2003

PRE-COPULATORY SEXUAL CANNIBALISM IN FISHING SPIDERS: THE ECOLOGY OF AN EXTREME SEXUAL CONFLICT

J. Chadwick Johnson
University of Kentucky, jcjohnson@ucdavis.edu

ABSTRACT OF DISSERTATION

J. Chadwick Johnson

The Graduate School

University of Kentucky

2003

PRE-COPULATORY SEXUAL CANNIBALISM IN FISHING SPIDERS:
THE ECOLOGY OF AN EXTREME SEXUAL CONFLICT

ABSTRACT OF DISSERTATION

A dissertation submitted in partial fulfillment of the
requirements for the degree of Doctor of Philosophy in the
College of Arts and Sciences
at the University of Kentucky

By
J. Chadwick Johnson

Lexington, Kentucky

Director: Dr. Andrew Sih, Professor of Biological Sciences

Lexington, Kentucky

2003

ABSTRACT OF DISSERTATION

PRE-COPULATORY SEXUAL CANNIBALISM IN FISHING SPIDERS:
THE ECOLOGY OF AN EXTREME SEXUAL CONFLICT

Pre-copulatory sexual cannibalism (pre-SC), or predation of a potential mate before sperm transfer, provides an ideal model system for behavioral ecology's current focus on inter-sexual conflict. Studying the North American fishing spider (*Dolomedes triton*), I tested three female-benefit hypotheses for pre-SC: indirect benefits, direct benefits, and aggressive spillover. First, pre-SC may reflect a mating bias providing females with 'good-genes' benefits. By manipulating each female's options with regard to the most cited phenotypic advantage in male spiders, body size, I show that while females exhibit no bias in their attack tendency on males of different body sizes, large males mate significantly more often than small males. Second, pre-SC may be explained by direct benefits if females use it as an adaptive foraging/mating trade-off. My work provides mixed support for this idea: (i) females vary attacks according to the availability of mates, (ii) females do not vary attacks according to the availability of food, and (iii) females derive discrete fecundity benefits from consuming a male. Finally, I tested the aggressive-spillover hypothesis, which posits that pre-SC is a by-product of selection for high levels of aggression towards prey in traditional foraging contexts. Path analysis indicated intra-individual, positive correlations between aggression in foraging contexts and the mating context, thus supporting the hypothesis. I conclude by stressing that pre-SC in a given species may rarely be explained by one hypothesis, and that studies accounting for multiple benefits that fluctuate as behavioral-ecological contexts shift should give a more realistic glimpse of behavioral ecology and evolution.

James Chadwick Johnson

7-15-03

PRE-COPULATORY SEXUAL CANNIBALISM IN FISHING SPIDERS: THE ECOLOGY OF AN EXTREME SEXUAL CONFLICT

By

J. Chadwick Johnson

Andrew Sih

Peter Mirabito

7-15-03

RULES FOR THE USE OF DISSERTATIONS

Unpublished dissertations submitted for the Doctor's degree and deposited in the University of Kentucky Library are as a rule open for inspection, but are to be used only with due regard to the rights of the authors. Bibliographical references may be noted, but quotations of summaries of parts may be published only with the permission of the author, and with the usual scholarly acknowledgements.

Extensive copying or publication of the dissertation in whole or in part also requires the consent of the Dean of the Graduate School of the University of Kentucky.

DISSERTATION

J. Chadwick Johnson

The Graduate School

University of Kentucky

2003

PRE-COPULATORY SEXUAL CANNIBALISM IN FISHING SPIDERS:
THE ECOLOGY OF AN EXTREME SEXUAL CONFLICT

_____

DISSERTATION

_____

A dissertation submitted in partial fulfillment of the
requirements for the degree of Doctor of Philosophy in the
College of Arts and Sciences
at the University of Kentucky

By
J. Chadwick Johnson

Lexington, Kentucky

Director: Dr. Andrew Sih, Professor of Biological Sciences

Lexington, Kentucky

2003

This work is dedicated to my beautiful soon-to-be wife Gina Hupton, my remarkable powerhouse of a mother Sandra Deer, Jim Johnson, the man I have tried to emulate, Jennifer Deer, the best friend a brother could hope for, Penny, who never wavers in her love and enthusiasm, and all of my friends and loved ones.

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF FILES

chadsphd.pdf, 1.08 MB

CHAPTER 1

Overview of the thesis

<u>Introduction</u>

The phenomenon of pre-copulatory sexual cannibalism (pre-SC), or predation of a potential mate prior to sperm transfer, has fascinated behavioral ecologists for the past century (reviewed in Elgar, 1992; Johns & Maxwell, 1997). Pre-SC is relatively widespread among invertebrates, suggesting that it has evolved independently several times, and reports are particularly prevalent for arachnids. Despite the apparent widespread distribution of pre-SC, relatively few studies have experimentally tested hypotheses of its functional significance. The goals of this paper are to describe my approach to understanding pre-SC and to summarize several tests of the functional significance of this behavior.

Pre-SC as extreme sexual conflict in multiple behavioral contexts

Elgar (1992) suggested that the relative scarcity of work on SC might be the result of a historical view of mating systems as "cooperative and harmonious ventures". Clearly, pre-SC does not fit into such a paradigm. Instead, pre-SC appears to be an ideal model system for the modern day study of mating systems, which emphasizes the role of inter-sexual conflict in explaining sexual behavior (Parker, 1979; Rowe et al., 1994; Choe & Crespi, 1997). Pre-SC provides an opportunity to study an extreme inter-sexual conflict of interest. Male interests are served by avoiding female attacks, obtaining matings and ensuring their own fertilization success. In contrast, female interests may sometimes be better served by preying on a male and foregoing the mating opportunity. Thus, unlike SC that occurs during or after sperm transfer (e.g. Andrade, 1996), pre-SC cannot be construed as a male mating strategy, and research on the adaptive significance of this behavior has instead focused on a search for female benefits that can explain why females would prey on a male before successfully mating with him (see below).

An understanding of pre-SC also requires that we view mating behavior as deeply intertwined with other aspects of an organism's life history. For all animals, mating decisions can be best understood in conjunction with a wide range of other relevant selection pressures (Rowe et al., 1994). For example, patterns of female mate choice in nature are often heavily influenced by predation risk and/or previous foraging success (Sakaluk, 1990; Crowley et al., 1991; Sih,

1994; Lima, 1998). In sexually cannibalistic species, mating, foraging and predator/prey issues are uniquely inseparable as males are simultaneously potential sperm donors and/or prey items, and females are simultaneously potential mates and/or predators. Thus, pre-SC offers an obvious intersection of foraging, mating and anti-predator behavior where the sexual conflicts of interest typical of many mating systems are compounded by asymmetries of interest regarding foraging and survival.

Review of hypotheses

In a widely cited review of sexual cannibalism, Elgar (1992) focused on two potential female benefits to explain pre-SC. First, females may obtain indirect benefits from pre-SC if they use attack behavior upon courtship as an extreme form of mate refusal (Elgar & Nash, 1988). Under such a hypothesis, female aggression should be biased towards males of certain phenotypes (e.g. small males), presumably resulting in a mating bias for males of the phenotype that is less often attacked. This 'good-genes' hypothesis has received little support as few studies have been able to demonstrate that females preferentially attack males based upon their size or other distinguishing phenotype.

An alternative, but not mutually exclusive, idea is that pre-SC could represent an optimal foraging/mating strategy if attacks/matings are predicated on each female's current need for the material benefits of food (fecundity) versus sperm (fertilization). Newman & Elgar (1991) developed this hypothesis with an economic model showing that pre-SC can be explained, even for virgin females, on the basis of the nutrient payoff to females that feed on a male rather than mating with him. According to this trade-off model, (1) pre-SC should benefit female fecundity and (2) the prevalence of pre-SC should depend on the levels of food/sperm limitation experienced by females (i.e. be most common when prey are limiting but mates are not).

Perhaps surprisingly, this intuitive, resource-optimization idea has also met with little empirical support. In one of the few explicit attempts to test this hypothesis empirically, Arnqvist & Henrikkson (1997) showed in the European fishing spider (*Dolomedes fimbriatus*) that female fecundity was unrelated to adult feeding history including pre-SC, and female attacks on males were not predicted by the level of sperm and food limitation experienced by a female. Notably, despite multiple mating opportunities, many virgin females in this laboratory

experiment attacked every single male provided, failed to mate, and thus produced no offspring. This fascinating result indicates strong fertility costs of pre-SC rather than foraging benefits.

Arnqvist & Henrikkson (1997) offered an alternative explanation for their results positing that pre-SC is "an indirect result of behaviour that is adaptive in previous life-history stages". This 'aggressive-spillover' hypothesis suggests that pre-SC represents a carryover of aggression from the juvenile foraging context, where high levels of foraging aggression might be selectively advantageous, to the adult's mating context. They hypothesized that genetic constraints on the behavioral expression of aggression produce intra-individual behavioral correlations across ontogenetic stages (juvenile feeding and adult mating). Selection thus shapes the suite of correlated aggressive behaviors rather than optimizing aggressive levels in each individual context. These three current hypotheses for pre-SC form the core of my dissertation work. Below I present experimental tests of each of these ideas using the semi-aquatic North American fishing spider (*Dolomedes triton*) as my study organism.

The foraging and mating systems of fishing spiders are reviewed in Chapter 4. With regard to pre-SC, adult female fishing spiders commonly attack males at any point during the copulatory sequence. However, laboratory mating trials indicate that females of the European fishing spider (*D. fimbriatus*) most frequently attack during pre-copulatory courtship (75% of trials), and that males are killed in approximately 5-10 % of these attacks (Arnqvist, 1992; Arnqvist & Henrikkson, 1997). For *D. triton*, laboratory mating trials showed that pre-copulatory attacks by virgin females occur in approximately 20% of pairings (see Chapter 4), a result that was recently confirmed under semi-natural field conditions (see Chapter 3). In addition, field studies of *D. triton* suggest that males represent a common contribution to the adult female diet (Zimmerman & Spence, 1989), and that male population density declines drastically, soon after adult female emergence (Zimmerman & Spence, 1992). Thus, sexual cannibalism appears to play an important role in the ecology of *Dolomedes*.

Hypothesis 1: Mate choice for indirect benefits:

If pre-SC acts as a way for females to invoke an extreme mating bias against certain male phenotypes, then females should attack non-preferred males and mate with preferred males. The most obvious phenotypic difference amongst *D. triton* males is body size, and large male body size in arachnids is associated with a number of benefits (Vollrath, 1987; Elgar & Fahey, 1996;

Arnqvist & Henrikkson, 1997). In addition, body size has been shown to be heritable in at least one spider species (Watson, 1998). Below I test the prediction that pre-copulatory attacks are directed primarily at small males and matings are most common with large males.

Over 100 penultimate-stage males were collected from the field. Upon maturity I weighed and digitally imaged males. Males from the middle 1/3 of the population size distribution were not used in the experiment. On sequential days adult virgin females from the same population were paired with a male from the large size class and a male from the small size class. Thus, each female could exhibit one of four possible strategies (e.g. attack males of both size classes, attack large male but not small male, attack small male but not large male, or attack neither male, see Table 1.1). To test the prediction that females switch their behavior biasing attacks towards small males I compared the relative frequency of attacking small males but not large males (tactic # 1c) versus attacking large males but not small males (tactic # 1b). To test the prediction that females switch their behavior biasing mountings and matings towards large males I compared the relative frequency of mounting/mating with large males but not with small males (tactic # 3b/4b) with mounting/mating with small males but not large males (tactic # 3c/4c).

Figure 1.1 shows the substantial amount of size variation both within and between sexes. Male size classes used in this experiment were statistically different in both mass (t_{61}=17.23, $p<0.0001$) and cephalothorax area (t_{62}=18.38, $p<0.0001$). Females showed no tendency to switch their attack behavior based on male size class. The tactic of attacking small males but not large males did not occur more often than the tactic of attacking large males but not small males (G=1.36, d.f.=1, $p>0.1$). Interestingly, females displayed tactics that failed to discriminate between male size classes (tactics # 1 and 4 from Table 1.1) more often than would be expected given the overall probability of attack on each size class (p(attack small)=0.30, p(attack large)=0.21). Thus, no evidence exists to suggest that females switch their attack strategy based on male size class. Instead, females are more likely to treat different-sized males similarly than they are to switch behaviors based on male size class.

Also from Table 1.1, it is apparent that females are not biasing mountings in favor of large males (G=0.69, d.f.=1, $p>0.1$). However, females are mating with large males but not small males more often than they mate with small males but not large males (G=2.93, d.f.=1, $.05<p<0.1$). This result is supported by additional analyses that do not take the above pair-wise

approach. In a comparison of large versus small virgin males that secured a mounting, large males were significantly more likely to transfer sperm successfully (11/13; successful males are the enlarged symbols in Figure 1.1) relative to the mating success of small males (2/13; χ^2=12.46, d.f=1, p=0.0004). Thus, mating does most often include the largest males, but this bias occurs after courtship has resulted in a mounting, and appears to be determined by the superior copulatory ability of larger males. Nevertheless, it remains a possibility that females subtly contribute to this bias by, for example, raising their legs high during the copulatory struggle such that large males have greater mating success.

Hypothesis 2: Adaptive foraging/mating trade-off:

If pre-SC is being used by adult females as an adaptive foraging/mating trade-off, then (1) adult feeding, and particularly eating a male, should benefit female fecundity, (2) attacks should be most frequent by food-limited females, and (3) attacks should be least frequent by sperm-limited females. First, I manipulated adult food availability by providing one group of adult females (n=24) with 3 crickets per week and another group of females (n=29) with 1 cricket per week. This adult food manipulation had a significant effect on fecundity (Table 1.2), especially when considering fecundity benefits accrued from second and third egg sacs (see Chapter 4). Furthermore, while consumption of a male did not significantly enhance fecundity in terms of traditional quantitative measures (e.g. egg sac mass or offspring number), it did produce more subtle fecundity benefits in two separate experiments (see Chapters 4 and 5). Specifically, the inclusion of males (0, 1, 2 or 3) in the female diet significantly improved a female's chances of successfully hatching an egg sac (binary logistic regression: n=59, log likelihood ratio= 7.57, d.f.=1, p=0.006). In addition, pre-SC significantly improved the ratio of egg sac mass to offspring number (r=0.434, t_{32}=2.46, p=0.01). Thus, male-derived nutrients appear to facilitate successful reproductive events and allow females to provide more egg mass per egg, but the addition of one or more males to the female's diet does not significantly increase offspring number among females that hatch an egg sac.

Second, despite the existence of discrete fecundity benefits of consuming a male in *D. triton,* no evidence exists to support the prediction that food limitation explains the prevalence of attacks. Experimentally induced food restriction did not result in increased rates of pre-SC, and female body condition (mass / cephalothroax area) has failed to predict pre-SC in three

independent studies of this population (see Chapters 4, 5 and 6). Finally, while a number of studies have examined the food-limitation side of Newman & Elgar's model, to my knowledge no one has manipulated sperm limitation to test the prediction that pre-SC should be most frequent in females that experience high mate availability. While some evidence suggests an increase in pre-SC amongst mated females relative to virgins (Wojcicki, 1992; Chapter 4), such studies are confounded by mating motivation and thus fail to test the crucial prediction that among virgin females, pre-SC should be more frequent when females 'perceive' males as abundant and less frequent when males are 'perceived' as limiting. This is, no doubt, a result of the fact that it is difficult to imagine how unmated females might vary in their experience of mate availability or sperm limitation.

One way in which virgin females could experience differences in male availability well before mating/pre-SC decisions are being made stems from the fact that adult males are sometimes found cohabiting with penultimate-stage females. I predicted that male-female cohabitation allows pre-reproductive females a means to assess the value of a male as either food or sperm. Thus, all else being equal, females housed with adult males through their penultimate molt ($n=19$) should be more likely to exhibit pre-SC than females housed with smaller juvenile females ($n=20$), or females housed alone ($n=21$). To prevent cannibalism of the cohabitant (guest) by the focal female (host), guests were housed in their own 16 oz., transparent plastic cup with the bottom cut out. This cup was covered at each end with mesh and rested on its side submerged in several inches of water in the host female's container. Thus, water-borne chemicals were continuously exchanged between host and guest but physical contact was prevented. It should be noted, however, that cohabitation frequently resulted in some physical contact as the two spiders would cling to opposite sides of the cup's mesh covering such that their legs touched. Results support the contention that pre-reproductive exposure to males heightens pre-SC. Juvenile females exposed to adult males attacked males in 38% of their mating trials, whereas juvenile females housed with either smaller juvenile females or no cohabitant at all attacked males in 29 % of their mating trials ($t =1.96$, d.f.$= 38.3$, $p_{1\text{-tailed}} =0.029$). While support for the trade-off hypothesis is mixed in *D. triton*, future work needs to continue to ask creative questions that get at the full expectation of the model, rather than merely looking for increases in offspring number for sexual cannibals.

Hypothesis 3: Aggressive spillover:

Finally, as noted above, a recent hypothesis suggests that pre-SC is not adaptive per se, but instead represents voracity (aggression towards food) that is selectively advantageous in previous ontogenetic foraging contexts. The spillover hypothesis posits that the fecundity advantages accrued by highly voracious juvenile females explain the appearance of potentially costly voracity towards males in the mating context. To test this idea I measured voracity in 60 individual females in (1) the juvenile foraging context, (2) the adult foraging context, (3) the adult's mating context, and (4) the anti-predator context (i.e. boldness to predators). Results support the sequence of predictions made by the spillover hypothesis (see Figure 1.2). Path analysis indicated significant, positive correlations between juvenile foraging voracity, fecundity, adult foraging voracity and pre-SC.   In addition, this suite of voracious behaviors was significantly positively correlated with boldness towards predators, defined as the proportion of a trial spent above water following a simulated predator disturbance (pre-SC: r_{59}=.243, t=1.89, $p_{1\text{-tailed}}$=0.032, hetero-specific foraging voracity: r_{60}=.317, t=2.54, $p_{1\text{-tailed}}$=0.007). Thus, an aggressive syndrome in *D. triton* appears to produce intra-individual correlations (spillovers) across both ontogenetic contexts (juvenile/adult) and behavioral contexts (foraging /mating /anti-predator). The existence and importance of behavioral correlations such as these is currently receiving renewed interest in animal behavior and may require that we shift our way of thinking about behavioral evolution.

<u>**Conclusions**</u>

In conclusion, pre-SC offers an ideal model system to study the complexity that emerges when male-female conflict is woven into multiple behavioral and ecological contexts. This dynamic interaction may often produce results that do not fall neatly into single-hypothesis categories. Instead, it may be that pre-SC in a given species is explained by multiple benefits that increase or decrease in importance as the context shifts. For example, pre-SC may largely be a way in which females diversify an otherwise monotonous diet when food diversity is limiting. In contrast, when the need for prey diversity is relaxed, pre-SC may be maintained through the overall benefits of a syndrome of high feeding voracity. However, a shift in ecological parameters, such as a reduction in the availability of males, should heighten the fertility costs of a spillover of aggression into the mating context. Under such circumstances, the maintenance of

pre-SC may shift back to material benefits derived from consuming a male and/or indirect benefits of mating with superior male phenotypes. Future experiments need to identify potential benefits and design experiments that examine how shifts in relevant behavioral and ecological contexts may result in fluctuations in female benefits.

Table 1.1　　The observed and expected frequency distributions of four distinct strategy sets (e.g. attack males of both size classes, attack one size class but not the other, or attack neither size class, *n=33*).

Event	Tactic	Large	Small	Observe	Expect	Obs-Exp
1. Attack	1a	yes	yes	5	2.12	2.88
	1b	yes	no	2	4.88	-2.88
	1c	no	yes	5	7.87	-2.88
	1d	no	no	21	18.12	2.88
2. Kill/Attack	2a	yes	yes	2	1.00	1.00
	2b	yes	no	1	2.00	-1.00
	2c	no	yes	2	3.00	-1.00
	2d	no	no	7	6.00	1.00
3. Mount	3a	yes	yes	1	1.64	-0.64
	3b	yes	no	5	4.36	0.64
	3c	no	yes	8	7.36	0.64
	3d	no	no	19	19.64	-0.64
4. Mate/mount	4a	yes	yes	1	0.86	0.14
	4b	yes	no	5	5.14	-0.14
	4c	no	yes	1	1.14	-0.14
	4d	no	no	7	6.86	0.14

Table 1.2   Least square means ± standard error (n) for two adult diet regimes. Food contrasts indicate support for the idea that adult food benefits fecundity.

Diet Regime	Fixed adult size (mm^2)	Number of spiderlings
Adult food		
Low	40.28 ± 2.05 (29)	474.13 ± 67.80 (18)
High	42.25 ± 2.05 (24)	612.65 ± 83.95 (12)

Figure 1.1 Regression of fixed adult body size on adult body mass (= body condition) demonstrating the substantial amount of size and mass variation that exists both within each sex and between the sexes (i.e. sexual size dimorphism).
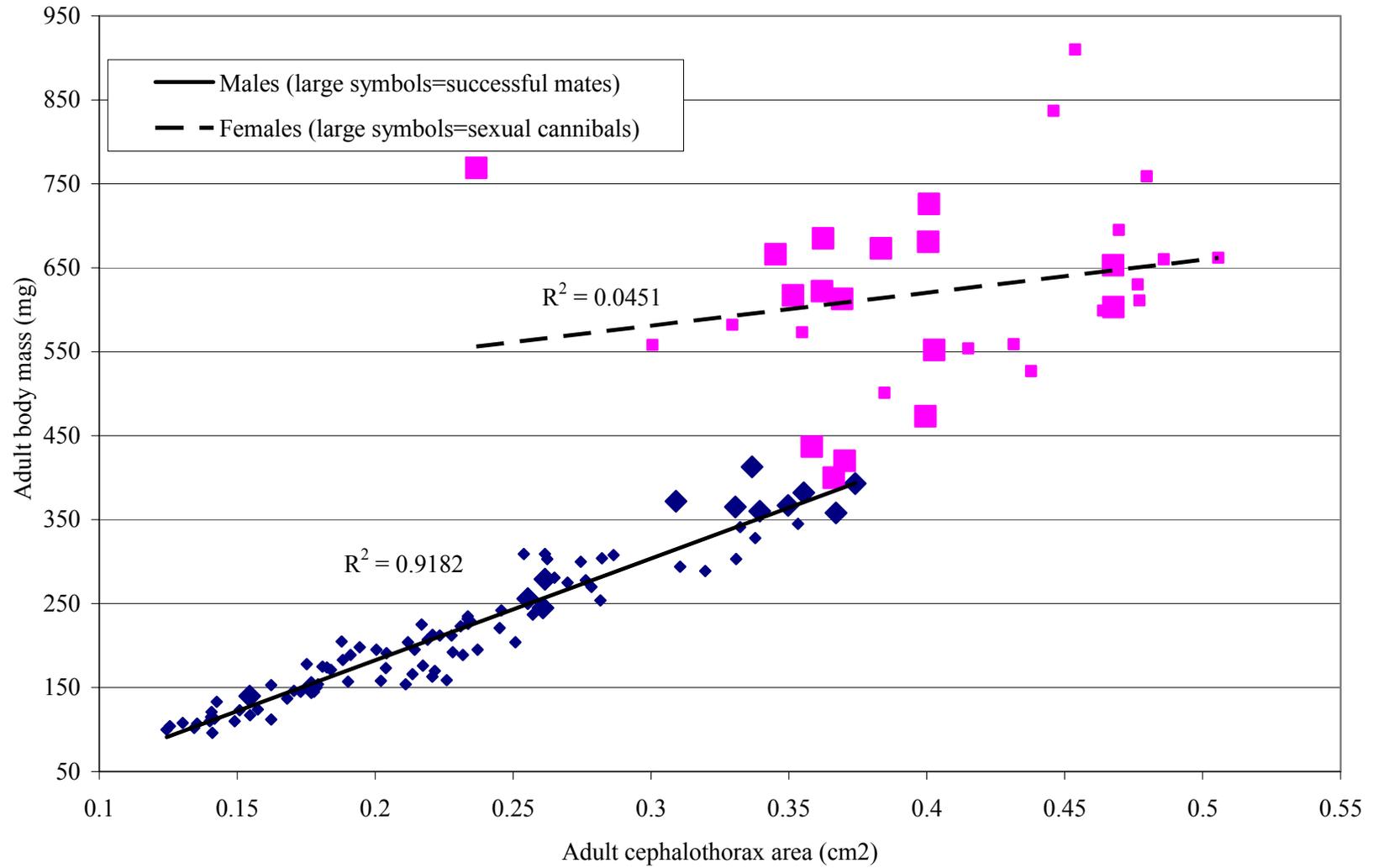
Figure 1.2   A test of the predictions of the aggressive spillover hypothesis. Note that we emphasize a new formulation of the spillover hypothesis with the statistically significant relationship between adult voracity/foraging success, adult mass with the egg sac and fecundity. All p-values are for 1-tailed t-tests.
*=p<0.05, **=p<0.01, ***=p<0.001, ****=p<0.0001
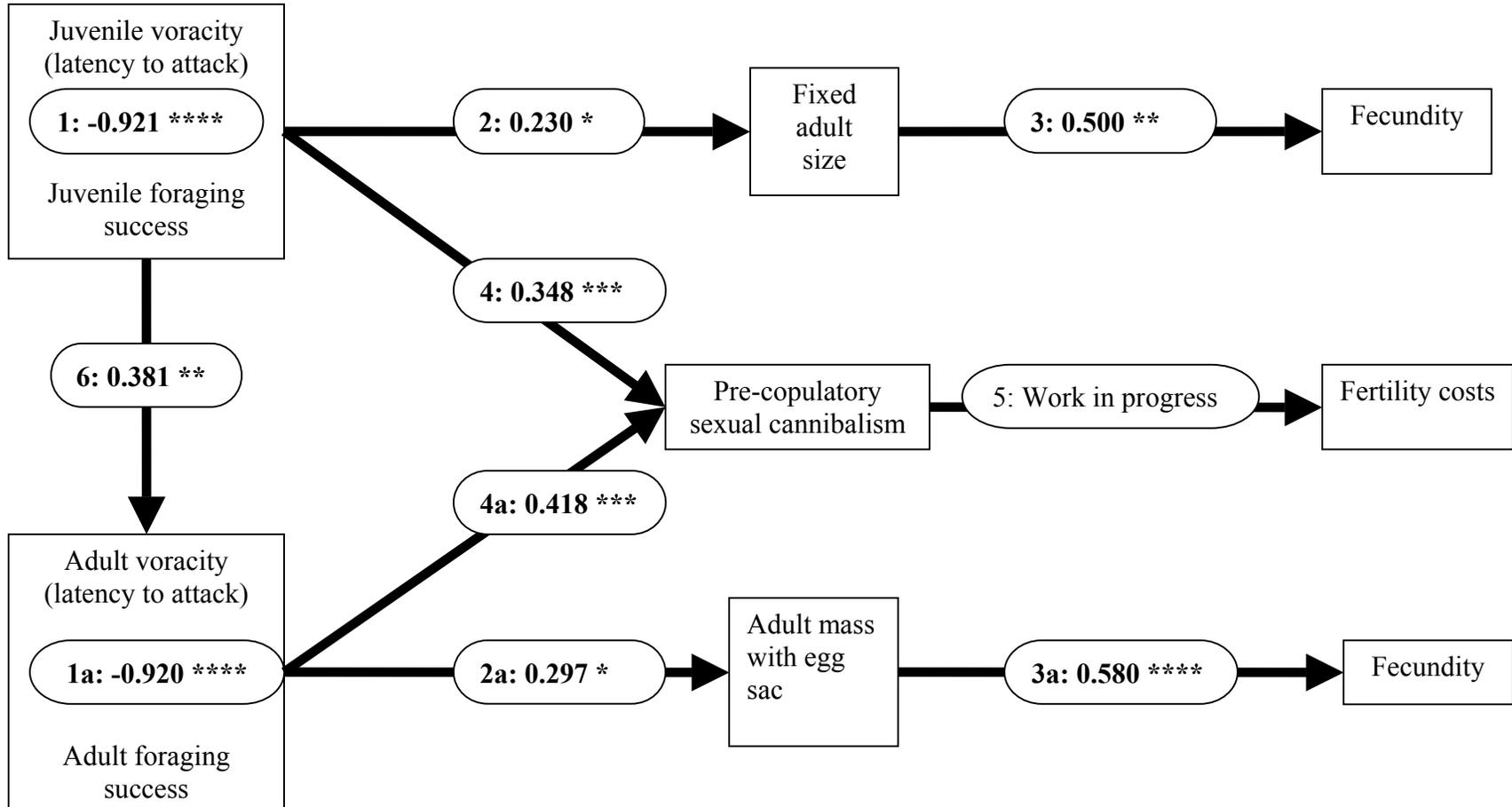
CHAPTER 2

Sexual cannibalism:

the ecology of an extreme sexual conflict

Summary

The phenomenon of sexual cannibalism (SC), or intra-specific, inter-sexual predation during courtship, copulation, or shortly thereafter, has fascinated and perplexed behavioral ecologists for the past century. SC is relatively widespread among invertebrates, suggesting that it has evolved independently several times, and reports are particularly prevalent for arachnids. Despite its apparent widespread distribution, most reports of SC are anecdotal, and much of what we know of the phenomenon comes from laboratory observations of mating behavior. Thus, evolutionary treatments of the functional significance of SC are uncommon, and the prevalence of SC in nature is known for only a handful of species. As a result, the behavioral and evolutionary ecology of SC remains an exciting field of research with much room for growth. Here the current state of work on SC is reviewed with an integrative approach that emphasizes the modern view of mating systems as being the product of inter-sexual conflict, set on a larger stage of interacting behavioral and ecological variables (e.g. mating status, food availability). A recurrent theme that emerges from considering such transient variables in the determination of inter-sexual conflict is that multiple, context-dependent explanations may be required to explain SC within any given species. This additional layer of complexity is rarely addressed in studies of SC, or studies of mating systems in general for that matter. The current review points out how studies that focus on the possibility of multiple, co-occurring benefits of SC may do the best job of promoting our ability to understand a complex behavioral and ecological phenomenon such as SC.

