexual cannibalism. Nevertheless, data on a wider range of species are needed to critically test this hypothesis.

These data suggest that male vulnerability to female cannibalistic attacks is related to SSD. Hence, sexual cannibalism should select for larger male size. Yet, phylogenetic analyses reveal that males are not evolving to become larger despite the potentially strong selective pressure of sexual cannibalism (e.g. Hormiga et al. 2000). For example, Hormiga et al. (2000) reconstructed ancestral states of male and female size in orb-weaving spiders and reported that most cases of SSD were due to increases in female size and that males rarely increased in size over evolutionary time. Males may not become larger because the cost of sexual cannibalism may be relatively low compared to the benefit of small size for males. The costs of sexual cannibalism to male fitness are especially low if cannibalism occurs after copulation and males have few opportunities for repeated mating (Andrade and Kasumovic 2005). For example, the probability of mortality for males while moving between female webs is 80 – 92 % in *Latrodectus hasselti* and 67 – 90 % in *Nephila clavipes* and, in both cases, even if males reach the female web they can expect competition with other males for the opportunity to mate (Christenson 1990, Vollrath and Parker 1992, Andrade 2003). In addition, small size of males may result in early maturation and faster climbing speed, both of which aid in scramble competition for females (Vollrath and Parker 1992, Moya-Larano et al. 2002).

Spiders species vary widely in the degree of SSD, which appears to be due to variation among species in the strengths of fecundity selection (Head 1995, Prenter et al. 1999, Hormiga et al. 2000) acting to increase female size and mortality selection (e.g. differential mortality model; Vollrath and Parker 1992) and other selective pressures (e.g. Moya-Larano et al. 2002) acting to maintain or decrease male size. This degree of SSD then has consequences for sexual cannibalism by affecting male vulnerability to female attacks. Such a situation, where selection in one context has implications for another context, has been termed a spandrel by Gould and Lewontin (1979), after the architectural feature that is a consequence of the confluence of two adjacent arches (see also Gould 1997). The concept of a spandrel was offered as an alternative to adaptationist explanations for the evolution of traits (Gould and Lewontin 1979). Viewing sexual cannibalism as a byproduct of SSD may explain why no general adaptationist hypotheses have emerged to account for the frequency and distribution of sexual cannibalism among taxa and may aid in understanding the evolution of this behavior.

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Table 1. The relationship between the degree of sexual size dimorphism (SSD) of a male and female in a given pairing and sexual cannibalism for several spider species. NA indicates that data were not available

Family	Species	Relationship Between SSD and Sexual Cannibalism	Average SSD in Body Length (Female / Male)	Citation
Araneidae	*Argiope keyserlingi*	positive	2.80	Elgar et al. (2000)
	Argiope aurantia	none	4.00	Foellmer and Fairbairn (2004)
	Araneus diadematus	positive	1.89	Elgar and Nash (1988)
	Argiope bruennichi	none	3.33	Fromhage et al. (2003)
Lycosidae	*Schizocosa ocreata*	positive	1.26	Persons and Uetz (2005)
	Hogna helluo	positive	1.73	Wilder and Rypstra (this study)
Pisauridae	*Dolomedes fimbriatus*	positive	1.91	Arnqvist and Henriksson (1997)
	Dolomedes triton	positive	1.75	Johnson (2005)
Tetragnathidae	*Nephila plumipes*	negative	4.20	Schneider and Elgar (2001)
	Nephila edulis	positive	3.83	Elgar et al. (2003)
	Nephila fenestrata	none	NA	Fromhage and Schneider (2005)
Theridiidae	*Latrodectus hasselti*	none	4.00	Andrade (1998)

Figure 1. The relationship between sexual size dimorphism (female carapace width / male carapace width) of randomly paired *Hogna helluo* and the frequency of sexual cannibalism.