Introduction

The phenomenon of sexual cannibalism (SC), or intra-specific, inter-sexual predation during courtship, copulation, or shortly thereafter, has fascinated and perplexed behavioral ecologists for the past century (Roeder, 1935; Bristowe, 1958; Robinson & Robinson, 1980; Polis, 1981; Elgar, 1992; Johns & Maxwell, 1997). Most cases of SC involve large predatory female invertebrates attacking their smaller male counterparts. SC is relatively widespread among the invertebrates, suggesting that it has evolved independently several times, and reports are particularly prevalent for arachnids. Elgar (1992) cites records of SC in four families of insects, a copepod, two familes of gastropods, four scorpion families and fourteen spider families. More recent additions to this list suggest that more taxa will be included as the number of species examined grows (Dick, 1995; Elgar et al., 2000; Knoflach & Van Harten, 2000; Schneider et al., 2000). Despite its apparent widespread distribution, most reports of SC are anecdotal, and much of what we know of the phenomenon comes from laboratory observations of mating behavior. Thus, evolutionary treatments of the functional significance of SC are uncommon, and the prevalence of SC in nature is known for only a handful of species. As a result, the behavioral and evolutionary ecology of SC remains an exciting field of research with much room for growth.

The goal of this review is to argue for an updating of our approach (conceptual and experimental) to the study of SC by comprehensively documenting the current state of work on the behavior, ecology and evolution of SC. I begin by presenting an integrative approach to SC and mating systems in general. First, mating system dynamics are largely a product of the resolution of conflicts of interest between the sexes (i.e. antagonistic coevolution). SC is but one possible outcome of one type of conflict between the sexes. Second, variation in ecological parameters (e.g. food availability, predation risk etc.) often determines the nature of this conflict resolution, and thus these variables can determine the occurrence of SC. In addition, SC can occur either before, during or after sperm transfer. Sex-specific costs and benefits of SC should vary at different points along this copulatory sequence. Thus, contextual variation, both ecological and behavioral, can profoundly affect inter-sexual conflict, which in turn can determine the explanation(s) for and prevalence of SC.

I then proceed to review the hypotheses proposed to explain SC, describing recent attempts to evaluate the hypotheses and identifying areas that deserve future attention (see Table

2.1 for an overview). In particular, I review the existing literature with special regard for how past studies have approached the complexity of SC, which stems, in part, from the above-mentioned contextual variability. I stress throughout the review that the conceptual sequence proposed here (variation in environmental context - variation in the resolution of inter-sexual conflict - variation in the explanation of SC) may often require that we consider multiple explanations for SC within a species across these variable contexts. Hypotheses are grouped and treated in the following order: male benefits, female benefits, and non-adaptive hypotheses.

Sexual cannibalism as sexual conflict

In the last thorough review of SC, Elgar (1992) suggested that the relative scarcity of work in this area may be the result of a historical view of mating systems as "cooperative and harmonious ventures". Indeed, SC does not appear to fit into such a paradigm. Instead, SC appears to be an ideal model system for the modern day study of mating systems, which emphasizes the role of conflicts of interest between the sexes in explaining sexual behavior (Parker, 1979; Davies, 1985, 1989; Elgar, 1992; Gross, 1994; Rowe et al., 1994; Clutton-Brock & Parker, 1995; Choe & Crespi, 1997; Elgar, 1998; Schneider & Lubin, 1998). According to this approach, mating system dynamics are largely determined by the ability of each sex to control four critical phases of mating: pair formation, copulation, fertilization, and parental investment (Brown, et al., 1997).   Such a theory further predicts two general classes of outcomes of inter-sexual conflicts. First, inter-sexual conflict may result in a stable compromise between the sexes ('persuasion' sensu Brown et al., 1997). Alternatively, inter-sexual conflicts can result in 'unresolvable evolutionary chases'—a situation in which selection regimes are constantly changing as each sex retaliates to the latest novel adaptation employed by the opposite sex to retain control over reproduction ('coercion and/or forcing' sensu Brown et al., 1997; see also Parker, 1979; Alexander et al., 1997).

SC provides an opportunity to study an extreme inter-sexual conflict of interest. Male interests are best served by avoiding female attacks, obtaining matings and ensuring their own fertilization success (but see 'Male benefits' below). However, female interests can be served by preying on a male, mating with a male, or mating with a male and then preying on the male. In addition to these traditional conflicts, female spiders are able to store sperm from multiple males (Austad, 1984; Elgar, 1998). As a result, once mating has occurred, there is the potential for

post-copulatory, inter-sexual conflicts between male mechanisms of sperm competition (Elgar, 1998) and female mechanisms of cryptic gamete choice (Eberhard, 1996, 1997, 1998).

Sexual cannibalism as an ecological phenomenon

In addition to stressing the importance of inter-sexual conflict, an understanding of SC also requires that we view mating behavior as deeply intertwined with other aspects of an organism's life history. Mating decisions for all animals, and for the sexual cannibal and her mate in particular, are only fully understood in conjunction with a wide range of other relevant selection pressures (Rowe et al., 1994). For example, patterns of female mate choice in nature are often heavily influenced by predation risk and/or previous foraging success (Real & Caraco, 1986; Sakaluk, 1990; Crowley et al., 1991; Sih, 1994; Lima, 1998). In sexually cannibalistic species, mating, foraging and predator/prey issues are uniquely inseparable as males are simultaneously potential sperm donors and/or prey items, and females are simultaneously potential mates and/or predators.

The complexity of behavioral strategies that emerge from such a situation require that we view SC as necessarily facultative, with each individual's strategy (e.g. attack or mate) being dependent upon both the behavioral and ecological context in which it occurs (e.g. variation in predation risk, food limitation and/or sperm limitation), as well as on the strategy adopted by other individuals. This is the approach taken by recent reviews of sexual selection in water striders (Rowe et al., 1994) and jumping spiders (Jackson & Pollard, 1997), and it should prove to be a valuable approach for all mating systems in which the sexual conflicts of interest typical of so many mating systems are compounded by asymmetries of interest regarding foraging and survival. For example, pre-copulatory SC in a hypothetical species may be the joint result of the direct, material benefits of feeding on a male (see 'Adaptive foraging' below), combined with the indirect, 'good genes' benefits of narrowing the pool of sires to only those males capable of avoiding an attack (see 'Mate choice/refusal' below). However, the relative importance of these mechanisms may fluctuate given the ecological context. Under conditions of severe food stress, SC may be largely driven by material benefits, with indirect benefits playing a relatively minor role. In contrast, given a relaxation of food stress, material benefits of SC may be reduced and indirect benefits may maintain SC during transient periods of food abundance.

Sexual cannibalism as a behavioral continuum

Hypotheses for SC have traditionally been split into two distinct categories reflecting the timing of a female's attack relative to copulation (Elgar, 1992; Johns & Maxwell, 1997). Because males cannot benefit from a scenario in which they are killed prior to sperm transfer, pre-copulatory SC (pre-SC) has traditionally been examined as either an adaptive female strategy or as a non-adaptive by-product of the female's aggressive, predatory nature. In contrast, post-copulatory SC (post-SC, i.e. female attack during or after sperm transfer) has the potential to benefit both males and females (Elgar, 1998). However, the majority of work on this topic has focused on ways in which male sacrifice after mating can be construed as an adaptive male tactic.

I will follow this traditional dichotomy to some extent. However, sexually cannibalistic females that commonly attack males before copulation often also attack males during and/or after copulation, and there is no *a priori* reason to expect that attacks before and after mating are explained by the same functional mechanism. This continuum of predatory options available to females opens up the possibility that more than one hypothesis may be required to explain SC at different points along the copulatory sequence. For this reason, I have chosen to structure this review around the mechanisms proposed to generate SC, rather than isolating pre-copulatory and post-copulatory mechanisms as previous reviews have done. Nesting the timing of attack within individual mechanisms illustrates how the costs and benefits of a particular sex-specific behavioral strategy can vary across the mating sequence. For example, pre-copulatory attacks in a hypothetical species may provide females with the adaptive foraging benefit suggested above. In contrast, in the same species, SC that follows successful sperm transfer may be explained as a paternal investment strategy by the complicit, suicidal male (see 'Paternal investment' below). Finally, ecological and behavioral contexts may commonly interact to produce multiple, context-dependent explanations for SC. For example, in the simplest such scenario, SC within a species may have four distinct explanations: pre-copulatory mechanisms in two ecological contexts, which are distinct from post-copulatory mechanisms in two ecological contexts.

Adaptive hypotheses (male benefits)

Perhaps one of the most intriguing suggestions regarding SC is that if it follows successful sperm transfer, it could actually be to the male's benefit. Verbal and quantitative models have investigated this possibility and generally suggest that if the benefits to male

suicidal investment are great, and the male's chances of future matings are low, then males could benefit from post-copulatory SC (Thornhill, 1976a; Parker, 1979; Buskirk et al., 1984). Below I review two traditional explanations for male complicity in post-copulatory SC. While these hypotheses differ in the proposed benefit gained by males, historically they have both been restricted to species in which males either facilitate or fail to resist SC during or following copulation. In addition, I address the recent suggestion of a male benefit to pre-copulatory sexually cannibalistic attacks; this benefit rests on the assumption that males escape any elicited attacks.

Paternal investment

Simmons & Parker (1989) define paternal investment via nuptial gift-giving as situations in which "a male gains via increasing an individual female's gametic output through the donation of a nuptial gift" (p.332). Nuptial gift-giving is common in arthropod mating systems (reviewed in Thornhill & Alcock, 1983) and can include prey items captured by the male for the female (Thornhill, 1976b; Austad & Thornhill, 1986), male glandular secretions (Gwynne, 1984; Sakaluk, 1984; Brown, 1997), irreplaceable body tissue (Dodson et al., 1983), and, in the case of post-copulatory SC, the male's entire body (Buskirk et al., 1984; Elgar, 1992). A long standing debate exists over whether the functional significance of nuptial gifts is best explained as male mating effort (see below) or paternal investment (debate recently reviewed in Vahed, 1998). The paternal-investment hypothesis for gift-giving requires that male material investment be used toward the production of offspring sired by the investing male (Parker, 1979), and this investment of somatic nutrients must increase female reproductive output relative to output in the absence of such nuptial provisioning.

While non-lethal nuptial gifts can carry high costs for males of some species (Sakaluk et al., 1987; Gwynne & Simmons, 1990), a suicide gift such as post-copulatory SC is presumably the most costly of all, as cannibalized males forfeit any future mating possibilities. Models of post-copulatory SC account for this high cost to males and consider ecological scenarios in which benefits of such investment could outweigh these costs. Buskirk et al. (1984) present a model suggesting that male sacrifice as a means to increase the number of offspring sired by the investing male is most likely to evolve when: (1) males have little chance of acquiring additional matings in the future (i.e. low residual reproductive value), and (2) male sacrifice results in a

18

significant increase in the number or fitness of offspring sired by the male. Short male lifespans, male biased sex ratios and/or high risk of predation associated with mate searching are all factors that reduce a male's residual reproductive value. The contribution a male's body can make toward female fecundity, and the degree to which female fecundity is nutrient-limited, are ecological factors influencing the material fitness benefits of male sacrifice.

What is the empirical evidence for post-copulatory SC as paternal investment; or, put differently, are there examples of male sacrifice in which the male may derive a fitness benefit through the donation of somatic nutrients? When Buskirk et al. published their model, no experimental evidence existed to support the paternal-investment hypothesis. They supported their ideas by noting several examples of sexually cannibalistic arthropod species with life histories consistent with the evolution of paternal investment. Subsequently, no studies have shown a male material fitness benefit stemming from post-copulatory SC. In fact, very few studies indicate that male consumption by the female has any significant effect on female fecundity (see 'Adaptive foraging' below for a list of references). In addition, contrary to the predictions of this model, neither the magnitude of male benefits from paternal investment, nor the number of additional male mating opportunities consistently influence the pattern of paternal investment (Peretti et al., 1999). Finally, Gould (1984) argued that instances in which males appear content to sacrifice themselves after copulation are very rare, suggesting the evolution of SC by paternal investment is unlikely.

Perhaps the best known example of male sacrifice is in the Australian redback spider, *Latrodectus hasselti* (Forster, 1992). Rather than resisting predation by their mates, male redbacks perform a ritualized somersault during copulation bringing them to rest in a prone position just in front of the female's mouthparts. Also favoring the hypothesis of paternal investment in this species is the fact that males have a low probability of acquiring future matings. Inter-specific predation risk on mate searching males is very high (Andrade, pers. comm.). However, the hypothesis of paternal investment and natural selection for male sacrifice in redback spiders has not received support. Male redbacks typically weigh 1-2 % of the female's body mass and are significantly smaller than most prey items taken by females. In addition, females often do not consume the complicit male (Andrade, 1996, 1998), suggesting that the male's body might not provide sufficient resources to promote female fecundity. Indeed,

experimental comparisons in this species indicate that female consumption of the male does not increase offspring production (Andrade, 1996).

Two other records of male complicity in SC come from the theridiid spider *Tidarren cuneolatum* and an araneid spider *Argiope aemula*. Males of these species make no attempt to avoid female attacks after they have transferred a full complement of sperm (Sasaki & Iwahashi, 1995; Knoflach & Van Harten, 2000). In fact, males were often found to be dead, presumably from fatigue, following their final insertion but immediately prior to the female's attack. Post-copulatory SC is frequent enough in these species to be considered an important component of their mating systems (100% and 98 %, respectively). While data on future mating opportunities for males are lacking, it might be presumed that the male's failure to attempt to escape indicates that he profits more from sacrificial paternal investment than he would from trying to obtain additional matings. Certainly for males dying of fatigue near the end of copulation, future matings are unlikely, and the donation of their body to their mate's reproduction at this point harbors little cost. Nonetheless ecological data such as operational sex ratios, typical male longevity, and predation risk associated with finding an additional mate are needed to evaluate the prediction that low male residual reproductive value favors a sexually cannibalistic paternal investment strategy.

Unfortunately, no data are available on material benefits associated with male sacrifice for these species. Instead, male consumption in *Argiope keyserlingi*, similar in size to its congener *A. aemula*, is not associated with increases in female fecundity (Elgar et al., 2000). Natural selection for paternal investment might seem unlikely in these species, as males represent a minute contribution to the mass of female egg sacs. Alternatively, male sacrifice may, in fact, yield fecundity benefits that are undetected in laboratory studies that fail to mimic natural levels of food stress. In other words, male consumption may only benefit female fecundity when prey are realistically limiting. Future studies need to either be conducted in the field where females are subject to natural levels of variation in food availability, or laboratory studies need to use field data to employ experimental food regimes that will not mask potential effects of male consumption on female fecundity. Recently, studies (e.g. Elgar et al., 2000) have discounted this possible confound of laboratory food regimes if female fecundity (number of eggs) in the experiment approximates fecundity in the field. This is a safe assumption only if

quantitative measures like egg number accurately reflect female fitness. As the next section points out, this may not always be the case.

SC as qualitative paternal investment

Studies of the functional significance of nuptial food gifts, along with studies of diet effects on reproduction in general, traditionally emphasize quantitative benefits (e.g. female mass, egg sac mass, egg number, offspring number) at the expense of more subtle qualitative fitness benefits of feeding (but see Brown, 1997). By mass, male arachnids often represent a very small contribution to the diet of their larger female counterparts. Thus, perhaps it should not be surprising that consumption of a male is rarely associated with significant increases in female mass, mass of the egg sac, or egg/offspring number (but see Birkhead et al., 1988; Elgar & Nash, 1988 under 'Adaptive foraging' below). Cannibalized males may instead offer paternal investment to their offspring in terms of the qualitative nature of the nutrient they offer females.

With regard to the possibility that males offer females qualitative foraging benefits, male consumption by female fishing spiders (*Dolomedes triton*) is associated with a significant increase in successful egg sac hatching of both first and second egg sacs, but is not associated with increases in the number of offspring produced in either egg sac (see Chapter 4). In addition, females that feed on males increase the mass of their egg sac relative to the number of offspring in that egg sac (see Chapter 5). Thus, SC as paternal investment may be a way in which the male ensures that his mate succeeds in hatching an egg sac comprised of well-provisioned eggs, regardless of the absolute number of eggs produced.

Further support for this idea comes from a study of the orb-web spider *Argiope keyserlingi* (Araneidae) (Elgar et al., 2000). Among females that produced offspring in this experiment, consuming at least one male did not increase offspring production relative to females that failed to feed on a male. Interestingly, of the 80 staged mating trials that resulted in post-copulatory SC, 37 of these females hatched an egg sac (46 % hatch success). In contrast, of the 58 mating trials that did not result in SC, only 10 of these females hatched an egg sac (17 % hatch success). It remains to be seen if discrete benefits of post-copulatory SC such as increases in the probability of successful egg sac hatching are common across species.

Several aspects of arachnid reproduction may favor the evolution of SC as a qualitative paternal investment strategy. First, studies of nutritional ecology have shown that arachnids

require a breadth of amino acids to maximize reproduction (Riechert & Harp, 1987), and that at least one species exhibits prey selectivity in order to optimize the diversity of prey-types in its diet (Greenstone, 1979). Males may offer females an opportunity to diversify their diet. Second, males may be qualitatively important prey items if they are more efficiently converted to energy than other prey items (Elgar & Nash, 1988). Finally, post-mating feeding in spiders is known to be associated with the onset of the accumulation of larger egg yolk granules (Foelix, 1996). Accordingly, cannibalized males may be investing in their offspring, not in terms of the crude mass they offer, but instead as a means of nutrient diversity, which is most efficiently converted to energy, and is readily available at a crucial time in egg development.

If such qualitative benefits are common, then we should not rely on a correlation between female mass and offspring number to determine the effect of SC on male and female fitness. Instead, future studies should look for benefits such as increases in female longevity, probability of successful reproduction, egg size, and possibly the size and vigor of offspring (e.g. Watson, 1998), to determine if selection on males is favoring the investment of qualitatively important nutrients via SC. The above debate also points out a larger problem in the analysis of fecundity data from studies such as these; many studies compare only reproductive output of those females that produce some offspring, excluding experimental animals that for whatever reason fail to produce offspring altogether. While the historical emphasis has been on comparisons of continuous measures like offspring number, comparisons of discrete measures such as percent of females that hatched an egg sac may be more biologically relevant, especially when ecological constraints make offspring number less important than individual offspring vigor and survivorship.

The necessity of male complicity

Historically studies of SC as paternal investment have been restricted to systems featuring male complicity with SC. However, males that suffer post-copulatory SC despite attempts to escape can still gain via paternal investment. For some species, paternal investment may be a facultative strategy that is selected for, and subsequently employed, only under certain ecological conditions. For example, the benefits of a paternal investment strategy should depend on food stress. Indeed, heightened food stress in a population should have the dual effect of (1) increasing the proportional fitness gain a male could receive by sacrificing his body toward his

mate's reproduction, and (2) lowering the number of available reproductive females, thus reducing the male's expected number of future matings. Both of these changes associated with food stress are predicted to increase the viability of post-copulatory SC as a paternal investment strategy. The optimal male strategy may be to sacrifice himself during periods of food limitation but not during periods of food abundance. Because most male spiders feed very little after maturation (Foelix, 1996), males may need to rely on their mate's motivational state to indicate current levels of food stress. In such a scenario, males do not benefit by facilitating their capture, but instead do best to always try and evade post-copulatory attacks, thus relying on female hunger and voracious motivation to dictate whether or not male consumption will be reproductively beneficial.

In sum, current empirical evidence does not support the hypothesis of paternal investment as a mechanism driving post-copulatory SC. However, historical preconceptions that males must be complicit in their capture, and that male consumption must yield quantitative increases in egg or offspring number, may have distracted researchers from instances of paternal investment. Future studies should investigate the possibility that paternal investment benefits fluctuate along with ecological parameters such as food availability, and should more explicitly examine the qualitative, nutritive addition a male's body offers the female.

Post-copulatory male mating effort

A second male-oriented explanation for post-copulatory SC suggests that males enhance their fertilization success by being consumed during or after sperm transfer (Elgar, 1992). Much like paternal investment, this male mating effort can take various forms in arthropod mating systems, with SC being an extreme form of this effort (Thornhill & Alcock, 1983). SC as male mating effort should evolve most readily when benefits of mating effort are high and additional male mating opportunities are few in number (Simmons & Parker, 1989; Hawkes et al., 1995; Vahed, 1998). In contrast to the paternal-investment hypothesis, male mating effort need not be associated with any material benefit gained by the receiving female and the offspring sired by the cannibalized male. Instead, the mating effort hypothesis simply requires that, all other things being equal, consumed males sire a higher proportion of a female's offspring than males that are not consumed. Thus, fertilization success and assurance of paternity are stressed in the mating effort hypothesis rather than material provisioning.

Mating effort appears to explain more cases of nuptial provisioning in insects than does paternal investment (reviewed in Vahed, 1998). Theoretical studies also appear to favor the evolution of mating effort over paternal care (Hawkes et al., 1995). In addition, there is good experimental evidence that male facilitation of post-copulatory SC functions as male mating effort in at least one species. While Andrade's (1996) work on redback spiders failed to support the paternal investment hypothesis (see above), it showed that consumed males copulated for twice as long as males that were not consumed. This, in turn, translated into twice as many offspring being sired by cannibalized males. Thus, male redbacks facilitate post-copulatory SC, probably have very few other mating opportunities, and derive a substantial paternity advantage by being consumed (Andrade, 1996). In addition, consumed male redbacks also derive paternity benefits by inducing a substantial refractory period in their mates that should reduce sperm competition (Andrade, 1996; see also Johnson et al., 1999; Knoflach & Van Harten, 2000 for similar suggestions in other species).

However, subsequent works have not indicated that post-copulatory SC serves a male mating effort function in other species. For example, Elgar et al. (2000) have shown that paternity in the sexually cannibalistic spider *Argiope keyserlingi* is under female control rather than male control (see 'Post-copulatory mate choice' below for a description). These authors echo the theme of the current review by pointing out that SC will likely be explained in different ways for different species because SC is the result of an antagonistic coevolution between the sexes that will not necessarily be resolved similarly in different species. Taking this idea one step further, there is no reason to expect SC within a species to be explained by the same mechanism across variable contexts.

Post-copulatory SC as male mating effort illustrates a means by which males can gain some post-copulatory control over their reproductive success. However, as has been the case in work on pre-copulatory sexual selection, trying to assign 'control' to one sex or the other can be problematic. Mating patterns that appear to reflect male manipulation of female reproduction may actually be subtly dictated by the female. For example, cryptic female paternity biases may be invoked, despite male attempts to control paternity, if a female's body condition determines whether or not SC occurs (e.g. see Andrade, 1998 under 'Post-copulatory mate choice' below). This cautionary note applies to findings of female control as well (e.g Elgar et al., 2000). The finding that females control paternity in *A. keyserlingi* may only apply under a relatively

restricted set of conditions, or alternatively may reflect the way in which data were analyzed. For example, Elgar et al., (2000) point out that female control of paternity in their study was restricted to mating trials in which SC occurred. Thus, events occurring prior to copulation that determine whether or not SC occurs in the first place could determine the importance of mechanisms that rely on the timing of SC.

Pre-copulatory male mating effort (sensory exploitation)

Hypotheses for SC have been, for the most part, restricted to situations in which females attack and successfully kill the male (Elgar, 1992). In contrast, a largely distinct literature has focused on how male courtship behavior might be shaped by the need to avoid SC (Platnick, 1971; Robinson & Robinson, 1980; Robinson, 1982). One unfortunate result of this historical dichotomy has been that male-oriented hypotheses for SC have been restricted to post-copulatory attacks (see above), as it was hard to see how males could benefit from pre-copulatory SC. However, for some species, the number of pre-copulatory attacks by females greatly exceeds the number of these attacks that are successful (Arnqvist & Henrikkson, 1997; Jackson & Pollard, 1997; Chapter 4). Males might benefit from **unsuccessful** pre-copulatory attacks if provoking such attacks is the most effective way of attracting a female's attention.

This line of thinking can be traced back to Clark & Uetz's (1992) finding that female jumping spiders (*Maevia inclemens*) mate preferentially with the male that moves first in simultaneous mate choice dyads. While SC is rare in this species (Jackson, 1980; Clark & Uetz, 1992), these authors suggested that, rather than preferring certain male morphological characters, females may simply mate with the male that first elicits her orientation response, which presumably evolved in the context of prey detection. In effect, these authors suggest a sensory exploitation mechanism for mate choice (Basolo, 1990; Ryan, 1990; Endler, 1992; McClintock & Uetz, 1996); females mate with males that exploit a pre-existing sensory bias that evolved in a non-mate discrimination context. Courtship in the water mite (*Neumania papillator*) takes this idea one step further. Males of this species vibrate their forelegs toward passing females at frequencies similar to that of typical prey items. Females, especially hungry females, then orient toward and clutch males as they would their typical copepod prey. Instead of harming males, this result benefits male mating success because females responding to these mimetic stimuli increase their rate of spermatophore acceptance (Proctor, 1991).

So males are not afraid to mimic prey stimuli in exchange for increased mating success when the risk of harm is minimal. However, to extend such a sensory exploitation hypothesis to account for unsuccessful pre-copulatory SC we must account for the very real risk males run of becoming prey items rather than mates. How could males use such a mate attraction strategy, while at the same time minimizing the risk of being killed by the female? Jackson & Pollard (1997) note that this sensory exploitation argument is in some ways similar to the aggressive mimicry practiced by jumping spiders of the genus *Portia*. One of *Portia's* predatory strategies is to invade the webs of a diverse array of hetero-specific spiders. By plucking and strumming the resident's web, *Portia* emits a series of web-borne vibrations that 'aggressively mimic' possible prey stimuli that the resident might encounter. However, the intruding *Portia* cannot be sure if the resident is of a size to be a potential prey item, or if instead it might be large enough to turn the tables and become the predator. To deal with this uncertainty, *Portia* is able to modulate the intensity of the resident's response to mimetic prey stimuli, effectively manipulating the rate at which the resident spider approaches by alternating between stimuli that lure the resident forward and stimuli that slow the resident's approach (Jackson & Wilcox, 1993).

This situation is not unlike the uncertainty that males face when they attempt to court a female that may be either a mate or a predator. Is it possible that some male spiders initially alert females to their presence with stimuli that the female perceives as potential prey, only later to switch to more traditional courtship techniques that presumably serve to reduce the chance of female attack? For such a strategy to be stable, costs would have to be low and benefits would have to be high relative to more traditional courtship strategies. The cost/benefit ratio of mimicking prey stimuli might be quite low for male spiders that are forced to reckon with hyper-aggressive females. If the chances of a pre-copulatory attack are very high regardless of a male's courtship strategy, perhaps even bordering on unavoidable, then using prey-like stimuli to attract the female's attention, and consequently provoking an attack early in courtship from the maximum possible distance, may be a more profitable strategy than traditional courtship if a female's predatory tendency cannot be tempered. Such an 'attack-provoking' strategy would yield the dual benefit of attracting the female's attention by exploiting her predatory tendencies, and dispensing with an initial pulse of female aggression in a relatively safe manner. Of course, this line of thinking is predicated on the notion that some female spiders are indiscriminate predators that attack courting males at astonishingly high frequencies disregarding the cost of

treating males as prey rather than as mates, an idea that is treated in some detail below (see 'Aggressive spillover'). Regardless, scenarios in which a risky, attack-provoking strategy might beat the strategy of traditional courtship are at least conceivable.

If males are mimicking prey stimuli as a courtship strategy, at least initially, shouldn't we see courtship behavior that appears to serve this purpose? Instead, on the surface at least, courtship seems to serve the traditional function of persuading the female not to attack. However, the incorporation of some prey-like stimuli into a broader courtship repertoire might not be immediately obvious (see below for an example). Only given careful monitoring and recording of prey and courtship stimuli could we hope to detect these subtle differences. Thus, two factors should guide us in our preliminary search for systems that might favor the evolution of such an extreme male strategy: (1) high frequencies of failed pre-copulatory attacks, and (2) some overlap between parameters of courtship and prey stimuli. Unfortunately, few studies have quantified either of these predictors. However, both criteria seem to be satisfied in fishing spiders (Pisauridae: *Dolomedes* spp.). Fishing spiders are voracious sit-and-wait predators on insects trapped on the water surface that emit stereotypical water-borne vibrations as they struggle (Carico, 1973; Bleckmann & Barth, 1984). Perhaps surprisingly, courtship is also primarily conducted via water-borne vibrations. Males court females by lightly tapping on the water surface with their forelegs (Arnqvist, 1992).

As for the first predictor, laboratory mating trials indicate that female European fishing spiders (*D. fimbriatus*) attack courting males in approximately 75 % of trials, and that males escape these pre-copulatory attacks 90-95 % of the time (Arnqvist, 1992; Arnqvist & Henrikkson, 1997). It should be noted that pre-copulatory attacks do not appear to be as common in the North American fishing spider *D. triton* (pre-copulatory attacks in 20% of trials, see Chapter 4). As for the second predictor, the sensory ecology of courtship and prey stimuli in *D. triton* is relatively well studied. To a large extent, these stimuli are distinctive; prey stimuli include higher frequencies (> 55 Hz), are irregular in cycle, and longer in duration (> 2 seconds), whereas courtship taps tend to contain lower frequencies (< 55 Hz), be more regular in cycle, and be shorter in duration (< 1 second) (Bleckmann & Bender, 1987). However, male fishing spiders often produce several courtship taps in rapid succession. Bleckmann & Bender (1987) argue that this increase in cycle irregularity may serve to make courtship distinct from abiotic stimulus sources, such as a falling leaf, that females will not pay attention to, while at the same time

maintaining the lower frequency and shorter duration that is characteristic of courtship and distinct from prey. A different interpretation of these occasional bouts of rapid courtship taps is that they serve to mingle prey-like stimuli (cycle irregularity) amongst courtship stimuli (low frequency and short duration) to cautiously exploit a female's sensory bias towards prey stimuli.

Future work needs to continue along these lines to better document the similarities and differences between courtship and prey stimuli in *Dolomedes* and other taxa that meet the criteria outlined above. This work should be aided by the development of protocols to record and play back such stimuli (e.g. for *Dolomedes* Bleckmann & Barth 1984). Specifically, playback of recorded courtship stimuli should be able to tell us exactly what stimulus components elicit female attacks. Support for the sensory exploitation hypothesis will come from playback experiments providing evidence that female attacks are elicited by parameters of courtship that resemble prey stimuli (e.g. irregular cycles). Further, our ability to record courtship during mating trials will allow us to address the prediction that males incorporating prey-like stimuli into their courtship will provoke more failed attacks and ultimately secure more matings than males that do not use prey-like stimuli to elicit failed attacks. Finally, the sensory exploitation hypothesis predicts that species exhibiting the highest frequencies of failed pre-copulatory attacks will also be the species with the most overlap between prey and courtship stimuli. For example, we need detailed measurements of courtship in *D. fimbriatus* to compare to *D. triton* in order to address the possibility that the higher frequency of pre-copulatory attacks in the former is due to the fact that male *D. fimbriatus* incorporate more prey-like stimuli into their courtship.

Summary

Despite male benefits of SC being somewhat counter-intuitive, work on post-copulatory SC has focused largely on this possibility. While the existence of post-copulatory male benefits might be expected to reduce sexual conflict over SC, this may not always be the case, especially if male benefits come into conflict with female interests (e.g. see 'Post-copulatory mate (gamete) choice' below). Note that because paternal investment enhances male fitness only to the extent that it enhances female fitness, it involves inherently less inter-sexual conflict relative to a strategy such as male mating effort. These two post-copulatory male benefits may often jointly explain SC within a species, with paternal investment being the dominant mechanism when material benefits are at a premium, and male mating effort being the dominant mechanism when

sperm competition and fertilization success are more important to a male's fitness than material provisioning. Pre-copulatory mating effort (sensory exploitation) is less likely to overlap with these other male benefits because it is founded on the premise of avoiding pre-copulatory attacks, rather than facilitating post-copulatory attacks. Instead, sensory exploitation is most likely to co-occur with other pre-copulatory mechanisms that feature indiscriminately aggressive females (see 'Mistaken identity' and 'Aggressive spillover' below). I will discuss the potential overlap between male benefits and other mechanisms of SC later in the review.

Adaptive hypotheses (female benefits)

Perhaps the most intuitive class of explanations for SC suggests that females benefit from these attacks. Below I review mechanisms driven by the female benefits of mate choice and adaptive adult foraging. Females can often benefit by attacking males at any point in the mating sequence; however, the costs of SC may be higher for pre-copulatory attacks if these attacks put females at risk of incomplete fertilization. Because mate choice and adult female foraging could explain pre and/or post-copulatory attacks, but the costs and benefits to females vary considerably across the mating sequence, I will outline each mechanism's pre and post-copulatory ramifications sequentially.

Pre-copulatory mate choice / refusal (indirect benefits)

One obvious result of SC before mating is that the pool of potential mates is reduced. Elgar & Nash (1988) suggested that pre-copulatory attacks could represent an extreme form of inter-sexual selection in that they may allow females to discriminate against a subset of males. Under such an adaptive model, SC occurs because the patterns of aggression that constitute SC result in indirect (good genes) benefits for the female and her resultant offspring. According to this idea, the benefits of a mating bias (i.e. mating with a high quality male) should exceed the potential costs inherent in attacking a male and thus passing up a mating opportunity (e.g. incomplete fertilization). Any beneficial, heritable feature of the male phenotype has the potential to be an indicator trait for sexual selection for indirect benefits.

Large male body size is one candidate for female choice in arachnids, as large males of many species have high foraging success and increased intra-sexual competitive abilities relative to smaller males (Vollrath, 1987). Perhaps SC is an evolutionary stable strategy because it

provides that females only mate with high quality males, which in many cases may be large males. In support of this idea, Elgar & Nash (1988) showed that small males of the orb-web spider *Araneus diadematus* were significantly more likely to be cannibalized by their mates than were large males. However, as they note, this effect was not produced by females preferentially attacking small males and mating with large males as would be the case if females were to display an 'active' mating preference for large males (see Wiley and Poston, 1996 for a discussion of the distinction between 'active' and 'passive' female choice). Instead, females attacked without regard for male body size, and large males were more successful at escaping these attacks, presumably due to increased strength, speed or agility associated with their large size. A similar large-male escape advantage has been shown in fishing spiders. In both the European (*D. fimbriatus*) and North American (*D. triton*) fishing spider, females fail to selectively attack with regard to male size (Arnqvist, 1992; Arnqvist & Henrikkson, 1997; see also Chapter 3). However, in both species male size is an excellent predictor of escape ability. In particular, in *D. triton,* what appears to be most important is for the male to be large relative to the attacking female (see Chapter 3). Thus, superior escape abilities can be added to the list of benefits of large male body size.

To a large extent, it remains to be seen if the large-male escape advantage demonstrated in these species translates into a large-male mating advantage. In *D. triton,* however, large males do mate significantly more often than small males. Interestingly, this effect stems from differences in male behavior rather than any 'active' mate preference females might express for large males. While females showed no size bias in terms of who they allowed to mount, large males transferred sperm in 11/13 mountings, whereas small males transferred sperm in 2/13 mountings (see Chapter 3). Thus, selection in this case appears to act on male size-dependent sperm transfer abilities, but does not seem to produce female mating biases for large males.

There is no reason, however, to believe that large male size is the only possible indirect benefit females could obtain from patterns of SC. For example, female orb-web spiders (*Nephila plumipes*) attack large males more often than small males (Elgar & Fahey, 1996). Indeed, small male body size in spiders is often attributed to the selective benefits obtained by males that are small enough to avoid detection and attack by females (Darwin, 1871; Robinson & Robinson, 1980). Thus, the patterns of aggression inherent in pre-copulatory SC may impose selection that

30

drives male body size in opposite directions depending upon the benefits of male body size across different species.

Studies of sexual selection are often confounded because it is difficult to separate out the influence of benefits to the different sexes. Studies of SC are not immune to this problem. The interpretation of good genes benefits to females outlined above presumes that SC is maintained because of the indirect benefits to females of obtaining high quality sires. However, it is difficult to rule out the possibility that selection on males is responsible for male-biased mating success in these species. Directional selection on male body size (in either direction) may exist because of benefits to the male, regardless of whether or not females receive indirect benefits from mating with these males. Alternatively, these male and female benefits may rarely exist in isolation from each other, and selection on both sexes may jointly explain the evolution of male body size and patterns of SC. The existence of strong inter-sexual conflict (i.e. benefits to one sex/costs to the other sex) may actually make the researcher's task of identifying functional explanations for SC relatively easy compared to cases where both sexes could benefit from mating patterns that result from SC.

Despite considerable research on female mate choice, and the indirect benefits of mate choice (e.g. good genes mechanisms as reviewed in Anderson, 1994), relatively little work has addressed sexually cannibalistic mating systems to ascertain whether pre-copulatory attacks represent a mating bias. Perhaps understandably, the majority of work on mate choice in sexually cannibalistic mating systems has focused on the material benefits females may accrue from preying on potential mates (see 'Adaptive foraging' below). For sexually cannibalistic females, the indirect benefits of mate choice may be dwarfed by the potential costs of mate refusal and failing to accept enough sperm to fertilize all of a female's eggs (Arnqvist & Henrikkson, 1997). However, there is no reason to prematurely dismiss the potential of mate choice for indirect benefits in these systems. In particular, studies that look for the layering of multiple mechanisms of SC may find that sexually cannibalistic females only express mating biases for indirect benefits in situations where material requirements (nutrition, sperm) have already been met. For example, females may only attack and refuse inferior males as mates when males are abundant, or alternatively, such preferences may be restricted to well-fed, multiply-mated females.

Post-copulatory mate (gamete) choice/refusal (indirect benefits)

Recent works in sexual selection have emphasized that female choice is only important in so far as it accurately reflects which male gametes are used to fertilize eggs (Eberhard, 1997, 1998). Regardless of female pre-copulatory behavior (mate or attack), multiply-mating sexually cannibalistic females retain the ability to bias paternity via their post-copulatory behavior. As pointed out in the previous section, however, studies of sexual selection have a difficult task in (1) determining which sex is in control of mating/fertilization biases, and (2) disentangling female benefits of female choice for certain male phenotypes from the benefits to males of having that phenotype. As for the first of these problems, Elgar et al. (2000) point out that post-copulatory SC as a means of cryptic female choice provides us with an obvious rejection behavior that is unambiguously controlled by the female. These authors showed that polyandrous female orb-web spiders *Argiope keyserlingi* (Araneidae) delay post-copulatory SC when mating with relatively small males, thus lengthening the duration of copulation with small males, and consequently biasing paternity in favor of small males (Elgar et al., 2000). Through patterns of post-copulatory SC dictated by the female, small males are allowed a fertilization advantage over large males. Further, in line with the theme of this review, additional, non-mutually exclusive hypotheses have been addressed and ruled out in this system; SC in *A. keyserlingi* is not explicable as a fecundity-promoting strategy by either sex, nor does it appear to benefit male fertilization success in a consistent fashion. This study clears both of the hurdles outlined above: the timing of post-copulatory SC in *A. keyserlingi* invokes a consistent, female-controlled paternity bias in favor of a certain male phenotype, but there is no covariance between this mechanism of female choice and the male trait being 'preferred'. This is the sort of approach that will be required as we begin to account for the complexity of SC.

Post-copulatory SC in redback spiders, initially thought to be driven by paternity advantages to consumed males (see Andrade, 1996 under 'Post-copulatory mating effort' above), may only apply when females are actually willing to consume males. Whether females consume complicit males is determined by female hunger level. Females in poor condition consume males during copulation, which in redback spiders effectively lengthens the duration of sperm transfer. In contrast, females in good condition do not cannibalize males and in effect shorten the duration of copulation (Andrade, 1996, 1998). Thus, at the very least, female hunger level invokes an indirect, cryptic paternity bias against males that are not consumed. No evidence

exists to suggest that females are also exhibiting 'active', post-copulatory preferences for males of certain phenotypes. For example, females do not preferentially consume mates based on male body size, nor do they preferentially consume males that are in good condition. Thus, redback females do not appear to bias paternity by preferentially consuming males that have genes for large body size or superior foraging abilities (Andrade, 1998).

The mating system of redback spiders and the elegant work that has been done recently to disentangle the functional significance of SC in this system provide a case study of the importance of sexual conflict in understanding the interactive and facultative nature of mating systems. Male redbacks benefit greatly from post-copulatory SC in terms of the extended copulation duration and increased paternity it affords. In addition, future mating opportunities for male redbacks are few. Presumably, the benefits of this suicidal strategy for males have led to its fixation in the population (i.e. males always do best by facilitating SC). However, females may or may not benefit by consuming males. Males offer little fecundity benefit to females, and as a result males are only consumed when females are in poor condition. Thus, the resolution of this inter-sexual conflict is highly dependent on ecological parameters influencing female condition. SC as male mating effort is generally an effective strategy when females are motivated to consume males, but is rendered less effective under conditions of high food availability. As pointed out by Andrade (1998), when SC occurs in redbacks, it represents a situation in which the interests of both sexes coincide. In the absence of SC, male mating effort is compromised, and females retain control over the paternity of their offspring. Presumably, male strategies that promote post-copulatory SC regardless of female interests would be favored if they were available to males.

Pre-copulatory adaptive foraging (direct benefits)

An alternative, but not mutually exclusive, adaptive hypothesis for pre-copulatory SC suggests that females may obtain considerable nutritional benefits by taking courting males as prey items. Regardless of whether male consumption is a novel form of mate choice, eating males rather than mating with them may be explained as an adaptive foraging strategy on the part of the adult female. The adaptive foraging hypothesis for pre-copulatory SC was suggested by the finding that females of the orb-web spider *Araneus diadematus* that consumed a single male added significantly to their body weight and presumably to their fecundity (Elgar & Nash, 1988).

Newman & Elgar (1991) later formalized the hypothesis with an economic model intended to determine whether potential costs to the virgin female associated with pre-copulatory SC (i.e. lost mating opportunities) could be outweighed by material benefits (i.e. enhanced fecundity) accrued through male consumption.

The adaptive foraging hypothesis suggests that females economically weigh a courting male's marginal value as a mate versus his value as a food item, and respond accordingly with the adaptive behavior (attack or mate) that maximizes female fitness. The model thus suggests that the two most important factors in determining the prevalence of SC are the degree to which other, non-male food sources are available to females (i.e. the intensity of food limitation), and the number of males a female can expect to encounter throughout the breeding season (i.e. the intensity of sperm limitation). Specifically, the model predicts that the likelihood of sexually cannibalistic attacks should (1) increase with decreasing food availability, (2) increase as unpredictability in food availability increases, (3) increase for non-virgin females relative to virgins, (4) increase as male size increases (large males presumably representing a greater nutritional reward than small males), and (5) decrease for virgin females as the breeding season progresses and male availability declines (Newman & Elgar, 1991).

Few studies have presented a comprehensive test of the assumptions and predictions made by the adaptive foraging hypothesis, and most relevant data come from studies examining only one or two of the model's predictions. However, two recent studies explicitly tested the model's assumptions and predictions using the European and North American fishing spiders, *Dolomedes fimbriatus* and *D. triton* (Arnqvist & Henrikkson, 1997; see also Chapter 4). Below I review the results of these studies, as well as other evidence pertaining to the adaptive foraging hypothesis for pre-copulatory SC.

Assumptions

If SC is to be explained as an adaptive trade-off between sperm (fertilization) and food (fecundity) by the adult female, then it must be shown that, by mating with a male, females can increase their fertilization rate, and that, by foraging on a male, females can increase their fecundity. Consistent with the first assumption, Arnqvist & Henrikkson (1997) present a data set suggesting that female fertilization rate for *D. fimbriatus* is a function of the number of palpal insertions a female receives (0, 1, or 2). Females in this laboratory experiment showed a

bimodal distribution of fertilization rates with one palpal insertion yielding approximately 33% fertilization and two insertions yielding 97% fertilization. It should be noted, however, that this trend was drawn from only six females with one insertion and a single female that received two insertions. While this is an extremely small sample to base any conclusions on, this trend was corroborated by a similar bi-modal distribution of fertilization rates for egg sacs collected from the field. Thus, Arnqvist & Henrikkson concluded that, as per the adaptive foraging hypothesis, virgin females and females with a single insertion will reap considerable fertilization benefits by choosing to mate with, rather than attack, a courting male.

Other works cast doubt on this conclusion. While the fertilization benefits of one mating over remaining unmated are not in dispute, whether females increase their fertilization rate by mating more than once is not clear (but see Fahey & Elgar, 1997 for a rare case in which copulation frequency is correlated with fertility). Fishing spider females (*D. triton*) that accept more than one insertion do not produce more spiderlings than females accepting a single insertion, suggesting that fertilization rate is not affected by multiple mating (see Chapter 4). However, this study used spiderling number as a measure of fecundity rather than number of fertilized eggs. Because unfertilized eggs might have been consumed by the female before emergent spiderlings were counted, egg fertilization was not measured.

More generally, selection may be intense on males to transfer enough sperm in one mating to fertilize all of a female's available eggs (Smith, 1984; Parker, 1998). This may be particularly true for sexually cannibalistic arthropods in which each additional courtship bout or mating can significantly heighten predation risk on males by females. A number of studies on sexually cannibalistic species have indicated that sperm stored from one mating provide females with enough sperm to fertilize eggs for multiple reproductive bouts (Jackson, 1980; Birkhead et al., 1988; Chapter 4; Andrade pers. comm). Additional work is needed to determine whether the adaptive foraging hypothesis' assumption that more matings equals greater fertilization rates is generally valid. To the extent that females do not need to mate more to secure sufficient quantities of sperm, the fertilization benefits of using males as mates are reduced, the costs of taking males as prey items are reduced, and females will benefit most by using subsequent males as a food source. Thus, as originally intended, Newman & Elgar's model is most useful for virgin female mating decisions. Beyond that, species-specific issues such as sperm storage duration, number of sperm transferred in a single palpal insertion, and the number of eggs

produced in a female's lifespan will determine whether females can obtain fertilization benefits from additional matings.

Also assumed by the adaptive foraging hypothesis is a strong positive relationship between female fecundity and adult feeding. To argue that adult females attack courting males in order to secure material fecundity benefits, one must first establish that differences in adult feeding can, in fact, translate into fecundity differences. Indeed, female feeding, size and fecundity are generally thought to be tightly linked in arachnids (Vollrath, 1987). Nonetheless, Arnqvist & Henrikkson (1997) found no evidence of a relationship between adult feeding and fecundity in *D. fimbriatus*, as adult food regimes did not explain differences in the number or size of eggs produced by females (see also Spence et al., 1996; Maxwell, 1999). Arnqvist & Henrikkson (1997) make the case that while foraging success is critical to female size and fecundity in arachnids, the majority of the available evidence suggests that feeding as a juvenile, rather than as an adult, is what best predicts fecundity. They review the evidence that female fecundity is most closely linked to fixed female size (i.e. cephalothorax area, leg length); measures that are set for life at adult emergence in most arachnids, and thus can only be enhanced via juvenile foraging success. By making this distinction between the fecundity effects of juvenile and adult feeding, Arnqvist & Henrikkson argue that a major underlying assumption of the adaptive foraging hypothesis is violated in many species. Therefore, to the extent that female fecundity is not limited by **adult** food availability, adaptive adult foraging is less likely to explain the occurrence of pre-copulatory SC.

However, the fecundity benefits of juvenile and adult feeding are difficult to separate (Beck & Connor, 1992). Arnqvist & Henrikkson (1997) suggest that fixed size is a preferable measure of female size because it reflects only juvenile foraging, whereas other measures of size (egg mass, female mass, offspring number) typically reflect both juvenile and adult foraging success. Thus, implicit in the reasoning they use for fixed size as a predictor of fecundity is the admission that both modes of feeding can contribute to fecundity. Other studies on fishing spiders suggest that females can enhance their fecundity via both juvenile and adult feeding, or through the interaction between foraging success at these different stages (Spence et al., 1996; see also Chapter 4). Despite a clear relationship between juvenile food availability, fixed size and fecundity in North American fishing spiders (Chapters 4 and 6), it seems quite possible that adult feeding and the resultant development of egg mass could provide fecundity benefits to

adult females. Indeed, Kreiter & Wise (2001) recently demonstrated that female fecundity is limited by adult food availability in at least one field population of *D. triton*. Nonetheless, it remains difficult to explain why other studies often fail to find a positive relationship between adult foraging and female reproductive success. For example, in Chapter 5 I show no effect of adult foraging success on *D. triton* female egg sac mass, offspring number or egg size. Interestingly, adult foraging in this species does increase the likelihood a female will hatch an egg sac successfully.

Even if adult food level produces significant fecundity benefits, males of many spider species may not represent a sufficient addition to the adult female's diet to be considered a possible fecundity benefit. Evidence that adult females obtain fecundity benefits by consuming males comes from only a few studies (Matsura & Morooka, 1983; Birkhead et al., 1988; Elgar & Nash, 1988; see also Chapter 5). It is interesting to note that two of these studies were done on mantid species. Male mantids generally represent a more substantial prey item to females than male spiders offer their females. Experiments involving spiders generally find no evidence that females gain mass, egg mass, or increases in the number of offspring produced following male consumption (Andrade, 1996; Spence et al., 1996; Arnqvist & Henrikkson, 1997; Fahey & Elgar, 1997; Elgar et al., 2000; Chapter 4; but see Elgar & Nash, 1988; Chapter 5). In sum, the importance of multiple mating to female fertilization success and the effects of adult feeding and male consumption on fecundity must be clarified before adaptive foraging can be considered a plausible explanation for pre-copulatory SC.

Predictions

As noted earlier, the adaptive foraging hypothesis predicts that female attacks should be more likely under the following conditions: (1) low food availability, (2) large male size, (3) non-virgin female mating stautus and (4) high male availability (i.e. early in breeding season). Arnqvist & Henrikkson (1997) found no support for any of these predictions in laboratory-staged mating trials. First, adult food availability (mean and variance) did not predict whether females exhibited pre-copulatory attacks (see also Chapters 4 and 6). In contrast, female feeding history, and hence motivation to feed, predicts the likelihood of pre-copulatory attacks in several other taxa (Liske & Davis, 1987; Birkhead et al., 1988; Hurd et al., 1994; Kynaston et al., 1994 for

mantids, but see Maxwell, 1999 for an alternative explanation; Peretti et al., 1999 for a scorpion; Dick, 1995 for a sex role-reversed amphipod).

Surprisingly absent from this list of organisms featuring an association between female hunger and pre-mating attacks are sexually cannibalistic spiders. Many reports on spiders indicate that female feeding history has no effect on pre-mating attack tendencies (Jackson, 1980; Breene & Sweet, 1985; Elgar & Nash, 1988; Arnqvist & Henrikkson, 1997; see also Chapters 4,5,6). One explanation for this is that strong selection on males to avoid SC during courtship (reviewed in Platnick, 1971; Robinson & Robinson, 1980) may have resulted in a reduction in pre-copulatory SC among spiders such that male courtship ability reduces the prevalence of SC in spite of female hunger. That is, selection for small male body size (Robinson & Robinson, 1980; Vollrath, 1980; Newman & Elgar, 1991; Elgar & Fahey, 1996), less vulnerable locations for mating (Elgar, 1991), and alternative male mating tactics (Robinson & Robinson, 1980; Austad & Thornhill, 1986; Prenter et al., 1994) may make female hunger a poor predictor of SC. Alternatively, the failure of hunger to predict attack likelihood may imply violation of the assumption that adult feeding and/or male consumption can benefit female fecundity (see above).

One recent study provides an exception to the above trend (Herberstein et al., 2002). Feeding history for mated female orb-web spiders (*Argiope keyserlingi*) does determine pre-copulatory attack likelihood. However, among virgin females of this species, pre-copulatory attack likelihood is not predicted by feeding history. Thus, pre-copulatory SC in this species illustrates an interaction between ecological context (food availability) and behavioral context (female mating status), the whole of which conforms to the adaptive foraging hypothesis; previous foraging success influences pre-copulatory SC, but only after females have met sperm requirements.

The adaptive foraging hypothesis also predicts that large males will be attacked more often than small males, as large males presumably provide a larger nutritional reward to females. As noted above, however, male size is generally a poor predictor of the likelihood of pre-copulatory attacks (Elgar & Nash, 1988; Arnqvist & Henrikkson, 1997; Andrade, 1998; see also Chapters 3 and 4). Nonetheless, consistent with this prediction, female Australian golden orb-weavers (*Nephila plumipes*) tend to attack large males more often than small males (Elgar & Fahey, 1996). However, these authors suggest that this bias is a mechanical one, in that females

fail to attack small males not because they offer insufficient nutritional rewards, but instead because these males are too small to be detected by females. No convincing evidence exists to support the foraging hypothesis' prediction that large males are eaten by females more often because they represent a larger foraging payoff for females.

Sperm availability should also affect the tendency for females to attack or mate with males. As sperm become more limiting, females should tend to use males as mates rather than as food items. Accordingly, the adaptive foraging model predicts that female mating status should influence the likelihood of pre-copulatory attacks; non-virgins should attack males more often than virgins. As noted above, mated female orb-web spiders (*Argiope keyserlingi*) exhibit more pre-copulatory attacks than virgin females (Herberstein et al., 2002). Also, for a Canadian population of the North American fishing spider (*D. triton*), pre-copulatory attacks were most prevalent by mated females (Zimmerman & Spence, 1989, 1992), a trend which was replicated in a laboratory experiment for the same species (see Chapter4). However, Arnqvist & Henrikkson (1997) did not find such an effect of mating status in *D. fimbriatus*.

However, tests such as these are confounded by differences in mating motivation between virgins and non-virgins. These comparisons fail to test the crucial prediction that among virgin females, pre-SC should be more frequent when females 'perceive' males as abundant, and less frequent when males are 'perceived' as limiting. In Chapter 5 I present what is, to my knowledge, the first attempt to experimentally manipulate female 'expectation' of male availability. By varying the cohabitation experience of juvenile females with mature males I show that juvenile female exposure to males siginificantly increases their propensity as adults to treat males as prey items rather than mates.

Finally, the adaptive foraging hypothesis predicts that as the breeding season progresses and male availability and/or opportunities to mate decline, virgin females should increasingly treat males as mates rather than as food items. Very few studies offer season-wide data on the likelihood of female attack, thus making it difficult to assess the viability of this prediction. Neither Arnqvist & Henrikkson (1997), nor Johnson (2001) found any effect of calendar date on the likelihood of female attack in fishing spiders. In natural populations many female spiders may have enough potential mates early in the breeding season to avoid the risk of progressing late into the breeding season as virgins. Indeed, selection may favor females that obtain

sufficient sperm and food reserves as quickly as possible to maximize their reproductive success (Vollrath, 1987).

In sum, the adaptive foraging hypothesis has received mixed support as an explanation for pre-copulatory sexually cannibalistic attacks. Needed are studies that carefully manipulate food and sperm limitation across the adult life cycle, and record female fertilization success, fecundity and the prevalence of pre-copulatory attacks. Even more useful would be studies that can accurately reflect natural levels of food and sperm limitation where they are known, conducted in settings realistic enough to ensure that mating behavior, and in particular male escape behavior, are accurately represented. While these are non-trivial tasks, they are necessary to understand the implications of SC as an adaptive foraging strategy.

SC as an adaptive foraging strategy by the female is somewhat similar to the paternal investment hypothesis reviewed earlier; the distinction being that paternal investment suggests a male benefit to providing females with a material benefit, whereas adaptive foraging only requires that the female derive a material benefit from SC. As such, the experimental refinements suggested for work on the paternal investment hypothesis also apply to the adaptive foraging hypothesis. Most importantly, future studies need to examine the possibility that females adaptively forage on courting males, not to obtain more food, but instead to obtain qualitatively important food. For example, experiments should investigate the effects of diet abundance and diet breadth on female fecundity and the likelihood of SC. In addition, future studies need to expand the analysis of female fecundity and fitness to include often overlooked measures, such as egg sac hatching success, to more fully address the possibility that pre-copulatory SC is adaptive female foraging.

Post-copulatory adaptive foraging (direct benefits)

The impetus for the adaptive foraging model was to try to determine why virgin females sometimes attack courting males, thereby foregoing a mating opportunity and running the risk of failing to get mated. However, as noted above, there is no clear consensus on the number of matings required by females to procure enough sperm to fertilize all of their eggs. If it is generally true that one insertion does not provide females with enough sperm to maximize fertilization success, then the adaptive foraging model can also be applied to post-copulatory attacks following a male's first insertion (action a_2 in Newman & Elgar, 1991). While receiving

40

a male's first insertion, the female must weigh a copulating male's value as a prey item versus the value of accepting a second palpal insertion from him.

While such post-copulatory adaptive foraging attacks were not the primary focus of the Newman & Elgar model, post-copulatory adaptive foraging may be more common than pre-copulatory adaptive foraging, as costs to females are reduced in post-copulatory attacks. First, as noted above, post-copulatory attacks by their very nature follow sperm transfer and thus do not involve as great a risk of incomplete fertilization as do virgin, pre-copulatory attacks. Second, the nature of post-copulatory attacks may make them more successful than pre-copulatory attacks. Copulating males are put in a very dangerous position following sperm transfer, and females often use this moment to take advantage of the close quarters required by copulation to turn, clutch, and kill males just following mating (Robinson, 1982; Elgar, 1992). Thus, post-mating attacks allow females the best of all scenarios: sperm are obtained, capture of the evading male is facilitated, and a prey item is consumed.

In support of a foraging explanation for post-copulatory SC, Andrade (1998) showed that female redback spiders in relatively poor condition (measured as mass / body size) are significantly more likely to consume their mates during sperm transfer than are females in good condition. Thus, the adaptive foraging hypothesis' prediction that hungry females cannibalize their mates more often than well-fed spiders appears to be supported in redback spiders, despite the fact that consumption of a male is not associated with fecundity benefits in this species.

Similarly, post-copulatory SC has been suggested to be a foraging strategy for virgin females of the golden orb-web spider *Nephila plumipes* (Schneider & Elgar, 2001). Relatively small virgin females that mature in poor condition are significantly more likely to cannibalize their mates after mating than virgin females that are in good condition. In addition, virgin females tend to capture large males more often than small males, suggesting that sexually-cannibalistic virgin females are maximizing their foraging efficiency. Interestingly, neither of these findings held for mated females of this species. For females having mated previously, poor female condition and large male size did not increase the probability of post-copulatory SC. The behavioral context of female mating status appears to play an important role that determines the patterns of SC for *N. plumipes*. While these results are consistent to an extent with an adaptive foraging explanation for SC, the hypothesis is not fully supported. First, and most importantly, there is no evidence in this species that adult female feeding and consumption of a male provide

material fecundity benefits to the female. Also, it is curious that mated female *N. plumipes* do not cannibalize males according to their foraging requirements, especially given the relaxation of sperm limitation that mating with two different males should produce. Some of these inconsistencies may be resolved when we consider the dynamic interaction between male and female interests (see 'Summary' below).

Summary

The female benefits of SC outlined in this section are in no way mutually exclusive of each other. In particular, indirect benefits of SC may co-exist with material benefits of SC, and the ecological and behavioral contexts suggested in this review to be so important should influence the relative magnitude of these benefits. Most obviously, SC may be an important foraging strategy when food is limiting. When food limitation is relaxed SC may be explained via good genes benefits. Also, female benefits are not necessarily mutually exclusive with male benefits. As noted above, post-copulatory foraging benefits to females are necessarily expected to arise from the male benefits of a paternal investment strategy. However, the converse need not be true; females can obtain foraging benefits from males regardless of whether males benefit from being killed following mating, and this may be a very common source of sexual conflict.