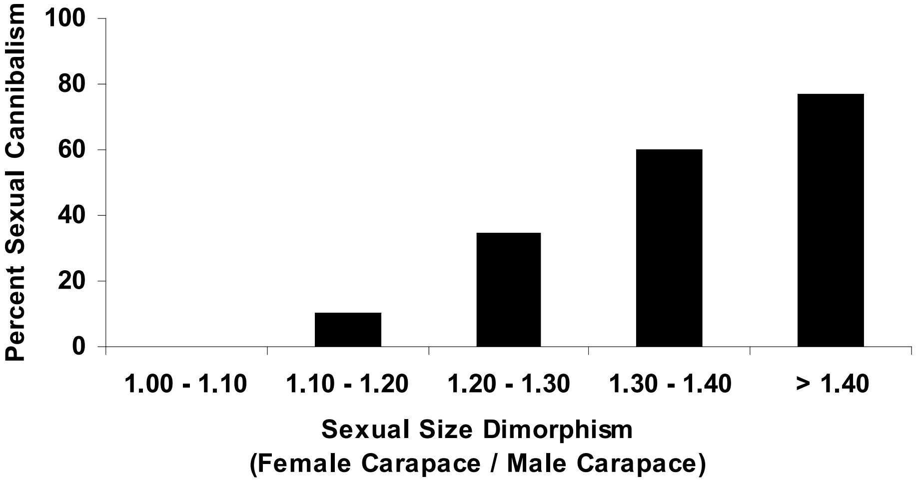
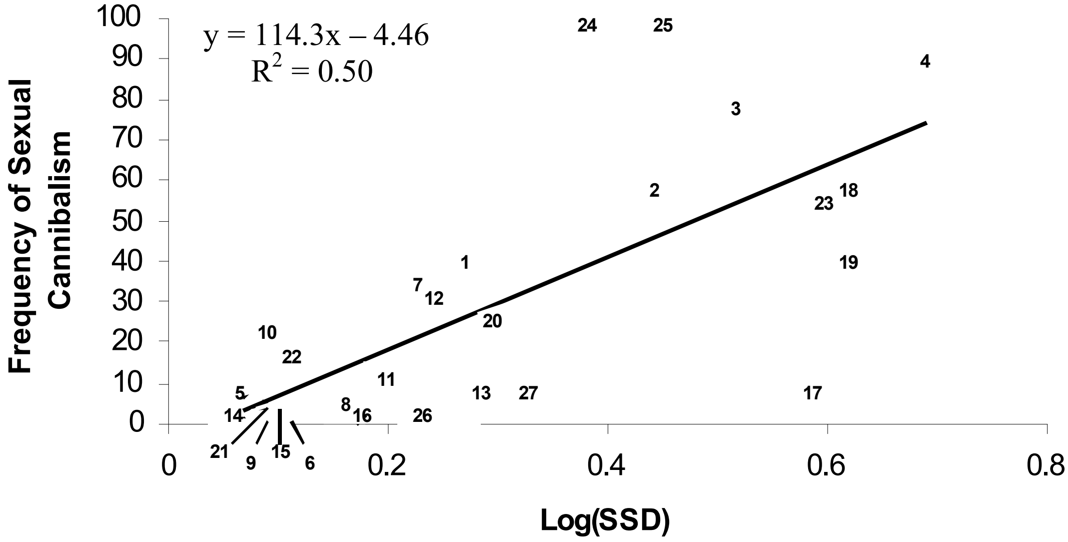
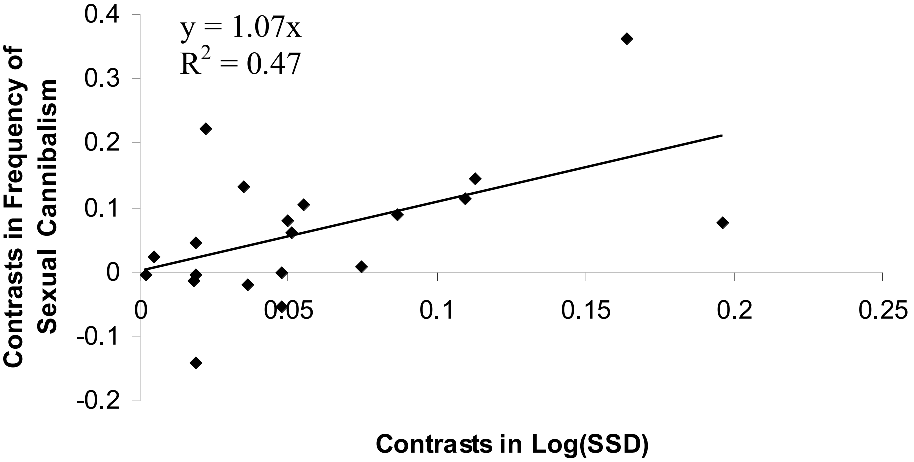