Behavioral and ecological context should influence the resolution of inter-sexual conflict over SC. For example, in the golden orb-web spider (*N. plumipes*), female mating status has a significant impact on male benefits of SC. Males that are killed following a mating with a virgin female (1) lose future mating opportunities, and (2) will likely have their sperm supplanted given the high probability that the female will mate again. In contrast, males mating with previously mated females are less likely to compete with the sperm of future males. Males mating with mated females actually double their fertilization success from 30 % of a female's clutch if they survive mating, to 60% if they do not survive mating. Thus, depending on the intensity of sperm competition and a male's future mating prospects, SC following a mating with a mated female may be a male's best strategy. In this species, SC by virgin females entails high levels of inter-sexual conflict, and appears most likely to be explained as a foraging strategy by the female. However, the shift of behavioral context to mated females produces a situation where SC may be best explained as post-copulatory male mating effort for paternity assurance.   This male benefit would seem to include a reduction in sexual conflict, however, it is unclear what benefits a

female (especially a well-fed female) obtains by eating the male. Thus, to the extent that males get a paternity benefit and females lose control over the paternity of their clutch, SC by mated females may be a better evolutionary strategy for the male than it is for the female.

Nor is it impossible for male and female interests to coincide in terms of indirect benefits. For example, large male body size may be jointly favored because it aids male escape success, and thus females mating with large males produce larger, fitter offspring. In contrast, a sensory exploitation benefit of pre-copulatory attacks to males cannot co-exist with female foraging benefits because the former assumes SC is unsuccessful, whereas the latter assumes females succeed in foraging on the male. However, sensory exploitation and indirect benefits for females could co-occur if patterns of SC provide that females only mate with males capable of exploiting female predatory tendencies and avoiding pre-copulatory attacks. The number of combinations possible is only limited by the amount of relevant environmental variation available and the extent to which resolutions of sexual conflict are affected by that variation.

‘Non-adaptive’ hypotheses

While most work on SC has emphasized the adaptive significance of the behavior, others have stressed that no adaptive mechanism need be invoked if the phenomenon is an anomalous, rare event. Despite the growing evidence in several taxa that SC is common enough to be viewed as more than an anomalous ‘mistake’ (e.g. Arnqvist, 1992; Sasaki & Iwahashi, 1995; Elgar & Fahey, 1996; Jackson & Pollard, 1997; Elgar et al. 2000; Knoflach & Van Harten, 2000), several non-adaptive hypotheses remain in the literature. Of particular interest is the recent ‘aggressive spillover’ hypothesis, which maintains that SC may be non-adaptive in the context of mating, instead being part of an adaptive syndrome of aggressive behaviors expressed in a multitude of contexts.

Male senility

Bristowe (1958) and Jones (1983) have suggested that SC could be the result of decreased agility and diminished courtship abilities in older males. The hypothesis of male senility predicts that older males should be at a significantly higher risk of SC than younger males. Accordingly, the hypothesis is consistent with findings that the probability of attack and kill are positively correlated with increasing male age, whereas successful matings should be

biased in favor of younger males. The few studies looking for a relationship between male age and SC have failed to find such a bias towards older males (Elgar & Nash, 1988; Andrade, 1996). For example, in an orb-weaving spider, *Araneaus diadematus*, increasing male age did not significantly increase female attack rate (# lunges / courtship time), nor did older males suffer lower mating success compared to younger males (Elgar & Nash, 1988).

It should be noted that demonstrating a positive relationship between male age and SC, or heightened mating success for young males, would not be sufficient evidence of male senility as a non-adaptive mechanism. Females may actually benefit by preferentially attacking and killing older males thereby biasing matings in favor of younger males, if young males are in some way superior mates (e.g. young males may be more likely to transfer a full complement of viable sperm). Rather than being a result of non-adaptive male senility, such a finding would be consistent with the adaptive foraging trade-off between a mate's value as a food item versus his value as a competent sperm donor. As is the case with most non–adaptive explanations, male senility is a difficult idea to test, and researchers may have to be content to show the presence or absence of functional benefits that may be more likely explanations of SC.   Thus, a rigorous demonstration of non-adaptive SC via male senility must show that attacks are the product of inferior courtship or compromised escape behavior by older males, and that females do not benefit in any discernible way by preying on these males. No such demonstration exists to date, and currently the hypothesis is apparently receiving little attention.

Mistaken identity

Alternatively, rare cases of SC could be construed as the female making a mistake. Gould (1984) suggested that the most likely explanation for SC is that it is simply a by-product of aggressive, predatory females attacking males as prey items before 'realizing' their potential value as mates. SC under such a scenario is then a function of females mistaking the identity of potential mates. While mistaken-identity has never been tested explicitly, several lines of evidence suggest problems with the hypothesis.

First, as noted above, the high frequency of SC in some species suggests that some functional benefit is responsible for its occurrence. In particular, pre-copulatory attacks carry an inherent risk to virgin females if they increase the probability that a female will fail to accept enough sperm to fertilize all of her available eggs (Elgar & Nash, 1988; Newman & Elgar,

1991). Thus, as the frequency of SC and the costs associated with SC increase, non-adaptive explanations have an increasingly difficult time explaining the maintenance of the phenomenon. Second, in many species, courtship appears to allow cautious males to alert the female to the presence of a mate rather than a prey item. Indeed, male courtship in arachnids has traditionally been assumed to counter female predatory tendencies (Platnick, 1971; Robinson, 1982). Thus, if SC is to be explained as mistaken identity, these mistakes are occurring despite presumably strong selection on males to avoid being mistaken as prey items.

Finally, in many species, sexually cannibalistic attacks do not resemble female attacks on non-male prey (Elgar & Nash, 1988; Elgar, 1991; Andrade, 1996, 1998; Jackson & Pollard, 1997). Females that only attack males under specified courtship and/or mating circumstances (e.g. Elgar & Nash, 1988; Elgar, 1991; Andrade, 1996, 1998) can hardly be seen as mistaking the identity of their mates. Secondly, in some spiders, the actual lunging motion toward courting males indicates that the female is not mistaken about the identity of her prey. When female jumping spiders (*Portia spp.*) attack potential mates, they do so with a twisting and lunging motion specific to conspecific males that approach them, and distinct from the attack used to capture other prey items (Jackson & Hallas, 1986; Jackson & Pollard, 1997).

Mistaken identity may be a much more plausible mechanism generating SC for species in which prey stimuli and courtship stimuli greatly resemble each other. For example, the sensory ecology of foraging and courtship in female fishing spiders (discussed in detail under 'Pre-copulatory mating effort' above) may make this group an excellent candidate for a sexual cannibal mistaking the identity of her mate. However, SC in fishing spiders violates one assumption of the non-adaptive, mistaken-identity hypothesis; it occurs quite frequently. In fact, Arnqvist & Henrikkson (1997) present a laboratory study in which females were so aggressive towards males that, despite multiple mating opportunities, they remained unmated throughout the entire experiment. This incomplete fertilization does not appear to be a result of laboratory artificiality, as they also present data suggesting that egg sacs in the field are sometimes incompletely fertilized. Thus, mistaking the identity of a male appears to carry enormous fitness consequences for both males and females. Presumably, pre-copulatory sexually cannibalistic attacks at such high frequencies and with such high potential costs could also be explained by some benefit to males (see 'Pre-copulatory mating effort' above) or females (see 'Aggressive spillover' below).

In sum, little evidence supports the contention that SC is strictly a non-adaptive by-product of inferior courtship by the male and/or mistaken identity by the predatory female. SC often occurs at high frequencies, and for some species is characterized by circumstances and predatory tactics distinct from those directed towards non-male prey. In addition, selection on males in many species has resulted in courtship behavior that appears to function largely as a way for males to identify themselves as mates and not prey items.

Pre-copulatory aggressive spillover

A recent hypothesis for SC reframes the mechanism of mistaken identity into a broader adaptive context. In rejecting the adaptive foraging hypothesis for the European fishing spider (see above), Arnqvist & Henrikkson (1997) proposed a novel alternative explanation positing that SC is not adaptive in the context of mating alone, but could be part of an adaptive syndrome of aggressive behaviors that are expressed in a multitude of contexts.

Arnqvist & Henrikkson (1997) found no fecundity benefits from adult female feeding, including SC, in *D. fimbriatus*. Instead, they found a close relationship between fixed adult size and fecundity. As a result, they present the argument that fecundity is more often linked to juvenile foraging success than adult foraging success. Only juvenile foraging success can affect measures such as cephalothorax area that are fixed at the adult molt. In addition, they documented a cost of pre-copulatory SC in the form of incomplete fertilization of egg sacs. They suggest that this cost is the direct result of overzealous, pre-copulatory aggressive behavior towards courting males. According to the aggressive spillover hypothesis, SC is maintained because the fecundity benefits of juvenile voracity outweigh the potential fertility costs of voracious behavior toward courting males. Thus, the spillover hypothesis suggests that the indiscriminate predatory 'mistakes' made by females under the mistaken identity hypothesis are an expression in the mating context of a general tendency towards voraciousness. Voracity is suggested to be a syndrome of correlated behaviors inherited jointly, and thus genetically constrained such that they are not optimally modulated across each individual context, but are instead maintained in multiple contexts due to the strong selective advantages of voracity in the juvenile foraging context.

The aggressive spillover hypothesis is based on the following four assumptions (Arnqvist & Henrikkson, 1997; see also links 1-4 in Figure 2.1). First, food acquisition and consumption

are positively correlated with voracity. In other words, voracious juveniles obtain more prey items than less voracious juveniles. Second, juvenile food acquisition and consumption are positively correlated with fixed adult size. In other words, more juvenile food leads to larger fixed adult sizes. Third, fixed adult size is positively correlated with fecundity. Combined, these first three asumptions maintain a direct, positive relationship between juvenile voracity, juvenile foraging success, fixed adult size, and female fecundity. Finally, the spillover hypothesis assumes that the expression of voracity is constrained across an individual's life-history such that it cannot be switched on and off according to its adaptive value in any particular context.

Arnqvist & Henrikkson (1997) provide a detailed review of the existing support for these assumptions. Because it is a relatively new hypothesis, the feasibility of aggressive spillover as an explanation for pre-copulatory attacks has only begun to be tested. Most notably, recent work on the North American fishing spider, *Dolomedes triton,* provides intriguing support for the hypothesis (see Chapters 4 and 6). In this spider, assumptions 1-4 are supported: juvenile voracity (defined as latency to attack), juvenile foraging success, fixed adult size, fecundity and pre-SC all show significant, intra-individual, positive correlations (see Chapter 6 and Figure 1.2). In addition, adult voracity and adult foraging success are also tied up in this syndrome suggesting (1) additional benefits to a voracity syndrome, and (2) that adaptive adult foraging and a voracious syndrome may be difficult to distinguish from each other.

Hypotheses such as aggressive spillover, which propose that behavioral correlations have the potential to shape patterns of animal behavior, are receiving renewed interest in behavioral ecology (Sih et al., 2003). Aggression has been one of the few behaviors addressed in the behavioral literature as a multi-context syndrome. For example, in taxa as diverse as fish and spiders, bold and aggressive behavior that is selectively advantageous in the context of inter-male competition is positively correlated with apparently disadvantageous boldness in the context of predator avoidance (Huntingford, 1976; Riechert & Hedrick, 1993; see also Chapter 6 and Figure 6.4). Bakker (1994) has shown that the behavioral syndromes making up these positive correlations are heritable, and that they are maintained across life-history switch points (i.e. juvenile aggression correlates positively with adult aggression). The aggressive spillover hypothesis merely extends this syndrome of aggression to include female reactions to males in the context of mating.

Future support for the spillover hypothesis could come in a variety of forms. First, we need more studies examining the relationship between voracity and fecundity. Spillover is only feasible to the extent that female fecundity benefits from juvenile voracity outweigh costs of voracity from the mating context. While Arnqvist & Henrikkson (1997) originally framed their hypothesis as a spillover of juvenile voracity into the mating context, a broader interpretation of the hypothesis is that fecundity benefits derived from the entire voracious syndrome (juvenile and adult voracity) combine to outweigh the costs of SC (SC defined here as voracity expressed in the mating context). As such, rather than being mutually exclusive with aggressive spillover, adaptive foraging benefits are part of the voracious syndrome responsible for spillover. Thus, findings of adult food limitation and material fecundity benefits of male consumption by females do not preclude a role for aggressive spillover.

Second, the aggressive spillover idea can explain high costs of overzealous SC in terms of incomplete fertilization of a female's eggs. Following Arnqvist & Henrikkson (1997), field assays of egg sac fertility are needed to determine if females actually pay a fertility cost of SC. In addition, documentation of other costly results of a voracious syndrome would indirectly support the hypothesis. For example, voracious individuals may be overly bold by failing to respond to predation risk appropriately, or they may attack inappropriately large prey items resulting in injury or death. In line with these predictions, the most voracious and fecund female *D. triton* are also the females with the weakest anti-predator response (see Chapter 6).

Finally, if hetero-specific foraging voracity is shown to be advantageous, and is positively correlated with pre-copulatory attack prevalence (see Chapter 6), then quantitative genetic work will be needed to establish the heritability of such a voracity syndrome. Offspring voracity should be positively correlated with parental voracity. The inheritance and expression of this aggressive syndrome should be tested in offspring of both sexes. Arnqvist & Henrikkson (1997) note that while the core of their hypothesis rests on the benefits of a voracious syndrome to juvenile females, the evolution of voracity may be enhanced if selection also favors juvenile male aggressiveness. If voracious juvenile males also have higher foraging success and grow to larger adult sizes, they should benefit in terms of inter-male competition and ability to escape female attacks. Further, they note that aggression is largely determined as a sex-linked trait in at least one arachnid (Riechert & Maynard Smith, 1989), and males are generally the heterogametic sex in spiders (Wise, 1983). Thus selection for an aggressive male phenotype expressed via the

male's one X chromosome may translate into "double doses of gene products regulating aggression" in females. Under such a scenario, SC by females can be seen as the product of a spillover of voracity from previous life-history stages (juvenile female feeding), as well as being the product of a spillover of voracity from the opposite sex. Ironically, genetic constraints may have trapped males in a situation where they suffer SC because of the selective benefits they receive from the very same syndrome of voracity that is responsible for SC.

Because the aggressive spillover hypothesis is grounded in the assumption that female indiscriminate predatory behavior is, on the whole, selectively advantageous, it should be more likely to be important in the same subset of systems for which mistaken identity is most plausible. For example, spillover may only be a viable mechanism underlying SC in cases where vibrations produced by males can readily be mistaken for non-male, prey stimuli. In many spider taxa, sexual size dimorphism is so pronounced (Elgar 1991,1992), that males may be too small to be detected as potential prey items (e.g. Elgar & Fahey 1996). In contrast, other spider groups do not exhibit such extreme sexual size dimorphism and males may be sufficiently large to elicit a predatory response. Thus, perhaps the moderation of sexual size dimorphism seen in some spiders makes them more likely candidates for mistaken identity and aggressive spillover.

Spillover might also be most likely for systems in which potential benefits of a voracious syndrome are great. For example, one parameter predictive of spillover is a strong, positive relationship between juvenile voracity and fecundity. This fact may make spillover more likely in taxa that rely most heavily on a voracious predatory response. For example, voracity may be particularly important to the foraging success and fecundity of cursorial spiders that are ambush predators, and thus do not rely on prey-ensnaring webs to initiate prey capture.

Post-copulatory aggressive spillover

The few works that have discussed the aggressive spillover hypothesis (Arnqvist & Henrikkson, 1997; Johns & Maxwell, 1997; Andrade, 1998; see Chapters 4 & 6) have all focused on pre-copulatory SC. Because the hypothesis is founded on the benefits of indiscriminate predatory behavior it would seem most plausible as a mechanism operating in concert with the onset of courtship stimuli. In addition, the reduced costs of post-copulatory attacks make a non-adaptive explanation less parsimonious than the more traditional adaptive explanations reviewed above. Thus, evidence that post-copulatory attacks are stimulated by generalized voracious

motivation, and that females suffer costs of post-copulatory SC will be necessary before aggressive spillover can be applied to post-copulatory SC.

Summary

Because traditional non-adaptive explanations posit no benefit to SC, they will rarely overlap with adaptive explanations. If SC can be shown to be the product of male senility or mistaken identity within a species, then it is unlikely to also be explained through any of the adaptive functions reviewed earlier. However, aggressive spillover is not truly a non-adaptive hypothesis. Because this idea holds that SC is adaptive in the broader context outside of mating, it is quite possible that benefits of aggressive spillover could combine with more traditional benefits to explain SC in spite of the presumed costs of aggressive spillover. For example, aggressive spillover may coincide with a male sensory exploitation benefit because both of these hypotheses are founded on the premise that a female's predatory nature overwhelms her ability to discriminate mates from prey. Indeed, male exploitation of such a pre-existing voracity bias illustrates one way in which selection on males can favor counter-adaptations to SC that promote male interests. Note that sensory exploitation by males and aggressive spillover by females may be an extremely stable combination because the male strategy reduces inter-sexual conflict. A sensory exploitation strategy not only benefits males, but to the extent that males are able to provoke attacks and avoid SC, it also favors overzealously aggressive females that might otherwise kill all potential mates thereby failing to produce offspring. Thus, males that exploit aggressive spillover to their own gain are, in effect, reducing the costs of spillover to females by ensuring that females will not kill all potential mates before copulation.

In addition, spillover may coincide with female benefits. As discussed above, the juvenile voracity benefits inherent in aggressive spillover may routinely combine with the adult foraging benefits of the adaptive foraging hypothesis to explain SC. Nor is spillover mutually exclusive with indirect female benefits. If spillover and sensory exploitation jointly explain pre-copulatory SC as suggested above, this combination may together yield the indirect female benefit of ensuring that only high-quality males capable of eliciting and avoiding female attacks sire offspring.

<u>Conclusion</u>

Although a comprehensible review of the literature on SC necessitated an approach that addressed individual hypotheses one by one, the thread running through this review, and the purpose of the summary sections, has been to point out the ways in which more than one of these mechanisms could be simultaneously at play in any given system. I have argued that SC, and mating systems in general, are dynamic affairs that are heavily influenced by the resolution of inter-sexual conflicts of interest. The resolution of these conflicts will shift given variation in behavioral and ecological parameters, and this will often require that more than one mechanism be employed to fully explain SC within any given system. Experiments that focus too narrowly on a single hypothesized adaptive benefit may miss the true complexity underlying the system. Finally, studies approaching mating systems from the male or female perspective exclusively disregard the importance of inter-sexual conflict and the ongoing evolutionary arms race between the sexes. Pre-copulatory SC appears on the surface to be a situation in which females dominate the sexual encounter at the expense of males. However, given the difficult and dangerous playing field created by sexually cannibalistic females, one cannot overlook the possibility that selection will favor male strategies, such as sensory exploitation, that shift the ongoing sexual conflict back in the favor of males. Modern day studies of SC, and mating systems in general, must account for the complexity that arises when males and females compete and co-evolve in variable environmental contexts.

Table 2.1   A comprehensive listing of the hypotheses for sexual cannibalism reviewed in Chapter 2.

HYPOTHESIS	MECHANISM	PRE-COPULATORY	POST-COPULATORY
Male-benefit • *Paternal investment*	Sacrificing males enhance female fecundity and production of offspring they sire	Not applicable	Supported by theory, no empirical support
• *Male mating effort (paternity assurance)*	Sacrificing males have higher fertilization success	Not applicable	Supported by theory. Empirical support for one species
• *Male mating effort (sensory exploitation)*	Males that elicit unsuccessful attacks have higher mating success than males not attacked	Viable, untested	Not applicable
Female-benefit • *Adaptive mate choice (indirect benefits)*	Patterns of aggression inherent in SC dictate that females derive indirect (genetic) benefits	Some evidence for male size bias	Evidence in several species for male size bias
• *Adaptive foraging (material benefits)*	Selection favors females that optimally trade-off males as food versus males as sperm	Supported by theory Empirical support mixed	Viable, untested
Non-adaptive hypotheses • *Male senility*	Inferior old male courtship and/or escape ability	Not supported	Not applicable
• *Mistaken identity*	Indiscriminate female predatory behavior	Viable, untested	Not applicable
• *Aggressive spillover*	Aggression spills over into mating context from other advantageous contexts	Preliminary support in one species	Reduced costs make spillover unlikely

Figure 2.1 The sequence of assumptions made by the aggressive-spillover hypothesis. Each arrow represents a positive correlation. Solid arrows depict the ontogenetic spillover suggested in the original formulation of the hypothesis. Dashed arrows represent the suggestion that voracity within the adult life history may spill over between behavioral contexts such as hetero-specific foraging opportunities and con-specific foraging opportunities that arise in the mating context (i.e. pre-SC).
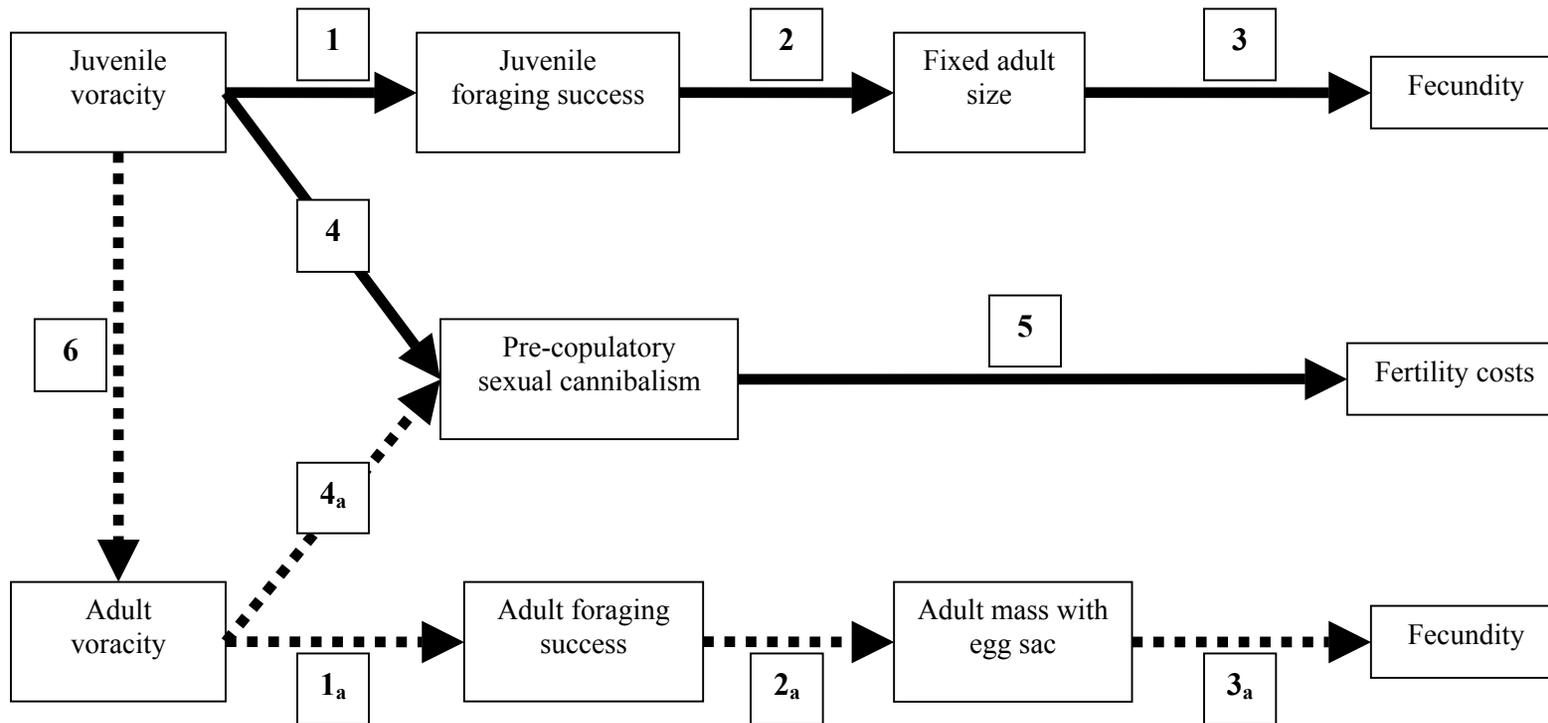
CHAPTER 3

The role of sexual size dimorphism in mating interactions of the

sexually cannibalistic spider *Dolomedes triton*

Summary

Some arachnids display extreme sexual size dimorphism (SSD) with adult females being several times larger than adult males. One explanation for SSD in species that exhibit pre-copulatory sexual cannibalism (female attack of the male prior to mating) is that smaller males may be less likely victims of predatory attacks by females. However, in some sexually cannibalistic species males are similar in size to females, suggesting benefits of large body size. Here, I report the results of an experiment designed to explore the ramifications of body size in mating interactions of the North American fishing spider (*Dolomedes triton*). Results suggest that male size does not influence courtship behavior, the likelihood of being attacked, or the male's ability to secure a mounting. However, large males were superior at transferring sperm once mounted, and as a result incurred fewer attacks during the struggle to transfer sperm. Alternatively, sexual cannibalism may be predicated on female size. Binary logistic regression indicated that female condition (mass/cephalothorax area) did not explain any of these behaviors from the copulatory sequence. However, adult female cephalothorax area was negatively related to the likelihood of pre-copulatory attacks. Finally, analysis of the ratio of female size to male size showed that when SSD is weak males are more likely to escape attacks and transfer sperm successfully. Results are discussed in light of several hypotheses for sexual cannibalism, and the benefits of large male body size illustrated here are put forth as potential explanations for the relatively moderate extent of SSD found in this sexually cannibalistic species.

Introduction

        The striking disparity in adult body size between males and females of many species (i.e. sexual size dimorphism: SSD) has inspired a wealth of explanations, and continues to be an active area of inquiry (Anderrson, 1994). Spiders are one group in which SSD is often extreme with adult females of some species being 10 times larger than adult males (Elgar et al., 1990; Elgar, 1992). Such studies of SSD in arachnids tend to use fixed measures of adult body size (e.g. cephalothorax length, leg length). Measures of fixed adult size are influenced exclusively by juvenile foraging success and, for the majority of spiders, are set for life upon the adult molt. In contrast, adult body mass is a more plastic measure of size that varies throughout the adult stage along with adult foraging success and energy expenditure. Throughout this paper, I will use the terms 'size' and 'mass' to make this distinction apparent.

        Recently, the extreme SSD found in some spider taxa has been the topic of a debate between models suggesting the evolution of 'dwarf males' (Vollrath & Parker, 1992, 1997), and others positing the evolution of 'giant females' (Head, 1995; Prenter et al., 1998, 1999; Hormiga et al., 2000). Essentially these models differ in that SSD via male dwarfism is suggested to arise by selective forces favoring diminutive males, whereas SSD via female gigantism arises by selective forces that favor the largest females. The 'dwarf-male' model suggests that extreme SSD is frequently observed in Arachnid systems because females are generally sedentary relative to males that experience high mortality through mate searching. This male-biased mortality will shift the operational sex ratio in favor of females. Such a shift should result in a scramble competition (Thornhill & Alcock, 1983) for relatively abundant females, rather than direct competition between males for access to a limited number of females. Under these circumstances, sexual selection on males should favor early maturation (protandry) and small male size, rather than the large male body size typically favored when males compete directly, sometimes physically battling each other for females. In contrast, the 'giant female' models argue that, across species, fecundity selection and variation in female size best explain the extent of SSD, whereas variation in male size often shows little effect on SSD (Prenter et al., 1999; Hormiga et al., 2000). In addition, proponents of the latter model point out that life history comparisons do not support the dwarf-male model when they are corrected for phylogenetic relatedness (Prenter et al., 1998).

The extent of SSD within any given species, however, should reflect selection acting on both male size and female size. In addition, body size for each sex will most often be the net result of a multitude of conflicting selection forces that sometimes favor drastically different optimal body sizes. Thus, realistic, taxon-specific selection pressures on body size (in both directions and for both sexes) need to be considered on top of these types of general models to fully understand SSD. One factor suggested to select for small male body size in a subset of spider taxa is the risk of pre-copulatory sexual cannibalism (i.e. female attack of the male upon courtship but prior to sperm transfer). Cambridge (1871), Darwin (1871) and later Robinson & Robinson (1980), suggested that small male spiders would benefit if their small size makes them less likely prey items for the female. This benefit could arise in one of two ways: smaller males may escape the notice of predatory females, or females may refuse to prey on diminutive males if they are inadequate prey items (Elgar, 1992; Elgar & Fahey, 1996).

Regardless of the exact mechanism, this hypothesis predicts that smaller males will avoid pre-copulatory attacks, and should subsequently secure more matings and sire more offspring relative to larger males. However, contrary to this idea, so called 'dwarf male' spiders and extreme SSD occur in several taxa that do not exhibit pre-copulatory sexual cannibalism. Perhaps more striking is the fact that SSD is much less pronounced in some species where females commonly attack males upon courtship (Elgar & Nash, 1988). Thus, despite a high risk of pre-copulatory sexual cannibalism, some male spiders do not show an extreme reduction in body size. What factors could explain the intermediate degree of SSD in these sexually cannibalistic species?

Several factors may favor large male size, and thus reduced SSD, despite the risk of pre-copulatory sexual cannibalism. First, large body size is generally associated with increased foraging success in Arachnids (Vollrath, 1987). For example, large juvenile males may have higher prey capture rates leading to growth/survival benefits. This benefit should be accentuated in cannibalistic systems where larger juveniles commonly feed on the smaller members of their cohort. Thus, larger juvenile males will have access to more prey items (both hetero-specific and con-specific), and will also be subject to fewer con-specific predators. Second, in systems characterized by direct male-male competition, sexual selection may favor large males that out-compete smaller males for access to females. Elgar & Fahey (1996) show such a benefit in the highly size dimorphic orb-web spider *Nephila plumipes*. In this species, selection to avoid

sexual cannibalism favors small males, whereas male-male competition favors large male body size. The result in this species is a great deal of variation in male body size. Third, large male size may actually be adaptive in terms of pre-copulatory sexual cannibalism if large size is associated with increased escape success. Indeed, several studies addressing the relation between male size and pre-copulatory attacks have found a large-male escape advantage (Arnqvist, 1992; Arnqvist & Henrikkson, 1997; see Chapter4). Finally, when the above benefits of male size exist, females may derive an indirect genetic benefit by mating with large males and/or rejecting/attacking small males (Elgar & Nash, 1988).

Study system

Here, I explore the ramifications of male body size in the sexually cannibalistic North American fishing spider *Dolomedes triton* (Araneae; Pisauridae). Fishing spiders are relatively large, cursorial ambush predators most commonly associated with the edges of aquatic habitat (Carico, 1973). Fishing spiders detect water-borne prey vibrations using sensory receptors located in their forelegs (Bleckmann & Barth, 1984). Prey items are most commonly insects trapped at the water surface (Carico, 1973; Barth, 1982; Zimmerman & Spence, 1989) however, fishing spiders derive their name from their ability, albeit infrequent, to attack, subdue and consume aquatic vertebrate prey (e.g. fish, frogs, salamanders) that are often significantly larger than the attacking spider (Bleckmann & Lotz, 1987; personal observation).

The *Dolomedes* mating sequence is initiated when a searching male encounters pheromonal cues from female silken drag lines (Carico, 1973; Arnqvist, 1992). Males then proceed with a stereotypic courtship sequence of leg waving and a slow regular tapping of the water surface or solid substrate. If not immediately attacked, males proceed cautiously, following the female's drag lines and approaching the female while continuing courtship. Males typically mount the dorsum of the female from behind and turn to face the opposite direction of the female. The male then leans sideways, usually between the female's legs II and III, and reaches to insert a single pedipalp charged with sperm into the female's epigynum, a paired structure located at the ventral junction between the cephalothorax and abdomen. Sperm transfer takes only a few seconds after which the male jumps off and retreats.

Adult female fishing spiders routinely attack males at any point during this copulatory sequence. However, laboratory mating trials indicate that females of the European fishing spider

57

(*D. fimbriatus*) most commonly attack during pre-copulatory courtship (75% of trials), and that males are killed in approximately 5-10 % of these attacks (Arnqvist, 1992; Arnqvist & Henrikkson, 1997). For *D. triton*, laboratory mating trials showed that pre-copulatory attacks by virgin females occur in approximately 20% of pairings (see Chapter 4). In addition, field studies of *D. triton* suggest that males represent a common contribution to the adult female diet (Zimmerman & Spence, 1989), and that male population density declines drastically, soon after adult female emergence (Zimmerman & Spence, 1992). Thus, sexual cannibalism appears to play an important role in the ecology of *Dolomedes*.

Fishing spiders are a particularly interesting group for several reasons. The family Pisauridae is one of only two spider families in which pre-copulatory sexual cannibalism is known to be common (see Table 7.4, Elgar, 1992). Orb-web building spiders from the family Araneidae, perhaps the family most frequently associated with pre-copulatory sexual cannibalism, are also the most sexually dimorphic group of spiders. Indeed, based on a sample of 97 species, female orb-web spiders routinely have a fixed body size twice that of males (Prenter et al., 1998), and this female size advantage can be much more dramatic in species such as *Nephila clavipes*, the model system used in the development of the dwarf-male hypothesis. In contrast, adult female *D. triton* are typically only 1.28-1.34 times the size of adult males (Carico, 1973; Johnson, unpublished data). Thus, fishing spiders offer us the opportunity to examine an exception to the rule that SSD should be extreme in spiders that commonly display pre-copulatory sexual cannibalism. Here I ask the question: why are male *D. triton* relatively large when they run a substantial risk of pre-copulatory sexual cannibalism? Specifically, I examine the ramifications of male body size throughout the copulatory sequence to see if this sexually cannibalistic mating system favors either extreme in adult body size.

Methods

One hundred-twenty males in their penultimate molt were collected in April, 2001 from a single pond in Central Kentucky. These males were maintained in the laboratory for 2 weeks in individual 425 ml. transparent, plastic cups each provided with 2 cm. of filtered water and a Styrofoam float (2.0 x 1.5 x 0.5 cm.).   During this holding period males were fed weekly 1 juvenile house cricket, *Acheta domesticus*, weighing approximately ¾ the spider's body mass. Upon their adult molt, males were weighed to the nearest milligram and video imaged. Adult

males were initially categorized according to their mass as either 'large' (top 1/3 of the population size distribution), 'intermediate' (middle 1/3 of the population size distribution), or 'small' (bottom 1/3 of the population size distribution). Individuals in the intermediate size class were returned to the field and the large and small males were included in the experiment. Digitized images were later used to measure the length and width of the cephalothorax. The area of the cephalothorax was then calculated as the area of an ellipse (= π x [cephalothorax width/2] x [cephalothorax length/2]).

Penultimate-molt females were collected from the same population in mid-May, 2001, weighed, imaged and maintained outdoors in individual, large (60 x 41 x 16 cm.), transparent, plastic containers. These containers were filled with filtered water to a depth of 2.0 cm. and each contained a large Styrofoam float (10 x 6.0 x 0.5 cm). Females were fed 1 adult cricket 3 times per week until they reached their adult molt. Forty-eight hours following their adult molt females were fed 1 adult cricket. Forty-eight hours following this feeding, females had their first mating trial.

To standardize the introduction of males to the female's container, I began each mating trial by attempting to touch the female's abdomen with the tip of a pencil. This invariably resulted in the female taking refuge under water on the under side of the Styrofoam float (see Carico, 1973 for a description of this anti-predator defense). Males were then introduced into the female's container as far from the submerged female as possible. Each female was presented with a sequence of mating trials in which the size class of male offered was alternated daily (i.e. small-large or large-small). Twenty females were randomly selected to be offered a large male first, and the remaining twenty females were offered a small male first. Males not initiating courtship within 15 minutes of introduction to the container were replaced with a male of the same size class. I then followed the copulatory sequence for 90 minutes recording the occurrence of and latency to (1) male courtship (defined as characteristic leg waving and/or tapping the water or solid substrate), (2) female re-surfacing, (3) female pre-copulatory attack, or (4) male mounting, (5) sperm transfer, and (6) female post-copulatory attack.

Statistical analyses

All statistical analyses were conducted using SAS (1988). Below I report the results from categorical analyses of the conditional likelihood of a copulatory event (e.g. occurrence of a

kill given an attack, or occurrence of a mating given a mounting). Analysis of the effect of male size class on the occurrence of various copulatory events was performed with a series of four-category G tests for goodness of fit. These tests pair each female's first trial with a large male with her first trial with a small male. Thus, each female could exhibit one of four possible strategies (e.g. attack males of both size classes, attack large male but not small male, attack small male but not large male, or attack neither male, see Table 1.1). To test the prediction that females switch their behavior biasing attacks towards small males I compared the relative frequency of attacking small males but not large males (tactic # 1c) versus attacking large males but not small males (tactic # 1b). To test the prediction that females switch their behavior biasing mountings and matings towards large males I compared the relative frequency of mounting/mating with large males but not with small males (tactic # 3b/4b) with mounting/mating with small males but not large males (tactic # 3c/4c). In addition, multiple logistic regression was used to simultaneously account for several male and female size variables in a further attempt to understand the occurrence of these copulatory events.

Results

This population of fishing spiders exhibits a substantial amount of variation in both adult male body mass and cephalothorax area (reported as mean ± s.e.), and these factors are highly correlated with each other (see diamond symbols in Figure 1.1). Within the size classes used in this experiment, small males (N=29) weighed 141.37 ± 5.39 mg. and had a cephalothorax area of 0.163 ± 0.004 cm^2. In contrast, males in the largest 1/3 of the population size distribution (N=35) weighed 314.68 ± 9.02 mg. and had a cephalothorax area of 0.304 ± 0.007 cm^2. For both measures this difference is statistically significant (mass: t= 17.23, d.f.=61, $p<0.0001$; cephalothorax area: t=18.38 , d.f.=62, $p<0.0001$).

The effects of male-size class

Males typically began courting within the first five minutes of a pairing and male size class did not influence the likelihood of courtship behavior (χ^2=0.95, d.f.=1, p=0.33). The sequence of male size classes experienced by females (SL, n= 17 vs. LS, n=16) had no effect on the occurrence of a copulatory event: (1) re-surfacing from refuge (χ^2=2.58, d.f.=1, p=0.11), (2) pre-copulatory attacks (χ^2=0.72, d.f.=1, p=0.40), (3) successful kills given an attack (χ^2=0.02,

d.f.=1, p=0.91), (4) mountings (χ^2=0.09, d.f.=1, p=0.77), or (5) matings given a successful mount (χ^2=0.71, d.f.=1, p=0.40). Therefore, I pooled females from the two sequence types and performed a paired contingency analysis with these 33 females.

Females showed no tendency to switch their attack behavior based on male size class. The tactic of attacking small males but not large males did not occur more often than the tactic of attacking large males but not small males (G=1.36, d.f.=1, p>0.1). Interestingly, females displayed tactics that failed to discriminate between male size classes (tactics # 1 and 4 from Table 1.1) more often than would be expected given the overall probability of attack on each size class (p(attack small)=0.30, p(attack large)=0.21). Thus, no evidence exists to suggest that females switch their attack strategy based on male size class. Instead, females are more likely to treat different-sized males similarly than they are to switch behaviors based on male size class.

Also from Table 1.1, it is apparent that kills/attack are not biased towards small males (G=0.34, d.f.=1, p>0.5), nor are mountings biased in favor of large males (G=0.69, d.f.=1, p>0.1). However, females are mating with large males but not small males more often than they mate with small males but not large males (G=2.93, d.f.=1, .05<p<0.1).

The above analysis treats single behaviors as part of a paired tact taken by individual females. Thus, behaviors are only considered from the female vantage point and each female was used as the experimental unit. However, the likelihood of a pre-copulatory kill, mounting and/or mating may be controlled by male behavior just as much as female behavior. Accordingly, I compared these measures across male size classes for all virgin males regardless of the female. For this larger dataset, male size class had no effect on the likelihood of a kill (χ^2=1.03, d.f.=1, p=0.31) or a mounting (χ^2=0.16, d.f.=1, p=0.69). However, the likelihood of sperm transfer given a successful mounting was contingent on male size class. Large virgin males were significantly more likely to successfully transfer sperm during a mount (11/13; successful males are the bold diamonds in Figure 1.1) relative to the sperm transfer success of small virgin males that obtained a mount (2/13; χ^2=12.46, d.f.=1, p=0.0004).

Unfortunately, the irregularity with which small males were able to successfully copulate precluded a formal comparison of the effect of male size on post-copulatory attacks and kills. Nonetheless, post-copulatory attacks occurred following 6 of 11 (55%) successful matings with large males and 4 of these 6 (67%) post-copulatory attacks were successful. Neither of the small males that succeeded in mating were attacked after copulation.

Other effects of body size

A multiple logistic regression model including fixed female size, female condition (mass scaled for fixed size), fixed male size, and the ratio of fixed female size to fixed male size showed some interesting results. Perhaps surprisingly, female condition did not predict any of the copulatory events measured. However, females of inferior fixed size were both more likely to re-surface during a trial (χ^2=4.40, d.f.=1, p=0.0358) and more likely to attack a male before sperm transfer (χ^2=10.40 d.f.=1, p=0.0013, bold squares in Figure 1.1 are the sexual cannibals). When viewed as a continuously-distributed variable, male size had no significant effect on the likelihood of a pre-copulatory attack (χ^2=0.32, d.f.=1, p=0.58). In agreement with the results of the male size class manipulation (see above), fixed male size was positively related to sperm transfer success (χ^2=8.91, d.f.=1, p=0.0028). The ratio of fixed female size to fixed male size predicted the likelihood of a kill given a pre-copulatory attack such that males that approximated the female's size were significantly more likely to escape an attack than were males that were dwarfed by the female (χ^2=6.08, d.f.=1, p=0.0136). In addition, successful matings were significantly more likely from pairs in which the ratio of fixed female size to fixed male size was small (χ^2=6.76, d.f.=1, p=0.0090).

Discussion

A substantial amount of within-sex and between-sex size variation was found in both fixed adult body size (cephalothorax area) and adult body mass for this population of fishing spiders. In terms of fixed size, large males are as large as smaller females. In contrast, small males may often be forced to court small females that are twice their size, or perhaps solicit copulations from large females that are four times their size (see Figure 1.1). Thus, the opportunity for selection to act upon male size and sexual size dimorphism appears to be present.

Body size effects on the copulatory sequence

Female re-surfacing from refuge

The large differences in male body size employed in this study produced no differences in a female's willingness to re-surface from refuge. While it is possible that a female is unable to detect the presence of a male tapping the water surface while she remains submerged

underwater, anecdotally it did appear that females often re-surfaced soon after the onset of courtship tapping. In addition, males often concentrated their courtship efforts in areas immediately adjacent to the submerged female, suggesting that they may be able to detect a submerged female's whereabouts (e.g. through detection of the freshest pheromonal silk lines left on the water). A submerged female's propensity to respond to prey and courtship stimuli is one issue under current investigation. Regardless, it may be impossible for a submerged female to detect fine-grained differences in the size of the male courting them (e.g. differences in water-borne stimulus amplitude) and the tendency to re-surface may have more to do with the female's state than the size of male courting her.

Adult female mass did have a significant effect on female re-surfacing behavior. While most females re-surfaced at some point during the trial, the heaviest females were most likely to remain submerged for the entire trial. This result suggests that either female's with the poorest recent feeding history are re-surfacing in order to improve their foraging success, or that only well-fed females have the energy reserves to remain submerged. Concerning the first of these possibilities, neither female mass nor female condition predicted the likelihood of a predatory attack on males. Thus, an adaptive foraging explanation for the re-surfacing tendencies of light females seems unlikely.

Pre-copulatory attacks

The overall frequency of pre-copulatory attacks in this study (20%), which was conducted outdoors using relatively large experimental containers, is identical to that reported from an earlier laboratory study which used much smaller containers (see Chapter 4). Thus, the occurrence of pre-copulatory sexual cannibalism in this species does not appear to be an artifact of laboratory conditions. When viewed as a paired tactic by females, the occurrence of these attacks was not based on differences in the body size of the courting male. In fact, females were much more likely to treat different-sized males similarly than they were to switch behaviors due to variation in male size. Such indiscriminate female behavior towards males of extremely different sizes suggests that female phenotype, rather than male phenotype, determines the likelihood of attack.

Females invoked no mounting bias with regard to male size (see below). Thus, if a female preference for attacking small males and allowing large males to mate exists, it must be

manifested after mounting. Indeed, more attacks occurred following mounting, during the male's struggle to inseminate the female, than occurred prior to mounting, and these copulatory attacks were heavily biased towards small males. Unfortunately, both of these types of attacks would fall under the historical label of pre-copulatory attack. As such, this large male advantage in terms of avoiding pre-copulatory attacks may instead be a by-product of the large-male advantage when it comes to transferring sperm (see Mating below). Future studies should consider the utility of delineating three phases of sexually cannibalistic attacks: courtship phase, mounting phase, and post-copulatory phase. As this data set illustrates, these three phases represent the whole of the courtship-copulation sequence much more fully than the historical division of pre-copulatory and post-copulatory attacks.

While it remains unclear if female attack behavior benefits large males, it is clear from Table 1.1 that small males are routinely attacked. Thus, small males do not appear to benefit by slipping under either (1) the predatory female's sensory threshold to detect potential prey items or (2) a female's behavioral threshold for the size of suitable prey items (Elgar & Fahey, 1996). Further confirming both of these points is the observation that adult female fishing spiders routinely detect, attack, and feed on prey items that are much smaller than even the smallest adult males (Zimmerman & Spence, 1989; personal observation).

The only female size variable that predicted pre-copulatory attacks was fixed adult size (cephalothorax area). Once again, this measure is fixed at adulthood, and thus can only be enhanced by juvenile processes such as juvenile foraging success and growth up until the adult molt. As such, there is no evidence that pre-copulatory attacks are motivated by a lack of **adult** foraging success (Newman & Elgar, 1991). Instead, it appears that females with the smallest fixed size, those that presumably had the poorest juvenile foraging success, are the most likely to practice sexual cannibalism. Indeed, this is exactly the suggestion of a recent paper (Schneider & Elgar, 2002). These authors suggest sexual cannibalism to be a component of adaptive adult foraging compensation for a history of poor foraging success through development. According to this idea, and consistent with the present data, pre-copulatory sexual cannibalism should be employed most often by females that emerge at small fixed adult sizes.

This interaction between juvenile feeding (fixed size) and adult feeding (adult mass) has been studied in *D. triton* previously (Spence et al., 1996). In addition, Chapter 4 provides support for the possibility that adult foraging success can effectively compensate for poor

64

juvenile foraging and small fixed size. Results from this direct manipulation of juvenile and adult food availability suggest that both juvenile and adult foraging have positive effects on fecundity. In particular, poorly-fed juvenile females from that study that were shifted upon adulthood to a high-food regime (1) far exceeded the fecundity of females held on a low-food diet throughout both juvenile and adult stages, and (2) did not differ significantly from the fecundity of females held on a low juvenile/high adult food regime (see Chapter 4). In addition, high adult foraging success in small females may allow for additional fecundity compensation by allowing these small females to produce multiple egg clutches (Chapter 4).

Troubling to the foraging compensation hypothesis, however, is the lack of evidence in *D. triton*, and most other spiders studied to date for that matter, that feeding on males has a quantitative fecundity benefit (Andrade, 1996; Spence et al., 1996 ; Arnqvist & Henrikkson, 1997; Fahey & Elgar, 1997; Elgar et al., 2000; Chapter 4; but see Elgar & Nash, 1988). Thus, small females may be able to compensate for poor juvenile foraging via increased adult foraging, but the addition of a single male to the adult female's diet does not appear to have a positive quantitative effect on fecundity, making it difficult to explain sexual cannibalism as any type of adaptive foraging strategy (but see Chapter 4 for the suggestion of a qualitative fecundity effect of sexual cannibalism).

As noted by Schneider & Elgar (2002), the finding that sexual cannibals are most often the females of the smallest fixed size is the exact opposite of that predicted by a recent, 'non-adaptive' explanation for sexual cannibalism. Arnqvist & Henrikkson (1997) hypothesized that pre-copulatory attacks stem, not from any adaptive foraging response by females, but instead from a spillover of aggression from advantageous contexts such as the juvenile foraging context, to potentially costly contexts such as the mating context. One prediction of this 'aggressive spillover' hypothesis is that pre-copulatory attacks should be most common in the largest adults who were the most voracious and successful juvenile predators. The present data, as well as one previous laboratory study (see Chapter 4) provide no support for this prediction. The aggressive spillover hypothesis is more directly addressed in Chapters 4 and 6.

Pre-copulatory kills

The frequency of successful kills per attack in this study (13/26) was significantly higher than in earlier work on this population of *D. triton* (see Chapter 4), as well as that reported for a

European congener (Arnqvist & Henrikkson, 1997). However, male size class had no effect on the male's ability to escape an attack. This contrasts with previous suggestions that superior speed and agility in large *Dolomedes* males allows them to escape more female attacks (Arnqvist & Henrikkson, 1997; see Chapter 4). However, disregarding the size classifications imposed in this experiment, male size relative to the attacking female's size was an important determinant of male escape ability. Apparently, when the largest males face an extremely large female, escape success remains poor despite large male size. Conversely, small males paired with relatively small females are often able to avoid pre-copulatory attacks. Thus, the heightened capture success seen in this experiment is almost certainly the by-product of using males from the extreme ends of the size distribution. Males of average size, which were not used in this experiment, should have a better chance of being large enough relative to their attacker to escape the majority of pre-copulatory attacks.

Mountings

Mounting was the only stage of the copulatory sequence that failed to be predicted by any measure of male or female size. Females appear to control this phase of pre-copulatory courtship as male suitors are often rebuffed by attacks, abbreviated 'false' lunges and/or leg waving by the female that prevents the male's attempts to mount. However, these rejection behaviors are not predicated on male size. Females are either unable to discriminate male size at this stage, have no preference for males of different sizes, or invoke such a bias at a later stage.

Matings

Finally, while a paired analysis showed that females mate with large but not small males more often than they mate with small but not large males, this result was not statistically significant (see Table 1.1). Nonetheless, sperm transfer offers a point at which large males are strongly favored in this mating system. The results from this experiment suggest that, regardless of events leading up to the transfer of sperm, small males rarely complete a mating successfully. This effect is particularly strong when the size dimorphism between a male-female pair is large. In other words, small males struggle in all cases, but completing a mating with a relatively large female may be impossible for a small male. In contrast, large males will have a relatively easy time transferring sperm unless they come into contact with an unusually large female. Females

may exacerbate this bias against small males if subtle movements during copulation (e.g. the raising of the legs high) make it even more difficult for a small male to reach the female's epigynum. Regardless of whether females are actively taking part in this mating bias, or simply creating a larger and more difficult "playing field" for smaller males, the result remains the same: matings with small males are rare, and when they do occur they will involve a small, presumably less fecund, female.

Conclusions

Small male fishing spiders do not benefit in any recognizable way during the course of the copulatory sequence in this sexually cannibalistic mating system. Small males suffer greater mortality in pre-copulatory attacks and are largely excluded from the gene pool through their poor sperm transfer performance. The question then is no longer 'why aren't males smaller when they are at risk of sexual cannibalism', but instead 'why aren't males bigger if size determines mating success'? Male body size is most likely limited by food availability and the benefits of emerging early. Indeed, the benefits of early emergence should be great in systems such as this where competition between males is more often via mate location and less often dependent on a male's ability to directly battle other males for access to a female. Nonetheless, multiple adult males are often found cautiously cohabiting with penultimate stage and recently-matured females (personal observation). It is not known if males ever come into conflict over females, but if they do the benefits of delayed maturation and large size might begin to approximate the benefits of early emergence at inferior sizes. Thus, optimal adult male body size in this species is most likely a delicate balance between the costs and benefits of early emergence at small size, the availability of resources allowing for growth to large sizes, and the costs and benefits of taking longer to mature at a large size. Results from the present study suggest that the benefits of large size during the copulatory sequence are considerable.

CHAPTER 4

Sexual cannibalism in fishing spiders (*Dolomedes triton*):

an evaluation of two explanations for female aggression towards potential mates

Summary

I manipulated juvenile and adult food availability in the fishing spider (*Dolomedes triton*) in order to test two hypotheses for sexual cannibalism. The adaptive foraging hypothesis posits that sexual cannibalism is an economic, adaptive foraging strategy on the part of the adult female. In contrast, the aggressive-spillover hypothesis suggests that pre-copulatory sexual cannibalism is misplaced aggression favored in previous life-history phases. Several results indicated support for the adaptive foraging hypothesis. First, increased adult food availability produced marginally non-significant fecundity benefits in female's first egg sacs and highly significant fecundity benefits in female's second egg sacs. Second, while consumption of a male did not result in more offspring in either egg sac, it did significantly increase the probability a female would successfully hatch an egg sac. Finally, mating trials revealed mixed support for the adaptive foraging hypothesis as, for the most part, female mating behavior (attack or mate) was not determined by the adaptive value a male represents (food item or sperm donor). Specifically, likelihood of a pre-copulatory attack was not determined by male size, date (an indirect estimate of male availability) or female nutrient load. However, mated females did tend to attack courting males more often than virgin females. The aggressive-spillover hypothesis was supported by several findings. Juvenile food availability had a significant positive effect on fixed female size which, in turn, had a significant positive effect on fecundity. Thus, the spillover hypothesis' assertion that strong fecundity selection acts on juvenile feeding and fixed adult size was supported. The possibility that the spillover and adaptive foraging hypotheses are not mutually exclusive is discussed, especially in light of the presence of high levels of sexual cannibalism both before and after mating.

Introduction

Sexual cannibalism, or intra-specific, inter-sexual predation of a male during courtship, copulation, or shortly thereafter, is a phenomenon which has fascinated and perplexed mating systems ecologists for the past century (Polis 1981; Elgar 1992; Johns & Maxwell 1997). Sexual cannibalism is relatively widespread among invertebrates, and is particularly prevalent amongst arachnids (Elgar 1992). Many hypotheses have been put forth to explain the evolution and maintenance of this behavior, however, little consensus has been reached. While post-copulatory sexual cannibalism, defined generally as cannibalism of the male by the female after sperm transfer, has received considerable experimental and theoretical treatment as a male strategy (Thornhill 1976; Parker 1979; Buskirk et al. 1984; Andrade 1996) and female strategy (Elgar 1998), fewer studies have addressed pre-copulatory sexual cannibalism. Consumption of the male prior to sperm transfer cannot be construed as an adaptive male tactic, thus hypotheses have focussed on explaining pre-copulatory sexual cannibalism from the female's perspective.

Elgar (1992) lists three possible explanations for pre-copulatory sexual cannibalism. First, Gould (1984) suggested that sexual cannibalism may simply be the non-adaptive product of mistaken identity if generally aggressive females attack males as prey items before 'realizing' their adaptive value as mates. Second, females may use discriminatory aggression towards potential mates as an extreme mechanism of mate refusal. Males of inferior phenotype (e.g. small males) may be attacked, while large males are the preferred mates. Finally, pre-copulatory sexual cannibalism may arise strictly as an adaptive female foraging strategy.

The adaptive foraging hypothesis for sexual cannibalism was first formalized by Newman & Elgar (1991), and it is essentially an economic model which suggests that females adaptively weigh a courting male's value as a mate versus his value as a food item. The model assumes strong effects of adult feeding on fecundity and that fertilization success is a function of the number of times a female mates. According to the adaptive foraging idea females should attack males when food is limited but mates are not. Thus, the hypothesis predicts that the likelihood of sexually cannibalistic attacks will 1) increase with decreasing food availability, 2) increase as variation in food availability increases, 3) be higher for non-virgin females relative to virgins, 4) increase as male size increases, and 5) decrease for virgin females as the breeding season progresses and male availability presumably declines.

69

Recently, Arnqvist & Henriksson (1997) found little support for the adaptive foraging hypothesis in the European fishing spider (*Dolomedes fimbriatus*) as adult feeding was not related to fecundity, and the likelihood of sexually cannibalistic attacks was not a function of male value as either a mate or a food item. The latter result was emphasized by the finding that despite multiple mating opportunities, many females cannibalized males to the extent that they remained unmated throughout the experiment. In addition, rather than being a result of adult feeding, variation in fecundity was best explained by fixed female size (measured as cephalothorax area and leg length). These measures are termed 'fixed' because they are set for life in arachnids at the final molt, and thus can only be influenced by feeding during immature stages.

The absence of obvious benefits to pre-copulatory sexual cannibalism, compounded by the documentation of a cost of sexual cannibalism in the form of the risk of remaining unmated, caused Arnqvist and Henriksson (1997) to suggest that the act of sexual cannibalism is not adaptive when viewed solely in the context of mating. Instead, this modern day variant of the mistaken-identity hypothesis suggests that apparently non-adaptive levels of aggression towards mates are, in fact, the result of a 'spillover' of high levels of aggression towards food (hereafter referred to as voracity) which are favored in previous life-history stages. In particular, they suggested that fecundity selection favoring juvenile voracity, which results in larger fixed adult size, might be so intense that it outweighs the costs of aggression at mating. Thus, this 'aggressive-spillover' hypothesis predicts that the most voracious juveniles will acquire the most food, attain the greatest fixed adult size, have the highest fecundity, and be the most likely to attack their mates (see Figure 2.1). In other words, if juvenile voracity is positively correlated with adult aggression towards mates, and the subsequent fecundity benefits of juvenile voracity are great, then this might explain apparently costly levels of aggression at mating.

Constraints-oriented explanations such as Arnqvist & Henrikkson's (1997) aggressive-spillover hypothesis are increasing in popularity as behavioral ecologists become more aware that behavioral correlations can play an important role in constraining adaptive behavioral expression (Price & Langen 1992; Sih 1992; Riechert & Hedrick 1993; Partridge 1994; Sih & Gleeson 1995; Sih et al., 2003). If, for example, the expression of anti-predator behavior is positively correlated across high and low risk contexts, perhaps due to genetic and/or physiological constraints, then strong selection favoring optimal anti-predatory responses at high

risk might favor seemingly non-adaptive anti-predatory responses at low risk. Hypotheses such as these presume that the genetic variance/covariance matrixes which underlie correlated traits are conserved to the extent that adaptive plasticity (e.g. no behavioral correlations) across contexts does not readily evolve (Houle 1991; Arnold 1992).

Surprisingly few studies have directly tested a behavioral correlation explanation such as the aggressive-spillover hypothesis. A few notable exceptions exist. Several works addressing the fear-aggression continuum have shown that in taxa as diverse as fish and spiders, the most aggressive individuals in territorial disputes are often also the boldest individuals when confronted with predation risk (Huntingford 1976; Riechert & Hedrick 1993). Thus, aggression or boldness as a syndrome is positively correlated across contexts as different as territorial defense and predator avoidance, a situation in which plasticity of aggression might be more adaptive. Working with sticklebacks (*Gasterosteus aculeatus*), Bakker (1994) showed that this positive boldness correlation is heritable and that it is maintained across different life-history switch points (i.e. juvenile aggression correlates positively with adult aggression). The aggressive-spillover hypothesis merely extends this aggressive syndrome to include positive correlations between juvenile voracity and adult female aggression towards courting males.

The present study is an effort to clarify the validity of the adaptive foraging and aggressive- spillover hypotheses for sexual cannibalism using the North American fishing spider (*Dolomedes triton*). First, I report the results of a manipulation of juvenile and adult food availability. I employed experimental food regime differences as a surrogate for natural levels of variation in voracity and food availability which are suggested to account for sexual cannibalism by the aggressive spillover hypothesis. By manipulating the juvenile food regime I was able to test several critical assumptions of the spillover hypothesis, namely that juvenile feeding determines fixed adult size and that fixed adult size determines fecundity. In contrast, the adaptive foraging hypothesis predicts that female fecundity is a function of food eaten as an adult. Second, by conducting mating trials I test the adaptive foraging ideas' assertion that the likelihood of sexual cannibalism is a function of the male's value as a mate or a food item. Specifically, female attacks are predicted to be more likely under the following conditions: 1) large male size, 2) high male availability (i.e. early in breeding season), 3) low food availability, and 4) non-virgin mating status. In contrast, the spillover hypothesis suggests that the likelihood of sexual cannibalism arises from an individual female's overall level of aggression, and thus

should show no adaptive pattern within the context of mating. Instead, the spillover hypothesis predicts that the likelihood of sexual cannibalism can be predicted from the juvenile female's level of voracity, and thus from her fixed adult size. This prediction of a positive correlation between juvenile voracity, fixed adult size and the likelihood of sexually cannibalistic attack is not addressed in the current study, as voracity is not measured in the present work. Instead, this crucial prediction of the spillover hypothesis is the focus of Chapter 6. Finally, while fecundity benefits from male consumption are potentially consistent with both hypotheses, the spillover hypothesis can account for costs of sexual cannibalism (incomplete fertilization) if the benefits of voracity in other contexts generally outweigh this risk.