Figure 2. The relationship between sexual size dimorphism and the frequency of sexual cannibalism in spiders using (a) species as data points (numbers refer to information in Appendix A) and (b) phylogenetically-controlled independent contrasts

A)



B)



APPENDIX A: Species Used in Phylogenetic Analysis

Table A1: List of the species used in the phylogenetic analysis along with the citation used to calculate the frequency of sexual cannibalism

Family	Genus	Species	Number	Source
Araneidae	*Araneus*	*diadematus*	**1**	Elgar and Nash (1988)
	Argiope	*keyserlingi*	**2**	Elgar et al. (2000)
	Argiope	*bruennichi*	**3**	Fromhage et al. (2003)
	Argiope	*aemula*	**4**	Sasaki and Iwahashi (1995)
Clubionidae	*Supunna*	*picta*	**5**	Jackson and Poulsen (1990)
Dysderidae	*Dysdera*	*crocata*	**6**	Jackson and Pollard (1982)
Lycosidae	*Hogna*	*helluo*	**7**	Walker and Rypstra (unpublished)
	Lycosa	*tarentula*	**8**	Moya-Larano et al. (2003)
	Pardosa	*milvina*	**9**	Schlosser (pers. comm.)
	Schizocosa	*ocreata*	**10**	Persons and Uetz (2005)
	Schizocosa	*retrorsa*	**11**	Hebets et al. (1996)
Pisauridae	*Dolomedes*	*triton*	**12**	Johnson (2001)
	Dolomedes	*fimbriatus*	**13**	Arnqvist (1992)
	Pisaura	*mirabilis*	**14**	Stalhandske (2001)
Pholcidae	*Pholcus*	*phalangiodes*	**15**	Rypstra and Hoefler (unpublished)
Salticidae	*Phidippus*	*johnsoni*	**16**	Jackson (1980)
Tetragnathidae	*Nephila*	*edulis*	**17**	Schneider et al. (2000)
	Nephila	*plumipes*	**18**	Schneider and Elgar (2001)
	Nephila	*clavipes*	**19**	Christenson and Goist (1979)
	Phonognatha	*graeffei*	**20**	Fahey and Elgar (1997)
	Tetragnatha	*elongata*	**21**	Danielson-Francois et al. (2002)
Theraphosidae	*Stromatopelma*	*griseipes*	**22**	Celerier (1981)
Theridiidae	*Latrodectus*	*hasselti*	**23**	Andrade (1998)
Theridiidae	*Tidarren*	*argo*	**24**	Knoflach and van Harten (2001)
	Tidarren	*cuneolatum*	**25**	Knoflach and van Harten (2000)
	Anelosimus	*eximius*	**26**	Rypstra (pers. comm.)
Thomisidae	*Misumena*	*vatia*	**27**	Morse and Hu (2004)

GENERAL CONCLUSIONS

The frequency of sexual cannibalism varies both within and among species of spiders (Elgar 1992, Elgar and Schneider 2004). Much of this variation may be due to variation in ecological and phylogenetic conditions. Certain ecological conditions may affect the motivation of females to attack males if they result in a higher benefit or lower cost of sexual cannibalism. For example, females may gain a greater benefit from engaging in sexual cannibalism if they are food limited (Chapter 1, Table 1) or may face a lower cost of cannibalism if there are many males in the population (e.g. Johnson 2005). Phylogenetic conditions (i.e. the evolutionary history) of taxa may also affect the occurrence of cannibalism. For example, the selective pressures of fecundity and mortality selection have shaped sexual size dimorphism among taxa (Vollrath and Parker 1992, Head 1995, Prenter et al. 1999, Hormiga et al. 2000, Moya-Larano et al. 2002) and this evolutionary history may then predispose species with higher levels of SSD to higher frequencies of sexual cannibalism. Hence, consideration of the biology of spiders (i.e. ecological and phylogenetic conditions) may provide insight into the phylogenetic distribution of sexual cannibalism among species.