Behavior and ecology of fishing spider feeding and mating

Fishing spiders (*Dolomedes* spp., Pisauridae: Araneae) are large, cursorial sit and wait predators most commonly associated with the edges of aquatic habitat (Carico 1973). In particular, *D. triton* is the most widely distributed species in North America, and is characteristically found along the edges of ponds and/or slow-moving streams. Fishing spiders forage by localizing vibratory prey stimuli and lunging at their prey (Bleckmann & Barth 1984). Prey items are most commonly insects trapped at the water surface (Carico 1973; Barth 1982; Zimmerman & Spence 1989), however fishing spiders are renowned for their ability, albeit infrequent, to attack and successfully subdue and consume aquatic vertebrate prey which often greatly outsize them (Bleckmann & Lotz 1987; personal observation).

The *Dolomedes* mating sequence is initiated when a searching male encounters female silken drag lines which elicit a stereotypic courtship sequence of male leg waving and a slow regular tapping of the water surface or solid substrate (Carico 1973; Arnqvist 1992). If not immediately attacked, males proceed cautiously, approaching the female and continuing courtship movements. Males mount the dorsum of the female, lean forward usually between the female's legs II and III, and insert a single pedipalp charged with sperm into the female's epigynum which is located at the ventral junction between the cephalothorax and abdomen. Sperm transfer takes only a few seconds after which the male jumps off and retreats. This process is often repeated and the male's second pedipalp is discharged. Mated females eventually produce an egg sac which they carry in their mouthparts and defend throughout its development

(approximately a 2 week period). Just prior to egg sac hatching females typically climb up in the vegetation and construct an elaborate nursery web for the emergent spiderlings.

Adult female fishing spiders are known to attack males at any point during this copulatory sequence. However, laboratory mating trials indicate that females of the European fishing spider (*D. fimbriatus*) most commonly attack during pre-copulatory courtship (75% of trials) and that males are killed in approximately 5-10 % of these attacks (Arnqvist 1992; Arnqvist & Henrikkson 1997). Field studies of *D. triton* suggest that males represent a common contribution to the adult female diet (Zimmerman & Spence 1989), and that male population density declines drastically soon after adult female emergence (Zimmerman & Spence 1992). Thus, aggression in the form of sexual cannibalism does appear to play a crucial role in the population ecology of *D. triton* and *D. fimbriatus*.

Methods

As a surrogate for individual variation in female voracity resulting in differential feeding rates, I directly manipulated female access to food in the laboratory. To measure the relative effects of juvenile and adult feeding rate on fecundity I manipulated food availability for each age class using a 2x2 factorial design. The adaptive foraging hypothesis assumes that female fecundity is determined primarily by feeding rate during adulthood (i.e. that consuming one or more males increases fecundity). In contrast, the aggressive-spillover hypothesis posits that juvenile feeding rate determines fixed adult size that, in turn, is the main determinant of female fecundity.

General protocol

Mature male and juvenile female *D. triton* that were approximately 1-2 molts (2-4 weeks) from maturity were collected in early May 1999 from ponds at the University of Kentucky's Ecological Research Facility, Lexington, Kentucky (38° 2' N, 84° 36' W). Throughout the experiment males and immature females were kept in 425 mL transparent plastic cups filled with filtered water to a depth of 2.0 cm. Styrofoam floats (2.0 x 1.5 x 0.5 cm.) were provided as a resting spot and underwater refuge. All spiders were weighed to the nearest milligram and images were digitally captured (Snappy 3.0) on the first day of the experiment. Females were

weighed and imaged every 2 weeks thereafter. Morphological measures were made by digitizing relevant points on the spider image and connecting these points.

Following Arnqvist & Henriksson (1997), I measured fixed adult size as the area of the adult cephalothorax (area of an ellipse= π x [cephalothorax width/2] x [cephalothorax length/2]). Immature female spiders were randomly assigned to one of four food availability treatments (n=15 for each group): 1) low juvenile food, low adult food; 2) low juvenile food, high adult food; 3) high juvenile food, low adult food; 4) high juvenile food, high adult food. Upon adult emergence, females were moved to individual plastic containers (14 x 10 x 8 cm.) filled with filtered water to a depth of 2.0 cm, and provided with Styrofoam floats (10 x 6 x 0.5 cm.). Adult female containers were also provided with an inverted 212 mL plastic cup with opposing sides cut out. These 'spider dens' served as an additional refuge for females and/or males during mating trials, but did not preclude me from being able to observe copulations.

Food regimes

Juvenile diets were initiated immediately upon collection and continued until adult emergence. Adult diets began the first day of adulthood and continued until death. Adult females were not fed while they guarded their egg sacs (approximately a 2 week period) because this is a time when females will not release the egg sac to attack and consume food items. Low food availability consisted of one weekly feeding of 1 house cricket (*Acheta domesticus*) weighing 50-75% of the spider's body mass, whereas high food availability consisted of 3 feedings per week of a cricket weighing 50-75% of the spider's body mass. Crickets were dropped upon the water surface in female containers. To minimize stressing the spiders, no cricket was offered if the previous food item had not been consumed.

Mating trials

Fourteen days into adulthood virgin females were paired in their respective containers with a randomly selected male spider and observed directly for a period of 2 hours, or until mating had taken place. Males not displaying the typical leg waving and tapping courtship behaviors were replaced after 30 minutes. I scored reaction to male courtship (i.e. attack or mate), whether an attack resulted in a successful kill, and the number of palpal insertions achieved by the male. Females failing to mate were paired with a different male one week later.

Mated females that had not yet produced an egg sac were paired one week later with a new male. Upon producing an egg sac females were left alone until the egg sac hatched. Two days after a hatching the nursery web was cut out of the female's container and all spiderlings were counted. Females that produced egg sacs that failed to hatch were not included in fecundity analyses.

Statistical analyses

Statistical tests were performed with SAS (1988). The effects of juvenile and adult food availability on fecundity were analyzed via two-way analysis of variance. Likelihood of sexual cannibalism was analyzed with binary logistic regressions for continuous variables (male size and date) and analysis of maximum likelihood for the discrete variable female feeding regime. A four category G-test for goodness of fit was performed to examine the effect of mating status (virgin, non-virgin) on the likelihood of sexual cannibalism. In this test the observed frequency of attack tactics was compared to an expected frequency derived from an estimate of the overall probability of pre-copulatory attack irrespective of female mating status.

Results

Food regimes and fecundity

Table 4.1 summarizes the effects of food regimes on juvenile growth, fixed adult size and fecundity. In accordance with the suggestion that juvenile feeding influences growth rate and development, low-food immature females pooled across adult diets ($n=27$) spent 21.5 days on their juvenile diets before molting into adults, while their high-food counterparts ($n=26$) matured after only 16.1 days. This difference in development rate is statistically significant (t-test with unequal variances: $t=2.10$, d.f.$= 41.2$, $p=0.04$). Despite being on their juvenile diets for a shorter period of time, high-food juveniles matured at significantly larger fixed adult body sizes than low-food juveniles ($t=2.11$, d.f.$=51$, $p=0.04$).

There was no significant effect of diet manipulation on the probability that a female would have an egg sac hatch (juvenile food effect: $\chi^2=0.97$, d.f.$=1$, $p=0.32$, adult food effect: $\chi^2=2.02$, d.f.$=1$, $p=0.15$). However, as predicted by the aggressive-spillover hypothesis, a two-factor analysis of variance showed that high juvenile food availability had a statistically significant positive effect on the number of spiderlings produced in a female's first egg sac ($F= 4.44$, d.f.$=1,26$, $p=0.04$). Adult food availability also showed a trend towards a positive effect on

the number of spiderlings produced in the first egg sac, but this effect was not statistically significant ($F=3.27$, d.f.=1,26, $p=0.08$). However, a similar analysis performed on a data set which excluded one outlying, well-fed juvenile that produced over one-thousand offspring showed a reversal of this pattern with adult food being statistically significant ($F=5.51$, d.f.=1,25, $p=0.03$), and juvenile food being marginally non-significant ($F=3.60$, d.f.=1,25, $p=0.07$). There was no interaction between food regimes on the number of spiderlings produced.

To further examine the relationship between juvenile food availability, fixed adult size and fecundity I performed an analysis of covariance with fixed adult size as the covariate. The model showed that fixed adult size was positively related to fecundity ($F=6.07$, d.f.=1,24, $p=0.02$), but that beyond this size effect, there was no additional effect of juvenile food regime on fecundity ($F=2.13$, d.f.=1,24, $p=0.16$). Interestingly, when fixed adult size is controlled, the effect of adult feeding on fecundity becomes statistically significant ($F=4.61$, d.f.=1,24, $p=0.04$).

Neither juvenile nor adult food availability affected the probability of hatching a second egg sac (hatching success ranged between 64 and 75 % across treatments). However, two-factor analysis of variance showed that the number of offspring in a second egg sac was significantly increased by high adult food availability ($F=20.63$, d.f.=1,17, $p=0.0003$), but not by high juvenile food availability ($F=1.72$, d.f.=1,17, $p=0.21$).

Palpal insertions and fertilization success

Arnqvist & Henriksson's (1997) sole finding that supported the adaptive foraging hypothesis was a significant rank correlation between the number of palpal insertions received by the female (0, 1, or 2) and the fertilization success of her first egg sac. In the current study, analysis of covariance controlling for fixed adult size showed a significant effect of the number of palpal insertions on spiderling production ($F=12.33$, d.f.=2,49, $p=0.0001$). However, individual contrasts showed this effect to be solely the result of females receiving no insertions producing no offspring. Females accepting a single insertion ($n=26$) produced on average 432 offspring in their first egg sac, whereas females with multiple insertions ($n=10$) produced 333 offspring ($t=0.75$, d.f.=34, $p=0.46$).

Likelihood of sexual cannibalism

With regard to sexual cannibalism, females have three behavioral options: 1) attack before mating, 2) accept one insertion then attack, and 3) accept two insertions then attack. Thus, results will be presented for the likelihood of pre-copulatory attacks confined to each female's first virgin pairing (option 1, $n=52$), and for the likelihood of post-copulatory attacks confined to each female's first pairing which resulted in a mating (option 2, $n=36$). Few females accepted 2 insertions from the same male, and none of these females attacked after a second insertion (option 3). Overall, option 1 occurred 11/52 times (21%) and option 2 occurred 19/36 times (53%).

Likelihood statistics are summarized in Tables 4.2 and 4.3. Binary logistic regressions showed that the likelihood of virgin female attack (pre or post-copulatory) was not affected by male size or time during the breeding season (an indirect indicator of male availability). Interestingly, a similar analysis on male size showed that large males tended to escape pre-copulatory attacks more often than small males ($\chi^2=3.66$, $n=50$, d.f.$=1$, $p=0.06$). However, females did not preferentially mate with large males ($\chi^2=2.15$, $n=36$, d.f.$=1$, $p=0.14$). Analysis of maximum likelihood showed no significant effect of either juvenile or adult feeding regimes on the likelihood of pre-copulatory or post-copulatory attacks. However, when pre and post-copulatory attacks were combined, poorly–fed adults did attack their mates more often than well-fed adults ($\chi^2=5.23$, $n=52$, d.f.$=1$, $p=0.02$). Contrary to the aggressive-spillover hypothesis, fixed female size was not positively related to the likelihood of pre-copulatory attack within each juvenile diet regime (low-food juveniles: $\chi^2=0.47$, $n=24$, d.f.$=1$, $p=0.49$; high-food juveniles: $\chi^2=1.52$, $n=25$, d.f.$=1$, $p=0.22$).

A four class *G*-test for goodness of fit (see Table 4.3) showed that females employ the tactic of not attacking as a virgin but attacking as a non-virgin (tactic #3) more often than can be explained by the expected frequency given an overall, experiment-wide attack probability of 29% ($G = 6.07$, d.f.$=2$, $.025<p<.05$). No females switched post-copulatory tactics between their virgin mating and their first non-virgin mating, thus precluding an evaluation of the likelihood of post-copulatory attacks given a female's mating history.

Costs and benefits of sexual cannibalism

Twenty-eight percent of females (15/53) failed to accept a palpal insertion despite multiple mating opportunities and thus remained unmated throughout the experiment. However, this 'cost' of remaining unmated cannot be attributed to sexual cannibalism in the present experiment as only 20% (3/15) of these unmated females behaved aggressively towards their potential mates. In fact, females accepting at least one insertion during the experiment were marginally more likely to attack a mate (17/38, 45%) than were the 15 females who remained unmated ($\chi^2=3.68$, d.f.=1, $p=0.06$).

Cannibalizing at least one male significantly increased the probability of having an egg sac hatch (1st egg sac: $\chi^2=8.09$, d.f.=1, $p=0.004$; 2nd egg sac: $\chi^2=4.31$, d.f.=1, $p=0.04$). However, amongst females that hatched an egg sac, analysis of covariance controlling for fixed adult size ($F=4.10$, d.f.=1,27, $p=0.05$), showed that females that killed and consumed at least one male did not produce more offspring than females that failed to cannibalize a male (1st egg sac: $F=0.02$, d.f.=1,27, $p=0.87$; 2nd egg sac: $F=0.06$, d.f.=1,19, $p=0.81$).

<u>Discussion</u>

The aggressive-spillover hypothesis assumes that selection acting upon juvenile voracity favors high juvenile feeding rates and results in larger fixed adult body size and ultimately increased fecundity. Because the spillover hypothesis contends that pre-copulatory sexual cannibalism is a carry-over effect, it suggests that the likelihood of sexual cannibalism is predicted by an individual female's overall level of aggression rather than any adaptive benefit of male consumption per se. In contrast, the foraging hypothesis rests upon the assumption that adult feeding translates into fecundity benefits, as well as the prediction that females treat courting males according to their relative value as a sperm donor versus food item. Finally, the hypotheses differ in that the adaptive foraging explanation predicts benefits to sexual cannibalism, while the spillover hypothesis can explain apparently overzealous, maladaptive sexual cannibalism if benefits to the aggressive syndrome outweigh this potential cost to female fitness.

Food availability and fecundity

In support of the aggressive-spillover hypothesis, high juvenile food availability had several beneficial effects. First, well-fed juveniles matured faster than poorly-fed juveniles. Thus, juveniles securing the most food may accrue a multitude of benefits inherent in early maturation (e.g. increased mate availability, reduced predation risk, broadening of diet, more time to produce multiple egg sacs). Further work will be required to determine if these subtleties offer early-maturing females a selective advantage.

High juvenile food availability also resulted in females of significantly larger fixed adult body size. This difference in fixed size accounted for a significant amount of the variation in fecundity attributable to juvenile food regimes. Thus, relatively modest increases in cephalothorax area can yield substantial increases in fecundity. While other works have noted a strong relationship between fixed size and fecundity in *Dolomedes* (Spence et al. 1996; Arnqvist & Henriksson 1997), this is the first study on fishing spiders to manipulate juvenile food availability, thus documenting the link between juvenile food, fixed size and fecundity.

It should be noted that these juvenile food effects on development time, fixed adult size, and fecundity were all produced in the present study by manipulating only the latter three weeks of the juvenile life cycle (1-2 molts). In natural populations, juvenile *D. triton* typically experience a two-year life cycle and are thought to go through 10-12 molts before adulthood (Carico 1973; Foelix 1982). Variation in juvenile food availability for the entire juvenile period should potentially yield even larger fecundity differences. Perhaps the most intriguing and persistent mechanism by which juvenile fishing spiders would consistently vary in their access to food is heritable variation in voracity. This is, of course, a key assumption underlying the aggressive-spillover hypothesis: voracious juveniles secure more food items (Hedrick & Riechert 1989; Uetz 1992), grow to larger fixed adult body sizes, and produce more offspring than their less voracious counterparts. Intense fecundity selection on juvenile voracity, particularly with no selection for juveniles to discriminate conspecifics from heterospecifics, could overwhelm any cost of indiscriminant aggression at mating and explain the maintenance of pre-copulatory sexual cannibalism.

In support of the adult foraging hypothesis, a high adult food regime yielded fecundity benefits, a finding in conflict with other recent works (Spence et al. 1996; Arnqvist & Henriksson 1997). Thus, both juvenile and adult food availability seem to impact fecundity in

this study, whereas their interaction did not affect fecundity. Spence et al. (1996) addressed the relative importance of fixed adult size and adult food availability to fecundity. They describe an interaction between fixed size and adult food availability for a Northern population of *D. triton* in which females of large fixed adult body size can only realize the fecundity benefits of their large size under conditions of high adult food abundance. Under experimental conditions of adult food limitation, a situation not naturally found in the field during the two years of their study, females were unable to translate fixed adult size into fecundity benefits. The present data (see Table 4.1) support their finding that fecundity in well-fed adults is determined by fixed adult size. However, in the present study, low-food adults also had their fecundity determined primarily by differences in juvenile food availability and fixed size. While these two studies differ in the magnitude of importance they place on juvenile food availability to fecundity, the recurring theme is that both juvenile and adult food appear to be important factors which ultimately determine fecundity.

In sum, the fecundity results presented here support the contention that intense fecundity selection acts on juvenile female fishing spiders to secure prey items and maximize fixed adult body size. That said, adult food availability clearly plays a significant role in determining fecundity through its effects on offspring number, in particular its effect on fecundity via offspring number in second egg sacs. It may be naive to expect food availability in one life-history phase to determine fecundity at the expense of the importance of food availability during other life-history phases. While statistical significance fluctuated given the specific test being done, at all times both modes of food availability explained a substantial amount of variation in fecundity.

It should be noted that the aggressive-spillover hypothesis does not require that adult food availability have no effect on fecundity. In fact, a broader interpretation of the spillover hypothesis would suggest that fecundity benefits derived from juvenile voracity and adult voracity towards hetero-specific prey combine to outweigh the costs of sexual cannibalism. Regardless, as long as the fecundity benefits of voracity (juvenile or adult) outside of the mating context are large enough to outweigh any cost of the spillover of aggression to the mating female, the spillover hypothesis remains a viable explanation for aggression towards courting males.

Sperm limitation

Fertilization success was not measured in the present study, therefore there is no way of knowing how many more offspring females could have produced if they had accepted more palpal insertions. Nonetheless, evidence of sperm limitation was lacking in the present experiment. Females accepting multiple insertions realized no fitness benefits above and beyond that achieved by females accepting a single insertion. The adaptive foraging hypothesis' assumption of a direct relationship between number of insertions and fertilization success is primarily a quantitative tool which allows the model to estimate expected reproductive output for females making decisions as to whether they should mate or cannibalize. Relaxation of this assumption strengthens the prediction of heightened sexually cannibalistic tendencies in mated females, but does not change any of the model's other qualitative predictions (see Figure 2 in Newman & Elgar 1991). If a single insertion typically provides a female with enough sperm for her lifetime (Jackson 1980; Foelix 1983), then mated females should value all future suitors, including their first mate attempting to achieve a second palpal insertion, as food more so than as mates. Indeed, this is one of the trends seen in the present study (see below).

It should be noted that Newman & Elgar's (1991) adaptive foraging hypothesis for sexual cannibalism is strictly a material benefits model which attempts to explain female mating decisions (i.e. attack or mate) based on the premium females place on males as sperm-donors or as food items. However, females may accept multiple mates for reasons other than attempts to maximize fertilization success. For example, much recent work addresses the hypothesis that females accept multiple mates, and thereby receive more sperm than they need to fertilize all of their available eggs, thus promoting sperm competition between males and cryptically choosing only the most competitive gametes (Eberhard 1998).

Likelihood of sexual cannibalism

Increasing male size and date (male availability) failed to enhance the probability of pre-copulatory or post-copulatory attacks. In line with Arnqvist & Henrikkson (1997), these data provide further evidence against the adaptive foraging hypothesis. There are several reasons one might not expect females to selectively attack large males despite the fact that they presumably represent the greatest nutritional reward. First, large males are better at escaping female attacks (present study; Arnqvist 1992; Arnqvist & Henrikkson 1997). Thus, females may avoid

81

attacking large males because they will incur greater resistance from such a male, and/or because females may expend more energy subduing a large male. Second, females may actively prefer to mate with large males in order to secure the indirect benefit of large body size for their offspring. However, no female mating preference for large males was noted in the present experiment. The latter suggestion, that females use pre-copulatory attacks/passivity as a drastic form of mate refusal/acceptance, is an often cited possibility which has rarely been tested experimentally (Elgar & Nash 1988; Elgar 1992). Finally, as suggested by the aggressive-spillover hypothesis and as seen in the current study, females may react aggressively to males regardless of their size, and only large males survive these attacks.

Note that all three of these explanations for female aggression at mating result in directional selection on male body size; however, they make very different assumptions about female discriminatory abilities. The first two alternatives predict 'active' preferences for cannibalizing small males and for mating with large males respectively, while the third suggests no aggressive discrimination on the part of the female. A parallel dichotomy exists in the modern day study of mate choice with the distinction some behaviorists draw between 'active mate choice' typified by adaptive female preferences for males of a certain phenotype, and indirect mechanisms of inter-sexual selection (Andersson 1994; Wiley & Poston 1996). The lack of evidence for adaptive female mating preferences for large males, combined with the lack of discrimination females show in choosing who they attack, support an indirect mechanism of inter-sexual selection characterized by stereotypically high levels of aggression regardless of male size, and a large male superiority in escaping female attacks.

If females make aggressive 'decisions' based on male material value (food or sperm), then as the season progresses and male availability declines, a virgin female should increasingly view a courting male as a mate, regardless of her nutrient load. However, no evidence of a seasonal decline in aggressive attacks was apparent in the present study. In nature females may routinely encounter enough males early in the breeding season that the risk of progressing unmated into a time of the breeding season when males are limiting might be unrealistic. Unfortunately, little is known about the number of courting males that females may have to choose from in nature. It is known, however, that sex ratios at the beginning of the season may vary a great deal. Zimmerman & Spence (1992) documented a 1:1 sex ratio in 1986 followed by 2:1 sex ratio biassed in favor of males in 1987. Thus, the limited available data suggest that

males may be quite abundant at times, and may not represent a limiting resource to females early in the season. Note that this line of thinking should remove the cost of aggression noted experimentally by Arnqvist & Henrikkson (1997). If males are abundant during the period soon after females reach sexual maturity, then regardless of their aggressive behavior females may never run the risk of remaining incompletely fertilized. In opposition to this suggestion is the finding of females in the field with incompletely fertilized egg sacs (Arnqvist & Henrikkson 1997). To document whether or not females in nature are, in fact, running a high risk of remaining incompletely fertilized by behaving aggressively towards potential mates, future empirical and theoretical work should focus on the temporal patterns of male abundance and female aggression towards males through the breeding season.

Perhaps the most intuitive prediction of the adaptive foraging hypothesis is that if females cannibalize potential mates as an adaptive foraging strategy, then attacks should be more prevalent for food-limited females. However, surprisingly few studies have shown a positive relationship between female hunger levels and the likelihood of sexual cannibalism in arachnids (e.g. Jackson 1980; Breene & Sweet 1985; Elgar & Nash 1988; Arnqvist & Henrikkson 1997; but see Andrade 1998). Similarly, in the present study, no effect of diet regime was found on the prevalence of pre or post-copulatory attacks individually. However, poorly-fed females did attack more often than well-fed females when pre and post-copulatory attacks were combined. Thus, the prediction of the adaptive foraging hypothesis is supported if both types of sexual cannibalism are included. It would seem reasonable that if sexual cannibalism is an adaptive foraging strategy it could include attacks before and after sperm transfer. Nonetheless, consistent with the spillover hypothesis' suggestion that females attack courting males indiscriminately, females do not appear to modulate their pre-copulatory aggressive behavior according to their hunger level.

The adaptive foraging hypothesis asserts that females should use their own mating status (sperm needs) as a factor in determining whether they will eat, mate, or mate and eat a male. The current study provides two pieces of support for this idea. First, attacks after an insertion occurred more than 50% of the time, whereas attacks before an insertion occurred only 21% of the time. Thus, females seem much more likely to attack a male after they have obtained sperm. Second, the observed prevalence of the tactic of not attacking as a virgin but attacking as a non-virgin exceeded that which is predicted by a distribution derived from the overall attack

prevalence regardless of mating status. Thus, female mating status seems to be an excellent predictor of the likelihood of sexual cannibalism.

Finally, the aggressive spillover hypothesis predicts that the likelihood of attack is a function of a female's overall level of voracity, and thus is predicted by her fixed size rather than any indicator of male adaptive value. The current study offers little to test this idea because juvenile voracity was not measured and variation in fixed size was artificially enhanced via variable juvenile food regimes. However, within juvenile food regimes no correlation was found between fixed size and the likelihood of sexually cannibalistic attack. Studies currently in progress will more adequately address this crucial assumption of the spillover hypothesis, namely that the most voracious juveniles will also be the adults that are most likely to attack their mates.

Costs and benefits of sexual cannibalism

The aggressive-spillover hypothesis posits no net benefit to male consumption, but instead stresses that benefits of aggression in other contexts must outweigh the cost of eating rather than mating with males. Laboratory studies such as this one might overestimate the cost of cannibalism by providing females with artificially low numbers of potential mates, thus increasing the chances a female will remain incompletely fertilized. Despite this fact, in the present study, no evidence was found that aggression towards mates was responsible for females remaining unmated or incompletely fertilized. Future field surveys of egg sac fertilization rates, along with experimental manipulations of male availability, should allow a better approximation of the costs of aggression to female fertilization rates. Such experiments will also evaluate the intriguing possible trade-off between the benefits of juvenile voracity in terms of large adult size (measured as the number of eggs manufactured) versus the costs of this aggressive syndrome to the adult female (measured as the number of unfertilized eggs / number of eggs manufactured).

In contrast, the adaptive foraging hypothesis requires that sexual cannibalism have adaptive benefits. In the present study male consumption was not responsible for the production of more offspring. In fact, few studies have shown such a quantitative benefit of sexual cannibalism or less extreme courtship food gifts (but see Andrade 1996). While eating a male did not yield more offspring, it did increase the probability that a female would hatch an egg sac. Thus, males may represent an important qualitative addition to the female's diet. First, studies of

nutritional ecology have shown that arachnids require a breadth of amino acids to maximize reproduction (Riechert & Harp 1987), and that some species will exhibit prey selectivity in order to optimize the diversity of amino acids in their diet (Greenstone 1979). Second, males may be qualitatively important prey items if they are more efficiently converted to energy than other prey items (Elgar & Nash 1988). Finally, post-mating feeding in spiders is known to be associated with the onset of the accumulation of larger egg yolk granules (Foelix 1982). Accordingly, males may represent adaptive foraging to females not in terms of the crude mass they offer, but instead as a source of nutrient diversity, which is most efficiently converted to energy, and is available at a crucial time in egg development.

The original inspiration for the aggressive-spillover hypothesis was Gould's (1984) suggestion that sexual cannibalism is maintained simply because generally aggressive females mistake the identity of courting males and attack them. Following Arnqvist & Henrikkson's (1997) suggestion that selection for a syndrome of aggression could explain apparently costly levels of aggression towards mates, I have presented data which support and link assumptions two and three of the spillover hypothesis: increasing juvenile food availability positively affects fixed adult size which, in turn, positively affects fecundity. Future work will standardize an assay of female aggressive tendencies to address the critical final assumption, that intra-individual, positive behavioral correlations in levels of aggression across contexts (juvenile voracity and adult aggression towards courting males) result in behaviorally constrained, pre-copulatory sexual cannibalism.

In conclusion, none of the evidence presented for or against either hypothesis mutually excludes the other hypothesis. For example, the trend for poorly-fed adult females to attack indiscriminately upon courtship, but to attack more often than their well-fed counterparts when post-insertion attacks are included, fits a hypothesis combining a spillover of genetically-constrained, pre-copulatory aggression with adaptive post-insertion aggression which corresponds to the predictions of the adaptive foraging hypothesis. Indeed, the optimal behavior for a hungry, virgin female is to mate and then feed on the male. Thus, the two hypotheses might explain sexual cannibalism at different stages of the mating sequence. While the elaborate nature of male courtship in fishing spiders (Carico 1973; Bleckman & Bender 1987; Bleckman & Lotz 1987) suggests that male signals are finely tuned to female sensory biases, it remains a possibility that pre-copulatory attacks may result from female aggressive tendencies, which are

favored outside of the mating context, overwhelming their discriminatory capacities. Subsequent to that, following successful insertions, females may cannibalize mates according to the predictions of the adaptive foraging model. Inter-populational and/or inter-specific variation in factors such as juvenile and/or adult food limitation may alter the relative importance of each hypothesis. For example, severe food limitation in the juvenile phase may accentuate benefits of juvenile voracity thus moderating the cost/benefit ratio of aggressive spillover. In contrast, food limitation during the adult phase should coincide with increases in sexual cannibalism according to the predictions of the adaptive foraging hypothesis. Sequential components of a complex behavioral continuum such as sexual cannibalism need not have the same mechanistic or evolutionary explanation.

Table 4.1   Least square means ± standard error (n) for four diet regimes. Food contrasts indicate support for both the adaptive foraging and aggressive-spillover hypotheses.

Diet Regime		Days on juvenile diet	Fixed adult size (mm^2)	Number of spiderlings
Juvenile	Adult			
Low	Low	20.40 ± 2.26 (15)	37.24 ± 2.00 (15)	386.00 ± 67.80 (9)
Low	High	22.92 ± 2.22 (12)	41.09 ± 2.20 (12)	539.71 ± 76.90 (7)
High	Low	17.07 ± 1.26 (14)	43.32 ± 2.10 (14)	562.67 ± 67.80 (9)
High	High	14.92 ± 1.30 (12)	43.41 ± 2.10 (12)	685.60 ± 91.00 (5)

Table 4.2   Likelihood of a sexually cannibalistic attack given variables predicted to be important by the adaptive foraging model.

Variable	Pre-copulatory attack			Post-copulatory attack		
	χ^2	*n*	*p*-value	χ^2	*n*	*p*-value
Male size	0.006	50	0.930	0.560	36	0.460
Date (male availability)	0.040	52	0.830	0.210	36	0.650
Female feeding regime (Juvenile food effect)	0.090	52	0.760	0.020	36	0.880
Female feeding regime (Adult food effect)	1.750	52	0.190	1.250	36	0.260

Table 4.3   The adaptive foraging tactic (# 3) is employed by females more often than can be explained by the expected frequency distribution given an estimated experiment-wide 29% probability of attack.

Tactic	Virgin	Non-virgin	Expected	Observed
1	Attack	Attack	1.76	1
2	Attack	No attack	4.32	2
3	**No attack**	**Attack**	**4.32**	**9**
4	No attack	No attack	10.59	9
	Total		21	21

CHAPTER 5

Pre-copulatory sexual cannibalism in fishing spiders (*Dolomedes triton*):

does male-female cohabitation influence female use of males as food versus sperm?

<u>Summary</u>

Pre-copulatory sexual cannibalism (pre-SC), or predation of a potential mate prior to sperm transfer, showcases an extreme inter-sexual conflict. Unlike sexual cannibalism occurring after mating, pre-SC cannot be construed as a male strategy. Thus, research on the adaptive significance of pre-SC has focused on female benefits. Here I test the idea that pre-SC represents an adaptive female trade-off between the material costs and benefits of mating with a male (foregoing food, securing sperm) and preying on a male (foregoing sperm, securing food). I pay particular attention to the rarely tested prediction that pre-SC should increase as a female's expectation of mating opportunities increases. I use the phenomenon of cohabitation between adult males and penultimate females as a means to increase female experience of mate availability. Results indicate that pre-reproductive cohabitation with mature males heightens the prevalence of pre-SC. This result has several important implications for the study of pre-SC. First, many previous studies may have incorrectly rejected the trade-off hypothesis because they focused exclusively on one side of the tradeoff – the potential foraging benefits of pre-SC. Future tests of this idea need to simultaneously manipulate both food availability and mate availability. Second, most experimental studies of pre-SC use adult females that were collected as juveniles and isolated during their penultimate molt. Such protocols may inadvertently provide females with experiences of artificially low mate availability. Thus these studies may have significantly underestimated the prevalence of pre-SC that occurs in the field under natural conditions of male-female cohabitation and interaction.

Introduction

The trade-off between foraging behavior and predation risk has been a core idea in the development of behavioral ecology (Krebs & Davies, 1991). More recently, studies have begun to include mating decisions into an integrative optimality approach to animal behavior (Rowe et al., 1994; Jackson & Pollard, 1997). Thus, understanding the manner in which an animal juggles these three requirements, foraging, mating and avoiding predation, is a central goal of modern behavioral ecology.

Pre-copulatory sexual cannibalism (pre-SC), or predation of a potential mate prior to sperm transfer, provides an ideal model system for this integrative approach. Pre-SC has been documented in several species of insects and arachnids, and has been noted as a frequent occurrence in at least two arachnid families: Pisauridae and Araneidae (Elgar, 1992). In systems characterized by pre-SC, the distinction between mating, foraging and anti-predator behaviors is blurred as males are forced to solicit copulations from potential predators and females have the option of mating with a male or instead trying to feed upon him. Thus, pre-SC showcases an extreme case of conflict between the sexes that, unlike sexual cannibalism that occurs following sperm transfer, cannot be construed as a male mating strategy (e.g. Andrade, 1996).

Pre-SC may also be costly for females. The cost of attacking a potential mate may be particularly high for virgin females in terms of lost mating opportunities. As a result, research on the adaptive significance of pre-SC has focused on female benefits that could outweigh such costs. Here I focus on the material costs and benefits to females of pre-SC. Specifically, I examine the material goods trade-off for females between mating with a male (foregoing food, securing sperm) and preying on a male (foregoing sperm, securing food).

The material benefits trade-off hypothesis for pre-SC was suggested by the finding that females of the orb-web spider *Araneus diadematus* that consumed a single male added significantly to their body weight and presumably to their fecundity (Elgar & Nash, 1988). Perhaps because this seminal finding addressed only the benefit of foraging on a male, the hypothesis has since been referred to as 'feeding opportunism' (Andrade, 1998), and 'adaptive foraging' (Schneider & Elgar, 2002; Chapter 4). However, these names do not do justice to the complete hypothesis (Newman & Elgar, 1991). In its entirety, this hypothesis is an economic model intended to determine whether potential costs to the virgin female associated with pre-SC

(i.e. lost mating opportunities) could be outweighed by material benefits (i.e. enhanced fecundity) accrued through the consumption of a male.

The trade-off hypothesis suggests that females economically weigh a courting male's marginal value as a mate versus his value as a food item, and respond accordingly with the adaptive behavior (attack or mate) that maximizes female fitness. The model thus suggests that the two most important factors in determining the prevalence of pre-SC are the degree to which other, non-male food sources are available to females (i.e. the intensity of food limitation), and the number of males that a female can expect to encounter throughout the breeding season (i.e. the intensity of sperm limitation). As such, the model assumes that (1) feeding on a male should enhance fecundity, and (2) mating with a male should enhance fertility. Given these assumptions, the model predicts that the likelihood of pre-copulatory attacks should (a) increase with decreasing food availability, (b) increase as unpredictability in food availability increases, (c) increase as male size increases (large males presumably representing a greater nutritional reward than small males), (d) increase for non-virgin females relative to virgins, and (e) decrease for virgin females as the breeding season progresses and male availability declines.

Two features of the current state of this hypothesis are noteworthy. First, this intuitive, resource optimization idea has met with very little support (reviewed in Arnqvist & Henrikkson, 1997). The fecundity benefit from feeding on a male, shown originally in *A. diadematus,* has not been replicated in any other spider species. Perhaps this should not be surprising given that male spiders are often very small prey items for the larger female (Elgar, 1991). However, one recent study suggested that feeding on a male may commonly have more subtle effects on offspring fitness (e.g. increased hatching success, and/or offspring vigor) rather than the traditionally studied possibilities such as increases in egg sac mass or offspring number (see Chapter 4). In addition, and perhaps even more damning against an optimal foraging explanation for pre-SC is that female hunger level rarely explains the prevalence of attacks. An optimal foraging explanation for pre-SC seems unlikely if attacks are not based on hunger and male consumption provides no material benefit (Arnqvist & Henrikkson, 1997).

Second, almost all tests of the trade-off hypothesis have been limited to the foraging side of the hypothesis. While occasional reference is made to the prediction that pre-SC should be more frequent in mated females relative to sperm-limited, virgin females (Wojcicki, 1992; see Chapter 4), such tests are confounded by differences in mating motivation between virgins and

non-virgins. These comparisons fail to test the crucial prediction that among virgin females, pre-SC should be more frequent when females 'perceive' males as abundant, and less frequent when males are 'perceived' as limiting.

A key issue for conducting naturally relevant tests of the effects of variation in male availability on pre-SC is: how might virgin females estimate the availability of males? Under what natural conditions would we expect some females to perceive male availability to be low, while others perceive it to be high? One way in which virgin females could experience differences in male availability well before mating/pre-SC decisions are being made stems from the fact that in many protandrous spider species adult males are known to cohabit with penultimate-stage females (Carico, 1973). This phenomenon is frequently associated with the male strategy to copulate with a female during her final molt, a time when females are especially vulnerable and unlikely to behave aggressively towards a male. However, opportunistic copulations such as these are rarely quantified and cohabitation between mature males and pre-reproductive females may instead provide a means by which females assess mate availability as high enough to make pre-SC a risk-free foraging strategy. Below I present a direct test of this prediction by manipulating female cohabitation experience through their penultimate molt and subsequently measuring each adult female's propensity for pre-SC. In addition, I also report correlational evidence pertaining to other expectations of the foraging/mating trade-off hypothesis.

Study system

Here I use the sexually cannibalistic North American fishing spider *Dolomedes triton* (Araneae; Pisauridae) as my study organism. Fishing spiders are relatively large, cursorial ambush predators most commonly associated with the edges of aquatic habitat (Carico, 1973). Fishing spiders detect water-borne prey vibrations using sensory receptors located in their forelegs (Bleckmann & Barth, 1984). Prey items are most commonly insects trapped at the water surface (Carico, 1973; Barth, 1982; Zimmerman & Spence, 1989) however, fishing spiders derive their name from their ability, albeit infrequent, to attack, subdue and consume aquatic vertebrate prey (e.g. fish, frogs, salamanders) that are often significantly larger than the attacking spider (Bleckmann & Lotz, 1987; personal observation).

The *Dolomedes* mating sequence is initiated when a searching male encounters pheromonal cues from female silken drag lines (Carico, 1973; Arnqvist, 1992). Males then proceed with a stereotypic courtship sequence of leg waving and a slow regular tapping of the water surface or solid substrate. If not immediately attacked, males proceed cautiously, following the female's drag lines and approaching the female while continuing courtship. Males typically mount the dorsum of the female from behind and turn to face the opposite direction of the female. The male then leans sideways, usually between the female's legs II and III, and reaches to insert a single pedipalp charged with sperm into the female's epigynum, a paired structure located at the ventral junction between the cephalothorax and abdomen. Sperm transfer takes only a few seconds after which the male jumps off and retreats. This entire courtship sequence is sometimes repeated allowing successful males to copulate a second time.

Adult female fishing spiders commonly attack males at any point during this copulatory sequence. However, laboratory mating trials indicate that females of the European fishing spider (*D. fimbriatus*) most frequently attack during pre-copulatory courtship (75% of trials), and that males are killed in approximately 5-10 % of these attacks (Arnqvist, 1992; Arnqvist & Henrikkson, 1997). For *D. triton*, laboratory mating trials showed that pre-copulatory attacks by virgin females occur in approximately 20% of pairings (see Chapter 4). In addition, field studies of *D. triton* suggest that males represent a common contribution to the adult female diet (Zimmerman & Spence, 1989), and that male population density declines drastically, soon after adult female emergence (Zimmerman & Spence, 1992). Thus, sexual cannibalism appears to play an important role in the ecology of *Dolomedes*.

Mature *D. triton* males, like males of many protandrous spider species, are often found cohabiting with penultimate-stage females. In fact, it is not uncommon to find 2-3 males in close proximity to an immature female (Johnson, personal observation). Male-female cohabitation is often associated with the male tactic to seize the female's final moult as an opportunity to mate at a point whne females are defenseless and unable to attack a suitor. However, this male tactic is rarely quantified, so it remains unclear what function male-femaale cohabitation serves.

Methods

The male availability side of the trade-off hypothesis was tested with an experimental manipulation of penultimate female exposure to mature males, whereas the food availability side

of the hypothesis was examined by monitoring the foraging success of females and correlating that with their propensity to attack courting males. Juvenile spiders (N= ~100 penultimate-stage males 1-2 weeks from adulthood and N= ~80 ante-penultimate-stage females approximately 3-6 weeks from adulthood) were collected from a large pond (~ 60 m^2) outside of Lexington, KY during the first week of April, 2002.

Upon collection all spiders were weighed to the nearest milligram and digitally imaged. Additional images were obtained following each spider's molt. Spiders were imaged while floating motionless in a cup of water. Image components (e.g. amount of water in the cup, distance of camera from spider etc.) were standardized and each day the imaging set-up was calibrated by imaging a piece of floating graph paper (2x2 cm). Images were later digitized (Sigma Scanpro) providing measures of the length and width of the cephalothorax. From these measures I calculated the area of the cephalothorax as the area of an ellipse (= π x [cephalothorax width/2] x [cephalothorax length/2]).

Experimental females (n=60) were maintained outdoors in individual, large (60 x 41x 16 cm.) plastic tubs. Containers were filled with filtered water to a depth of 2.0 cm. and each contained a large Styrofoam float (10 x 6.0 x 0.5 cm) and an inverted 20 oz. opaque, plastic cup. A rectangle (3 x 6 cm.) was cut out of the cup's side to allow the spider to use the cup as a refuge. Females were offered one adult house cricket (*Acheta domesticus*) 3 times weekly from the time of collection until the production of an egg sac (see below). Prey items were available for 30 minutes after which they were removed if not eaten. This level of food availability has been used previously (see Chapter 4) and is suitable to promote successful reproduction. Juvenile males were housed in individual transparent, plastic cups (425 ml.) each containing filtered water (100 ml.) and a Styrofoam float (2.0 x 1.5 x 0.5 cm.). Males were fed one 4-week old house cricket weekly.

The cohabitation manipulation began upon male maturation, approximately 10-20 days prior to female maturation. This manipulation involved the addition of a cohabitant (guest) to each relevant juvenile female's container for a minimum of 10 days. Each juvenile female (host) was housed with either a recently matured male (n=19), a much smaller juvenile female (n=20), or no guest at all (n=21). To prevent cannibalism of the guest by the host, guests were housed in their own 16 oz., transparent, plastic cup with the bottom cut out. Mesh sheets were fastened to both open ends of the cup with rubber bands and the cup was rested on its side partially

95

submerged in the host female's container. Thus, water-borne chemicals were continuously exchanged between host and guest but physical contact was prevented. In addition, every fifth day, hosts and guests swapped containers for 2 hours. This had the duel effect of (1) allowing hosts direct contact with their guest's physical environment (e.g. silken draglines left on the Styrofoam), and (2) allowing guests to leave silken draglines on the water and Styrofoam float of their host's container. It should be noted that, while direct physical contact was prevented, cohabitation frequently resulted in limited contact as the two spiders were often found clinging to opposite sides of the cup's mesh covering such that their legs touched. Females of the no-guest control group were housed with an empty cup. Guests were rotated every second day to another female's container within the same treatment group. In this way, females housed with males were exposed to a series of males ensuring that they experienced an environment indicative of a high abundance of potential mates.

Females were fed two days following their adult molt. Spanning adult days 4-7, females were paired with a sequence of four different males. Males were introduced as far from the female as possible. I then recorded the following variables: occurrence of and latency to male courtship, pre-copulatory attack/kill, or male mounting, palpal insertion, and post-copulatory attack. Egg sacs are produced ~ 7-10 days following a mating (Johnson, unpubl. data). Egg sacs, unfortunately, cannot be removed from the female's grasp without ripping the outer lining of the egg sac. As a result, I estimated the mass of the egg sac as the difference between the female's mass while clutching the egg sac one day following its production and the female's mass one day following her adult emergence. Egg sacs were considered to hatch successfully if live offspring emerged from them. The number of live spiderlings emerging from an egg sac was counted and used as a measure of fecundity. Because females and/or emerging spiderlings can consume unfertilized eggs, I did not have an estimate of the number of infertile eggs in hatched egg sacs. Because a subset of females produced second egg sacs, I performed separate fecundity analyses including and excluding offspring from second egg sacs.

Results

Foraging, pre-SC and fecundity

All tests reported are 1-tailed unless otherwise noted. Several measures of female reproductive success can be used to examine effects of female foraging on both hetero-specific

prey and con-specific males (pre-SC). Here I report the results of a series of three multiple linear regressions using mass of the egg sac, offspring number and the ratio of egg sac mass to offspring number as the dependent variables. Fixed adult size, female foraging success on hetero-specific prey, and female foraging success on con-specific males (pre-SC) were used as independent variables in all three of these equations. In addition, I report results from a logistic regression using hatching success of the egg sac as the categorical variable with the same three independent variables.

Fixed adult size, adult foraging success, and pre-SC kills explained a significant amount of variation in the mass of the female's first egg sac ($r=0.441$, $F_{3,46}=3.69$, $p=0.018$). Table 5.1 demonstrates that of these three independent variables, pre-SC kills had the most dramatic impact on the mass of the egg sac, whereas adult feeding on crickets had no significant effect on egg sac mass. While offspring number in the first egg sac was significantly related to the model ($r=0.513$, $F_{3,28}=3.33$, $p=0.034$), offspring number in egg sacs 1 and 2 combined did not show such a relationship ($r=0.378$, $F_{3,28}=1.56$, $p=0.221$). This distinction arose from the fact that fixed adult size has a significant positive relationship with offspring number in egg sac 1, but this effect is much weaker when offspring number from egg sac 2 are included. Notably absent from either analysis on offspring number was an effect of adult feeding on hetero-specific prey or con-specific males (see Table 5.1). The ratio of the mass of egg sac 1 to the number of offspring in that egg sac was also significantly predicted by this combination of model parameters ($r=0.497$, $F_{3,28}=3.07$, $p=0.044$). Fixed adult size was significantly negatively related to this ratio, pre-SC kills were significantly positively related to this ratio, and adult feeding on hetero-specifics had no significant relationship with this ratio (Table 5.1). Finally, logistic regression indicated that hatching success of the first egg sac was significantly predicted by these three variables ($\chi^2 = 16.73$, d.f.=3, $p=0.001$). Adult feeding on both crickets and con-specific males contributed to increased hatching success (Table 5.1).

Food effects on pre-SC

Contrary to the predictions of a foraging explanation for pre-SC, female attacks on males were not associated with a poor history of foraging success. Instead, pre-SC was most common amongst females with the highest foraging success ($r=0.418$, $t_{57}= 3.47$, $p=0.0005$). In addition, adult female condition (mass/cephalothorax area) at the time of a pairing was not negatively

related to the prevalence of female attacks, but was instead positively related to the prevalence of female attacks ($r=0.231$, $t_{57}=1.76$, $p=0.042$). Taken together these results suggest that pre-SC is most commonly practiced by females with a relatively successful recent history of foraging success rather than the females with the highest foraging requirements.

Mate abundance effects on pre-SC

While an ANOVA indicated that the cohabitation manipulation had a marginally non-significant effect on the prevalence of pre-SC by virgin females ($F_{2,57}=1.81$, $p=0.09$), pairwise contrasts indicated significantly higher rates of pre-SC in the male cohabitation treatment ($n=19$) relative to the other two groups ($t_{38.3}=1.963$, $p=0.029$). Surprisingly, attacks were more likely from virgin females relative to mated females. Using McNemar's test for significant changes of correlated proportions, females were significantly more likely to attack as a virgin but not as a non-virgin (32/54, 59%) than they were to attack as a non-virgin but not as a virgin (4/54, 7%; $G=24.54$, d.f.=1, $p<0.0001$). Finally, logistic regression showed no increase or decrease in attacks as the breeding season progressed ($\chi^2=0.231$, d.f.=1, $p=0.63$).

Discussion

This study addressed three aspects of the trade-off hypothesis for explaining variation in pre-SC: (1) the assumption that adult female foraging, and feeding on males specifically, increases female fecundity; (2) the prediction that hungrier females should be more likely to engage in pre-SC; and (3) the prediction that virgin females that have experienced a higher encounter rate with males should be more likely to engage in pre-SC. The results provided mixed support for (1), failed to support (2), and supported (3). I next discuss each of these results in more detail.

The use of multiple indicators of female reproductive success provided insight into how females may derive benefits of adult food (including pre-SC). Mass of the egg sac was significantly enhanced by adult female feeding on males but not feeding on crickets. This is a surprising result given that hetero-specific prey are often considerably heavier than adult males. Elgar & Nash (1988) suggested that foraging on a con-specific male may allow females to convert prey mass to energy more efficiently than foraging on hetero-specifics does. This

possibility could explain why pre-SC is correlated with increases in egg sac mass and foraging on crickets is not.

Interestingly, neither form of adult female foraging (on crickets or males) had any positive influence on offspring number, a result that appears to contradict the foraging side of the trade-off hypothesis (Arnqvist & Henrikkson, 1997 and references therein). Instead, fixed adult size, a morphological measure that indicates successful juvenile foraging and growth, was a strong predictor of offspring number (see also Chapter 4). Offspring number is almost certainly an important parameter of female reproductive success. However, it may not be feasible for females to increase the number of offspring in an egg sac via foraging that occurs following the adult molt. Studies that integrate behavioral questions such as these with reproductive physiology may shed some light on this question. For example, we need to know at what developmental point female egg number is set. If this occurs at a developmental stage prior to the adult molt, then expectations that adult female foraging and pre-SC should influence offspring number have been poorly informed.

Instead, adult female foraging, including pre-SC, appears to promote reproductive success in more subtle ways. First, pre-SC proved to increase the amount of egg sac mass devoted to each egg. This relationship did not hold for foraging on hetero-specifics. Egg size may play a large part in determining female reproductive success. Thus, it may be the case that the size of offspring produced is more important than the number of offspring produced. If this is the case, then offspring size should be included in future studies. Here, females that killed and ate more males significantly increased the ratio of egg sac mass to offspring number. One could argue that this ratio is the best indicator of female fitness, short of offspring vigor, because it reflects the amount of resource provided per offspring. *D. triton* offspring, like many spiderlings, rely exclusively on nutrients obtained from their egg yolk until they reach a size that permits them to subdue live prey items (Carico, 1973). The ratio of egg sac mass to offspring number is one possible indicator of the head start a female provides each of her offspring through egg mass provisioning.

In line with previous work on this species (see Chapter 4), adult foraging on both crickets and males increased the likelihood that a female's egg sac would hatch successfully. Taken together these results indicate that (1) juvenile foraging and the size at maturity significantly impact continuous measures of reproductive success, in particular, offspring number, (2) adult

foraging on hetero-specific prey has little influence on these continuous measures, and instead improves egg sac hatching success, and (3) pre-SC has several beneficial effects on reproductive success, but increased offspring number is not one of these. Future studies should continue to measure as many indicators of reproductive success as possible in an attempt to decipher where females derive foraging benefits and where they are lacking.

It should be noted, however, that correlating female foraging success/pre-SC with measures of reproductive success is not the ideal way in which to test these ideas. As has been pointed out recently in the literature (e.g. Schneider & Elgar, 2002), future studies hoping to show fecundity benefits of pre-SC need to separate the motivation to feed from the effect of feeding. In other words, we need to see the effect of pre-SC on reproductive success divorced from other factors that may be correlated with pre-SC such as overall female foraging voracity.

This experiment represents a third independent study of this population that fails to support the prediction that pre-SC attacks are motivated by adult foraging requirements. In addition, studies of other *D. triton* populations (Spence et al., 1996) a European congener (Arnqvist & Henrikkson, 1997) and a variety of other spider taxa (Jackson, 1980; Breene & Sweet, 1985; Elgar & Nash, 1988) have found similar results. Instead, in this study, pre-SC was practiced most often by females having experienced the highest adult foraging success, a result opposite to that expected if pre-SC serves female foraging requirements.

Perhaps the lack of an effect of foraging requirements on pre-SC is due to the fact that no study to date has looked at the interaction between foraging requirements and female expectations of sperm availability. This was, ironically, the essence of Newman & Elgar's original model. The present study indicates that pre-SC in virgin females is influenced by female experience of male availability through differences in cohabitation. This may be a frequent mechanism by which females assess whether pre-SC is a risk-free foraging strategy in their current environment. Past attempts to find a relationship between foraging requirements and pre-SC may have failed because variation in female 'expectations' of mate availability were masking an effect of female food requirements. Future tests need to simultaneously manipulate both food availability and female 'perception' of mate availability to complete a satisfactory test of this hypothesis.

Note that pre-SC attacks in this experiment were actually more prevalent from virgin females than from non-virgin females. This result does not coincide with the prediction that

attacks occur according to each female's need for sperm. Instead, this result may be strong evidence that virgin/non-virgin comparisons are misleading. While a material benefits, trade-off hypothesis, such as the one being tested here, predicts higher levels of pre-SC from non-virgins, this prediction assumes that the motivational state of virgins and non-virgins is identical. In fact, by virtue of being a mated female, non-virgins may have given up a considerable degree of control over their motivational state. The act of sperm transfer may set female physiological processes in motion (e.g. the further development of egg deposition) that curtails both foraging and mating motivation.

If female experiences of sperm limitation through pre-reproductive interactions with adult males do indeed affect rates of pre-SC, then past studies may have drastically underestimated the prevalence of pre-SC in nature.   Experimental studies of pre-SC routinely collect animals as penultimate juveniles and house them individually until maturity to ensure they are virgins when mating trials are conducted. One unfortunate by-product of this protocol is that it imposes an experience of artificially low mate availability on females across the board. The prevalence of pre-SC we see in experimental studies using such isolation protocols prior to mating trials may be a fraction of what would be observed if females had been allowed to mature under natural conditions of male-female cohabitation and interaction as they were in this experiment.

Table 5.1   The effects of fixed adult size, adult hetero-specific foraging success and pre-SC

kills on several measures of female reproductive success.

Egg sac mass, $n=50$	Standardized coefficient (r)		
		t	$P_{\text{1-tailed}}$
Fixed adult size	0.196	1.38	0.090
Adult hetero-specific foraging success	-0.009	-0.062	0.475
Pre-SC kills	**0.346**	**2.43**	**0.009**

Offspring number egg sac 1, $n=32$	Standardized coefficient (r)		
		t	$P_{\text{1-tailed}}$
Fixed adult size	**0.465**	**2.73**	**0.006**
Adult hetero-specific foraging success	0.032	0.185	0.427
Pre-SC kills	0.109	0.622	0.269

Offspring number egg sacs 1 + 2, $n=32$	Standardized coefficient (r)		
		t	$P_{\text{1-tailed}}$
Fixed adult size	**0.308**	**1.68**	**0.052**
Adult hetero-specific foraging success	0.052	0.274	0.393
Pre-SC kills	0.124	0.658	0.258

Egg sac mass/offspring number, $n=32$	Standardized coefficient (r)		
		t	$P_{\text{1-tailed}}$
Fixed adult size	**-0.373**	**-2.17**	**0.019**
Adult hetero-specific foraging success	-0.033	-0.188	0.426
Pre-SC kills	**0.434**	**2.46**	**0.010**

Hatching success of egg sac 1, $n=32$	Standardized coefficient (r)		
		t	$P_{\text{1-tailed}}$
Fixed adult size	NA	-0.936	0.174
Adult hetero-specific foraging success	**NA**	**2.53**	**0.006**
Pre-SC kills	**NA**	**1.71**	**0.044**

CHAPTER 6

Pre-copulatory sexual cannibalism in fishing spiders (*Dolomedes triton*):

a test of the aggressive-spillover hypothesis

<u>Summary</u>

Pre-copulatory sexual cannibalism, or predation of a potential mate prior to sperm transfer, offers an ideal model system for the current focus on sexual conflict in the study of animal mating systems. Historically, studies have attempted to show female benefits from this practice. Alternatively, a recent hypothesis suggests that pre-copulatory sexual cannibalism may actually be costly for females. The 'aggressive-spillover' hypothesis posits that attacks on males are the by-product of strong selection for high feeding voracity (aggression towards prey) throughout ontogeny, which should result in large adult size and high fecundity. As such, pre-copulatory sexual cannibalism per se may not provide benefits, but instead may be costly if sexually cannibalistic females do not mate enough to fertilize all of their eggs. This view, that behaviors may often be correlated across disparate contexts (e.g. aggression in foraging and mating contexts), is receiving renewed interest and may require a dramatic shift in the way we think about behavioral evolution. Here, by simultaneously and quantitatively testing alternative hypotheses, I show that pre-copulatory sexual cannibalism in the fishing spider (*Dolomedes triton*) is better explained as a component of a syndrome of correlated aggressive behaviors than it is by any traditional, context-specific adaptive hypothesis.

Introduction

Pre-copulatory sexual cannibalism (pre-SC), or predation of a potential mate prior to sperm transfer, has been documented in a number of insect and arachnid families (Elgar, 1992). Pre-SC offers behavioral ecologists an ideal model system for at least two reasons. First, pre-SC provides a dramatic example of inter-sexual conflict, a current focus in the study of animal mating systems (Elgar, 1992; Choe & Crespi, 1997; Johns & Maxwell, 1997). Rather than disputing, for example, the duration or frequency of mating, here the sexes differ in that males benefit from avoiding attacks and acquiring matings, but females often instead use the male as a prey item. Thus, unlike sexual cannibalism occurring during or after successful sperm transfer (e.g. Andrade, 1996), pre-SC offers no benefits for the cannibalized male, and researchers have instead focused on documenting female benefits to make adaptive sense of this behavior.

In addition to stressing the importance of inter-sexual conflict, an understanding of pre-SC also requires that we view mating behavior as deeply intertwined with other aspects of an organism's life history. Mating decisions for all animals, and for the sexual cannibal and her mate in particular, are only fully understood in conjunction with a wide range of other relevant selection pressures (Rowe et al., 1994; Jackson & Pollard, 1997). For example, patterns of female mate choice in nature are often heavily influenced by predation risk and/or previous foraging success (Real & Caraco, 1986; Sakaluk, 1990; Crowley et al., 1991; Sih, 1994; Lima, 1998). In sexually cannibalistic species, mating, foraging and predator/prey issues are uniquely inseparable as males are simultaneously potential sperm donors and/or prey items, and females are simultaneously potential mates and/or predators. Thus, studies of pre-SC may provide a model system for future studies of mating systems that seek to understand the implications of inter-sexual conflict set on an expansive stage that integrates selection pressures stemming from foraging requirements, mating requirements and predation risk.

In the last comprehensive review of sexual cannibalism, Elgar (1992) focused on two adaptive explanations for pre-SC. First, females may obtain indirect benefits from pre-SC if they attack males as an extreme form of mate refusal (Elgar & Nash, 1988). Under this hypothesis, female aggression is biased towards males of certain phenotypes (e.g. small males), presumably resulting in a mating bias for males of the phenotype that is less often attacked. This mate-choice hypothesis has received little support as no one has been able to demonstrate that females

preferentially attack males based upon their size or other distinguishing phenotype (Elgar & Nash, 1988; see also Chapter 3).