The evolution of sexual cannibalism among spiders is poorly understood. Many hypotheses have been proposed for the occurrence of sexual cannibalism including female foraging, aggressive spillover, mistaken identity, mate rejection and male sacrifice (Elgar 1992, Andrade 1996, Arnqvist and Henriksson 1997, Elgar and Schneider 2004). Each of these hypotheses has received some level of support in some species. Hence, one hypothesis for the evolution of sexual cannibalism in spiders in general is that this behavior has a polyphyletic origin (Elgar and Schneider 2004).

However, there are problems with the polyphyletic hypothesis for the origin of sexual cannibalism in spiders. One problem is that there are alternate interpretations for some of the hypotheses for sexual cannibalism. One major line of support for the polyphyletic hypothesis is the very specialized male sacrifice hypothesis, which has only received support in a few sexually cannibalistic species (Andrade 1996, Miller 2007). This hypothesis posits that males of some species encourage females to consume them because, by being consumed, the males gain a paternity advantage (Andrade 1996). So, male sacrifice is thought to have led to high frequencies of sexual cannibalism in some species. However, all species with male sacrifice also have high degrees of sexual size dimorphism (Miller 2007). My research in Chapter 4 shows that the frequency of sexual cannibalism increases linearly as sexual size dimorphism increases.

Hence, an alternate explanation is that male sacrifice and the associated paternity adaptations were a response to high levels of sexual cannibalism due to the high degree of sexual size dimorphism in these species. Unfortunately, it would be difficult to test between these alternate explanations for the relationship between male sacrifice and high frequencies of sexual cannibalism.

Another problem with the polyphyletic hypothesis is that SSD, which is a measure of male vulnerability to female attacks, explains much of the variation in the frequency of sexual cannibalism among taxa. Hence, there is evidence that the foraging hypothesis may be a unifying explanation for variation in the frequency of sexual cannibalism. The foraging hypothesis posits that sexual cannibalism can be explained as the female foraging on the male as a food item. As with most predator – prey interactions, both predator motivation (i.e. female hunger; Chapter 1, Table 1) and male vulnerability (i.e. sexual size dimorphism; Chapter 4, Figures 1 and 2) affect the occurrence of sexual cannibalism. Female hunger even affects the occurrence of sexual cannibalism in *L. hasselti*, which is the model system for the male sacrifice hypothesis (Andrade 1996, 1998). The idea that sexual cannibalism is a foraging decision by the female is not surprising given that spiders frequently engage in cannibalism of juveniles and intraguild predation of other spiders (Polis 1981, Polis et al. 1989, Wise 1993, 2006). Sexual cannibalism is only unique from more general cannibalism in that it occurs between adults of the opposite sex and happens either before, during or after mating. Interestingly, reverse sexual cannibalism, in which males consume females, occurs in two species of spiders in which males are sometimes larger than females (Schutz and Taborsky 2005, Cross et al. 2007). Reverse sexual cannibalism poses no benefit to the male other than nutrition and provides further evidence that sexual cannibalism may simply be a foraging decision by a larger individual, which in spiders is typically the female (Head 1995). The idea that sexual cannibalism in spiders arose through the foraging hypothesis is a more parsimonious explanation for the evolution of sexual cannibalism, compared to the polyphyletic hypothesis, and has support from a data set including a wide range of species.

Sexual cannibalism has intrigued biologists for centuries (Howard 1876, Prete and Wolfe 1992). Yet the evolution of this behavior and its consequences for fitness in males and females has only been studied intensively for several decades (Buskirk et al. 1984, Newman and Elgar 1991, Elgar 1992, Elgar and Schneider 2004). The data available, thus far, display wide variation in the frequency within and among species and in the factors responsible for this variation. While there is some data to support the framework proposed in this dissertation (Chapter 1, Figure 1), there are many gaps in our understanding that remain to be studied. Further research on this framework utilizing experimental and comparative approaches should enhance our understanding of the evolution of sexual cannibalism in spiders and praying mantids.

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