An alternative, but not mutually exclusive, idea is that pre-SC provides adult females direct, material benefits if it is used as an optimal foraging strategy. Newman & Elgar (1991) developed this adaptive foraging hypothesis with an economic model showing that pre-SC can be explained, even for virgin females, on the basis of the nutrient payoff to females that feed on a male rather than mating with him. According to the adaptive foraging idea, pre-SC should (1) increase female fecundity and (2) depend on levels of food and sperm limitation experienced by females (i.e. be most common in poorly-fed, mated females and least common in well-fed, virgin females).

Perhaps surprisingly, this intuitive, resource-optimization idea has also met with little empirical support. In one of the few explicit attempts to test the adaptive foraging hypothesis empirically, Arnqvist & Henrikkson (1997) showed in the European fishing spider (*Dolomedes fimbriatus*) that female fecundity was unrelated to adult feeding history including pre-SC, and female attacks on males were not predicted by the level of sperm and food limitation experienced by a female. Notably, despite multiple mating opportunities, many virgin females in this laboratory experiment attacked every single male provided, failed to mate, and thus produced no offspring. These authors concluded that (1) if females receive no fecundity benefits from adult feeding, and specifically feeding on males, then pre-SC cannot be explained as an adaptive adult foraging strategy, and (2) if overzealous aggressive behavior towards males causes some females to suffer sperm limitation, then pre-SC may have fertility costs rather than foraging benefits.

Arnqvist & Henrikkson (1997) offered an alternative explanation for their results positing that pre-SC is "an indirect result of behaviour that is adaptive in previous life-history stages". More specifically, they suggested that pre-SC represents a spillover of aggression from the juvenile foraging context, where high aggression might be selectively advantageous, to the adult mating context. The idea is that genetic constraints on the behavioral expression of aggression produce intra-individual behavioral correlations across ontogenetic stages (juvenile feeding and adult mating). Selection then shapes the suite of correlated aggressive behaviors rather than optimizing aggressive levels in each individual context.

This 'aggressive-spillover' hypothesis is grounded in a series of assumptions outlined in Figure 2.1. First, juvenile foraging success is assumed to be positively related to the level of

aggression displayed towards prey as a juvenile (hereafter referred to as juvenile voracity). Second, increased juvenile foraging success is assumed to translate into substantial increases in measures of adult body size, such as cephalothorax area, that are fixed at adulthood and thus influenced exclusively by juvenile feeding. Third, differences in juvenile voracity, juvenile foraging success and fixed adult body size translate into differences in fecundity. Arnqvist & Henrikkson (1997) argue that, especially in Arachnids, adaptive foraging benefits and female fecundity are more often linked to juvenile foraging success than adult foraging, including pre-SC.

Given this series of assumptions, the original formulation of the spillover hypothesis suggests that fecundity selection heavily favors high levels of *juvenile* voracity. Juvenile voracity is, in turn, suggested to be positively correlated with voracity expressed by the adult in the mating context (pre-SC). If pre-SC is indeed a spillover of voracity from previous ontogenetic foraging contexts where it was beneficial, then pre-SC need not provide any benefit, and instead may result in fertility costs if the most voracious juveniles attain the largest fixed size, have the highest fecundity, but also exhibit costly levels of aggression towards males.

Recently, Johnson (2001) provided support for assumptions 2 and 3 by demonstrating a significant effect of juvenile food availability on fixed adult size and fecundity in the North American congener *D. triton*. However, this work also noted fecundity advantages to adult food availability. Indeed, it would seem unlikely that voracity would spill over from the juvenile foraging context to the adult's mating context, somehow bypassing adult, hetero-specific foraging contexts. I suggest that a natural extension of the spillover hypothesis is that juvenile and adult voracity are likely to be positively correlated (link # 6 in Figure 2.1), resulting in heightened adult foraging success and fecundity benefits via increases in egg sac mass (dashed lines $1_a - 3_a$ in Figure 2.1). Thus, I predicted that fecundity selection should favor high levels of both juvenile and adult voracity, which are both correlated with pre-SC, thus leading to potential fertility costs for the most voracious females.

The aggressive-spillover hypothesis mirrors previous suggestions that spiders exhibit positive, and potentially costly, correlations between their aggression towards con-specific intruders and their boldness towards predators (Riechert & Hedrick, 1993). More broadly, the aggressive-spillover hypothesis is an excellent example of the renaissance of constraints-oriented explanations in animal behavior and the general hypothesis that behavioral syndromes (suites of

correlated traits) might be important in behavioral evolution (Sih et al., 2003; Sih et al., in review).

Note that a behavioral syndrome explanation for pre-SC, or for animal behavior in general, does not deny the existence of some level of traditional, context-specific adaptation. For example, females may dramatically down-shift their voracity when facing courting males relative to their voracity towards hetero-specific prey items. If in doing so female voracity in each context clusters around the optimal level of voracity for that context (e.g. Figure 6.1), then this would fit the traditional paradigm of behavioral flexibility and context-specific adaptation. However, the occurrence of some level of adaptive discrimination does not preclude a role for behavioral syndromes in explaining voracious behavior and pre-SC. Instead, the behavioral-syndromes hypothesis predicts that within the adaptive modulation that goes on across contexts, individuals that rank relatively high for voracity in context A, also rank relatively high for voracity in context B (e.g. Figure 6.2). Indeed, the strength of a behavioral-syndromes explanation lies in the extent to which voracity in context A is better explained by that individual's level of voracity in context B than it is by the optimal level of voracity in context A. For these reasons, I examine the results for consistency with both traditional, context-specific hypotheses and behavioral syndromes explanations such as the aggressive-spillover hypothesis.

Here I use the North American fishing spider (*D. triton*) as my study organism to present the first direct test of the aggressive-spillover hypothesis. Using Figure 2.1 as a framework, I test the following assumptions of the spillover hypothesis: (1) juvenile voracity, juvenile foraging success, fixed adult size, and fecundity are positively correlated, (2) adult voracity, adult foraging success, egg sac mass, and fecundity are positively correlated, and (3) juvenile voracity, adult voracity and pre-SC are positively correlated. Following the elegant work of Riechert & Hedrick (1993) on the funnel web spider (*Agelenopsis aperta*), I also examine the anti-predator context to test the idea that boldness towards predators is also included in the proposed syndrome of aggressive behaviors. The existence of fertility costs in nature and the heritability of the proposed voracity syndrome are the subject of ongoing experiments.

The behavior and ecology of *Dolomedes*

Foraging

       Dolomedes are relatively large, cursorial ambush predators most commonly associated with the edges of aquatic habitat (Carico, 1973). Fishing spiders detect water-borne prey vibrations using sensory receptors located in their forelegs (Bleckmann & Barth, 1984). Prey items are most commonly insects trapped at the water surface (Carico, 1973; Barth, 1982; Zimmerman & Spence, 1989) however, fishing spiders derive their name from their ability, albeit infrequent, to attack, subdue and consume aquatic vertebrate prey (e.g. fish, frogs, salamanders) that are often significantly larger than the attacking spider (Bleckmann & Lotz, 1987; personal observation).

Mating

       The *Dolomedes* mating sequence is initiated when a searching male encounters pheromonal cues from female silken drag lines (Carico, 1973; Arnqvist, 1992). Males then proceed with a stereotypic courtship sequence of leg waving and a slow, regular tapping of the water surface or solid substrate. Males proceed cautiously, following the female's drag lines and approaching the female while continuing courtship. If not attacked or rebuffed, males typically mount the dorsum of the female from behind and turn to face the opposite direction of the female. The male then turns sideways, usually between the female's legs II and III, and reaches to insert a single pedipalp charged with sperm into the female's epigynum, a paired structure located at the ventral junction between the cephalothorax and abdomen. Sperm transfer takes only a few seconds after which the male jumps off and retreats. If a mating is successful, this process is sometimes repeated by the same male and the male's other pedipalp is used to inseminate the female's other epigynal opening.

Sexual cannibalism

       Adult female fishing spiders routinely attack males at any point during this copulatory sequence. However, laboratory mating trials indicate that females of the European fishing spider (*D. fimbriatus*) most commonly attack during pre-copulatory courtship (75% of trials), and that males are killed in approximately 5-10 % of these attacks (Arnqvist, 1992; Arnqvist & Henrikkson, 1997). For *D. triton,* laboratory mating trials showed that pre-copulatory attacks by

virgin females occur in approximately 20% of pairings (see Chapter 4), a result that was recently confirmed under semi-natural field conditions (see Chapter 3). In addition, field studies of *D. triton* suggest that males represent a common contribution to the adult female diet (Zimmerman & Spence, 1989), and that male population density declines drastically, soon after adult female emergence (Zimmerman & Spence, 1992). Thus, sexual cannibalism appears to play an important role in the ecology of *Dolomedes*.

Avoiding predators

Fishing spiders commonly employ an anti-predator behavior in which the spider dives underneath the water and clings to submerged substrate (e.g. under floating aquatic vegetation, on submerged rocks or, in the case of the experimental containers, the underside of a Styrofoam float). While submerged, the spider is enveloped in an air capsule, and thus, when healthy, can re-surface completely dry. Bishop (1924) and Carico (1973) reported submergence durations of upwards of 30 minutes in *D.* triton, as well as other Nearctic species. My more recent work indicates that 30 minutes under water is routinely seen in *D. triton*, and the current record holders (*n*=3, all healthy adult females) remained continuously submerged for an entire 90 minute trial (Johnson, unpublished data). To my knowledge, no one has documented the physiological cost of submergence. As for behavioral ecological costs, time spent submerged most likely involves lost foraging opportunities (*Dolomedes* primarily detect prey items through water surface vibrations) and may allow aquatic predators (e.g. sunfish) to prey on the spider.

Methods

The experimental approach taken here was a longitudinal study focused on quantifying female behavior in multiple behavioral contexts. The study followed 60 focal females from the ante-penultimate juvenile stage, through to adulthood until death (approximately 5-6 months). Throughout this entire period foraging trials and anti-predator trials quantified female foraging success and boldness toward predation risk (see below). In addition, upon adulthood, mating trials quantified female behavior towards mates.

Penultimate-stage males and juvenile females approximately 3-6 weeks (1-2 molts) from adulthood were collected from a large pond (~ 60 m^2) outside of Lexington, KY during the first week of April, 2002. Upon collection all spiders were weighed and digitally imaged. Males

were maintained in individual transparent, plastic cups (425 ml.) each containing filtered water (100 ml.) and a Styrofoam float (2.0 x 1.5 x 0.5 cm.). Males were fed one 4-week old house cricket (*Acheta domesticus*) weekly. Prey items were removed if not eaten after 24 hours. Males were digitally imaged following their final molt. When not being used in mating trials males were maintained in the laboratory under a natural photoperiod.

Experimental females (*n=60*) were maintained outdoors in individual, large (60 x 41 x 16 cm.) plastic tubs. When observational trials were not in progress, screened lids covered these tubs to allow airflow, while at the same time preventing escape of the spider and/or entry of prey items (e.g. earwigs, wolf spiders) and predators (e.g. birds, lizards). Containers were filled with filtered water to a depth of 2.0 cm. and each contained a large Styrofoam float (10 x 6.0 x 0.5 cm) and an inverted 20 oz. opaque, plastic cup. These cups had a rectangle cut out (3 x 6 cm.) to allow the spider to use the cup as a refuge. These refuges were also invariably where females chose to build their nursery webs in preparation for the hatching of their egg sac.

Female containers were positioned in 6 circular stations each consisting of 10 tubs. This design allowed an observer to sit in the middle of a station and conduct behavioral trials for 10 females at a time without creating any disturbance. Stations received direct sunlight ranging from 2-3 hours during the middle of the day. Each week female containers were provided with fresh water and randomly re-located to a different station to control for micro-habitat differences between stations. Females were weighed and imaged weekly for the duration of the experiment.

Foraging trials

Females underwent thirty-minute foraging trials twice weekly throughout the experiment. Feeding regimes of this regularity and prey size (see below) have been used in the past and have resulted in successful growth to adulthood and offspring production within the range of that seen in the field (Chapter 4; Johnson, unpublished data). Foraging trials were conducted on females as juveniles and adults, but not when adult females were carrying egg sacs. Females rarely attack prey while carrying an egg sac in their mouthparts (Johnson, personal observation). To begin each trial, one 4-week old cricket was introduced to the water surface approximately 30 cm. from the female. Throughout the trial, I recorded the location and activity of predator and prey with spot checks at every 2 ½ minute interval, noting the time at which attacks and kills occurred. I used the inverse of latency to attack as a measure of voracity in both juveniles and adults.

Crickets that survived the trial (i.e. were not attacked or were attacked and discarded while still alive) were removed at the end of a trial such that females failing to secure prey during a trial did not have another feeding opportunity until their next trial.

Mating trials

Mating trials ran for 90 minutes and were conducted 4 times per week beginning on each female's 3rd day following adult emergence and continuing until egg sac production (~ 7-10 days following mating; Johnson, unpublished data). Males were chosen randomly with the exception that females never encountered the same male twice. The introduction of males was conducted in the same manner as the introduction of crickets. Males not initiating typical courtship leg waving and tapping behavior within the first 15 minutes of a trial were replaced. The location and activity of each spider (male and female) was recorded at 2 ½ minute intervals and I noted the time at which pre-copulatory attacks, kills, mountings, matings and post-copulatory attacks occurred. I used the latency to attack a courting male as a measure of voracity in the mating context. In the case of matings, I recorded the duration of sperm transfer using a stop-watch.

One day following egg sac production females were weighed while clutching the egg sac in their mouthparts. The difference between this measure and the mass of the female one day following her adult molt was used as an estimate of the mass of the egg sac. Females were allowed to tend their egg sac until it hatched, and the number of live offspring emerging from the egg sac was counted and used as an estimate of female reproductive success.

Anti-predator trials

Anti-predator assays were performed twice weekly throughout the experiment (i.e. on juveniles, adults and adults guarding their egg sac) and ran for 30 minutes. The goal here was to provoke submergence behavior. Females that did not submerge in response to the removal of their lid were firmly poked with the tip of a pencil. The few females that still remained on the surface after this time were scored as unwilling to submerge and received a submergence duration score of 0 seconds. During anti-predator trials no stimulus/resource (i.e. prey/food or courtship/mate) was present on the water surface. Thus, anti-predator scores consisted simply of the latency to re-surface in response to a 'predator', and because females would often re-surface and submerge again over the course of a trial, I also calculated the proportion of a trial spent

submerged. Females were scored as re-surfacing when at least 4 legs had returned to the water surface.

<u>Statistical analysis</u>

I used univariate correlations to examine the strength of relationships suggested by the aggressive spillover hypothesis (Figure 2.1). In addition, multi-variate path analysis was employed to evaluate alternative pathways to pre-SC (Sih et al., 2002). This approach allows for the consideration of multiple behavioral mechanisms and evaluates the relative contribution of several pathways to the overall expression of pre-SC. Finally, analysis of variance was used to detect differences in submergence behaviors across ontogeny and behavioral contexts.

Results

Foraging trials and feeding voracity

Contrary to adaptive adult foraging explanations for feeding voracity, body condition (mass/cephalothorax area) did not predict the occurrence of predatory attacks on hetero-specific prey ($r=0.09$, $F_{55}=0.433$, $p=0.51$). As a result, this commonly used index is not employed as a covariate in the analyses below. Here I sequentially address predictions 1, 2, 3 and 6 of the aggressive spillover hypothesis (see Figure 1.2), leaving treatment of sexually cannibalistic behavior for the section on mating trials.

First, the measure of juvenile voracity, 1/latency to attack a prey item, was strongly, positively correlated with juvenile foraging success ($r_{57}=-0.921$, $F=266$, $p<0.0001$), thus supporting assumption 1. Therefore, for the remaining analyses I refer jointly to voracity/foraging success and use only foraging success (proportion of foraging trials in which the spider fed, arc-sin transformed) for statistical comparisons. Analyses using latency to attack produced no notable differences in results. Second, juvenile voracity/foraging success was positively correlated with fixed adult size ($r_{53}=0.23$, $t=1.69$, $p=0.049$). Third, fixed adult size (cephalothorax area) was significantly, positively correlated with fecundity ($r_{32}=0.50$, $t=3.16$, $p=0.002$). As for assumption 6, juvenile feeding voracity and adult feeding voracity were significantly, positively correlated ($r_{52}=0.381$, $t=2.92$, $p=0.003$), thus supporting the suggestion of an ontogenetic spillover of voracity from juvenile to adult.

While the original formulation of the aggressive-spillover hypothesis emphasized this ontogenetic spillover of advantageous juvenile voracity towards hetero-specific prey to potentially costly adult voracity towards mates, voracity may also be correlated within the adult life history. Beneficial voracity in the adult hetero-specific foraging context may spill over into the adult mating context. Indeed, as shown in links $1_a - 3_a$ of Figure 1.2, adult voracity towards hetero-specific prey (1/latency to attack) was significantly positively related to adult foraging success (r_{57}=-0.920, t=-17.82, $p<0.0001$), adult foraging success was positively related to egg sac mass (r_{50}=0.297, t=2.15, p=0.018), and egg sac mass was positively related to fecundity (measured as offspring number; r_{32}=0.722, t=5.71, $p<0.0001$).

Mating trials and pre-copulatory sexual cannibalism

Females exhibited pre-SC attacks in 32% of mating trials. Males were killed in 50/109 (46%) of these attacks. The proportion of pre-SC attacks exhibited by a mature female spider was an excellent indicator of that female's propensity to actually kill and cannibalize courting males; the propensity to attack males was significantly, positively correlated with the number of males a female killed (r=0.51, $F_{1,57}$=19.59, $p<0.0001$). This propensity to attack males was not however, related to a female's mating frequency (r=0.136, $F_{1,56}$=1.05, p=0.31), or the likelihood she would hatch an egg sac (χ^2=0.862, d.f.=1, p=0.35).

In univariate correlations, both juvenile and adult voracity/foraging success were significantly, positively correlated with pre-SC (juvenile: r_{52}=0.348, t=2.62, p=0.012; adult: r_{52}=0.420, t=3.46, p=0.0005). Figure 6.3 presents a more detailed, multi-variate path analysis of several, biologically relevant routes to pre-SC. Arnqvist & Henriksson's original idea, that juvenile voracity spills over directly into the mating context resulting in pre-SC is not supported by the multivariate analysis (pathway A: r_{50}=0.218, t=1.43, p=0.159). Juvenile females that attack the most prey items are not the same females who after maturation tend to practice pre-SC most often. However, I found strong intra-individual correlations between adult voracity in the hetero-specific foraging context and adult voracity towards males in the mating context (pathway C: r_{50}=0.272, t=1.80, p=0.039). Finally, the traditional adaptive foraging thought on pre-SC predicts that adult female condition (mass/fixed size) will have a significant, negative relationship with the occurrence of pre-SC. In contrast, these data suggest a non-significant

positive trend, with females in the best condition being the most frequent sexual cannibals (pathway B: r_{50}=0.178, t=1.36, p=0.179).

Path analysis also allows for an examination of indirect pathway effects on a dependent measure. Thus, while juvenile voracity does not spill over directly into the mating context, the combined effect of juvenile voracity via both its direct effect and its indirect effect through its correlation with adult voracity is substantial ($.218^{direct}$ + $.381(.272)^{indirect}$ = r=.322,). None of the traditional, adaptive indirect pathways in Figure 6.3 proved to be significantly related to pre-SC. In addition, pre-SC did not provide females with fecundity benefits. Binary logistic regression showed that the number of males consumed (0, 1, 2, 3, or 4) was not related to offspring number after controlling for female condition at adult emergence (n=35, t=0.373, p=0.711).

Anti-predator trials and submergence behavior

I found significant differences in submergence behavior across three anti-predator contexts (juvenile, adult, adult while carrying an egg sac), two foraging contexts (juvenile, adult), and the mating context (see Figure 6.4, $F_{5,285}$=26.36, p<0.0001). There were no ontogenetic differences in submergence time within anti-predator trials or within foraging trials. Submergence behavior in anti-predator trials was significantly reduced when adult females were carrying/guarding their egg sac (n=84, t=3.06, p=0.004). The most dramatic reduction in submergence behavior, however, occurred during foraging trials. In foraging trials, females (juveniles and adults) spent significantly less time submerged than they did during (1) juvenile and adult anti-predator trials (n=120, t=11.05, p<0.0001), and (2) adult anti-predator trials while carrying an egg sac (n=84, t=3.05, p=0.005). Perhaps surprisingly, females spent a great deal of time submerged during mating trials, more closely resembling their behavior during anti-predator trials than their behavior during foraging trials (n=119, t=7.77, p<0.0001).

On the surface it appears that females exhibited an adaptive reduction in submergence behavior when (1) food was available and (2) egg sacs were present. In contrast, females did not reduce their submergence behavior when mates were available. However, none of these results accounts for the possibility that submergence behavior is the product of a syndrome of boldness rather than context-specific adaptation. To address the extent to which this suite of submergence behaviors are inter-correlated I examined intra-individual correlations across contexts (see Table

114

6.1). Throughout I employ a sequential bonferroni-adjustment for the fifteen tests performed to determine the statistical significance of submergence behavior correlations across contexts.

Within the juvenile stage, time spent submerged was not correlated between anti-predator trials and foraging trials, whereas within the adult stage submergence time was significantly correlated across these behavioral contexts. Across ontogeny, the proportion of time spent submerged as a juvenile and as an adult in anti-predator trials was correlated, but fell short of statistical significance given the sequential bonferroni requirement here of 0.005. Staying within the anti-predator context, the submergence behavior of adults carrying an egg sac did not correlate with either juvenile or pre-egg sac adult submergence behavior. Indeed, submergence behavior while carrying an egg sac did not correlate significantly with any other context. Within the foraging context, juvenile and adult submergence behavior was highly correlated. Finally, the amount of time females spent submerged in mating trials was highly correlated with all other contexts except for egg-sac carrying females and the juvenile anti-predator context. In sum, the propensity for submergence behavior (1) spills over across ontogeny within behavioral contexts (both anti-predator and foraging), (2) spills over across the foraging and anti-predator contexts for adults but not juveniles, (3) is not correlated with other contexts during the egg sac guarding phase, and (4) routinely spills over to the mating context from previous life-history stages and other behavioral contexts (anti-predator and foraging).

Finally, submergence behavior in the anti-predator trials (juvenile and adult) was significantly negatively correlated with pre-SC (r_{59}= -0.243, t=-1.89, $p_{1\text{-tailed}}$=0.032, and hetero-specific foraging voracity (r_{60}= -0.317, t=-2.54, $p_{1\text{-tailed}}$=0.007).

Discussion

Our results support the idea that pre-SC represents a spillover from a broader syndrome of correlated voracious behaviors rather than adaptive foraging. Replicating a previous study (see Chapter 4), I documented a link between juvenile voracity/foraging success, fixed adult size and fecundity. In addition, I have documented strong correlations between juvenile voracity, adult voracity in the hetero-specific foraging context, adult voracity in the mating context (i.e. pre-SC), and boldness towards predators. Voracity in *D. triton* appears to spill over across both ontogeny (juvenile-adult) and behavioral contexts (foraging-mating-anti-predator). Multi-variate analyses suggest a stronger role for spillover across behavioral contexts than ontogeny.

However, the possibility of a strong correlation between juvenile voracity and pre-SC cannot be entirely ruled out as juvenile fishing spiders develop for two years before reaching maturity. Juvenile foraging trials only quantified voracious behavior during the final 2-3 weeks of the juvenile period. Future work should aim to document voracity correlations across the entire juvenile life cycle.

To date, only a few studies have approached the study of correlated behavioral traits from an evolutionary/ecological viewpoint (Sih et al, in review). Particularly lacking are longitudinal studies that follow animals across ontogeny looking for intra-individual correlations at different points in development. In one notable exception, Bakker (1985) showed strong positive correlations between juvenile and adult female aggression towards conspecifics in the three-spined stickleback (*Gasterosteus aculeatus*). Several other works have shown potentially costly correlations within ontogenetic stages but across behavioral contexts. For example, Wilson et al. (1993) described a shy-bold continuum in juvenile pumpkinseed sunfish (*Lepomis gibbosus*) in which consistent individual differences in boldness affected predator risk, diet choice and parasitic infection. Similarly, Sih et al (2002) demonstrated a positive activity correlation for larval salamanders (*Ambystoma barbouri*) in the presence and absence of predatory fish. Individuals with high activity levels in the absence of predation risk acquired more resources and developed faster. However these same individuals were also more active in the presence of predators. Finally, Riechert & Hedrick (1993) showed that funnel web spiders (*Agelenopsis aperta*) that were most aggressive in contests with conspecific intruders were the same individuals that were boldest towards potential predators. This aggressive/bold syndrome was later shown to also correlate with wasteful killing (killing but not fully consuming prey) in the foraging context (Maupin & Riechert, 2001). These data support the existence of such an aggressive/voracious/bold syndrome in *D. triton* and suggest that these correlations also surface in the form of pre-SC in the mating context. Whether voracity in the mating context involves fertility costs, and the extent to which the demonstrated behavioral syndrome is heritable are the subjects of ongoing work.

While these results fit the aggressive spillover hypothesis, they did not support alternative hypotheses. Voracity was not predicted by female condition and pre-SC did not allow females in this study to produce more offspring. Indeed, such negative findings are commonplace in the few studies that have attempted to test the adaptive foraging hypothesis in spiders (Andrade,

1996; Spence et al., 1996; Arnqvist & Henrikkson, 1997; Fahey & Elgar, 1997; Elgar et al., 2000; Chapter 4; but see Elgar & Nash, 1988). Pre-SC in this experiment also did not accord with a recent variant of the adaptive foraging hypothesis: adult foraging compensation (Schneider & Elgar, 2002). This idea suggests that adult foraging, including pre-SC, is driven by an adult female's need to compensate for poor foraging success as a juvenile. This hypothesis predicts pre-SC to be most frequent among females with the poorest juvenile feeding history and thus the smallest fixed adult size. While an earlier experiment on this population of fishing spiders provided some preliminary evidence that the smallest females were most often those that attacked courting males (see Chapter 3), I found no such evidence in the present experiment. In fact, the present data indicate a non-significant positive relationship between fixed size and pre-SC (r_{59}=0.211, t=0.163, p=0.108), a result which is more consistent with the spillover hypothesis than any form of adaptive adult foraging.

Particularly intriguing are the data that suggest a link between voracity and boldness towards predators. While it has been argued that fear and aggression are distinct motivational states governed by separate genetic mechanisms and hormonal axes (Riechert & Maynard-Smith, 1989), it is interesting to note that several studies have found behavioral correlations between aggressive and bold behavior (Huntingford, 1976; Wilson et al. 1993; Bell, unpublished data; present study). Unfortunately, these studies represent a very limited number of taxa so the general link between fear and aggression remains to be established.

I suggest that behavioral syndromes such as the one documented here may be very common and that this will require a dramatic shift in the way we think about and study animal behavior similar to that occurring in the field of behavioral endocrinology (Ketterson & Nolan, 1999). We can no longer atomize the behavioral repertoire of an animal and expect to fully understand why it behaves the way it does. Instead, I suggest that future studies should examine the same individuals in multiple developmental and behavioral contexts to address the extent to which seemingly different behaviors (e.g. juvenile foraging behavior and parental care) are correlated in their expression. In many situations we may find evidence of both traditional, context-specific benefits and behavioral spillover. For example, there is no doubt that pre-SC may yield context-specific foraging/fecundity benefits in some ecological contexts (e.g. under extreme food limitation). Our task will then be to disentangle the relative importance of context-specific and context-general effects on behavior and fitness.

Such studies will face many of the same challenges and address many of the same issues currently being confronted in other sub-disciplines of evolutionary ecology. For example, if studies of syndrome benefits are to adequately disentangle adaptation from exaptation, they will have to embrace an integration of behavioral, mechanistic and historical (phylogenetic) approaches (Autumn et al., 2002). Similar to the work being done on the 'non-adaptive' sensory exploitation hypothesis for mate choice (Ryan & Rand, 1999), a thorough understanding of the mechanisms underlying trait/syndrome expression, as well as the evolutionary history of the taxa of interest, will be necessary to determine current and past evolutionary explanations for adaptive behaviors and adaptive syndromes.

Second, the existence of behavioral syndromes may help explain the maintenance of variation in traits that heavily influence fitness. The lek paradox (Kirkpatrick & Ryan, 1991) may be, in part, resolved by the understanding that selection acts on behavioral tendencies that are expressed in multiple contexts. To the extent that these contexts are variable in space and time (e.g. food/mate availability or predation risk on different ponds or across the breeding season) we may not expect to see the exhaustion of genetic variation for behavioral tendencies expressed in a suite of contexts because different behavioral types will perform better in different contexts.

In conclusion, the existence of a voracious syndrome of behaviors throughout developmental and behavioral life-history contexts may go a long way to help explain the phenomenon of pre-SC. These data clearly suggest that future work cannot ignore the potential of a syndromes explanation. Next steps in this and other systems should include (1) the search for potential costs of syndromes, (2) evidence that syndromes are heritable, (3) mechanistic studies aimed at deciphering what common factor (e.g. shared genes or hormones) is responsible for coupling certain behaviors and how they might be de-coupled, and (4) ecological studies on the effects of fluctuations in the availability of critical resources (e.g. food or mates) and how such fluctuations impact the evolution and maintenance of syndromes. Progress such as this will significantly advance our understanding of the potential that behavioral syndromes have for influencing the dynamic process of behavioral evolution.

Table 6.1 Correlations among submergence behaviors in the anti-predator context (A-P) for juveniles, adults and adults with egg sacs, the foraging context for juveniles and adults and the mating context for adults. [*]indicates statistical significance given a sequential bonferroni adjustment

$r=$, $n=$ $p=$	Juvenile A-P	Juvenile foraging	Adult A-P	Adult foraging	Adult mating	Adult A-P w/egg sac
Juvenile A-P	————					
Juvenile foraging	0.128, 41 0.427	————				
Adult A-P	0.370, 37 0.024	0.148, 46 0.330	————			
Adult foraging	0.09, 43 0.550	**0.512, 51 <0.0001[*]**	**0.497, 53 <0.0001[*]**	————		
Adult mating	0.393, 43 0.009	**0.503, 51 <0.0001[*]**	**0.560, 53 <0.0001[*]**	**0.624, 59 <0.0001[*]**	————	
Adult A-P w/egg sac	0.02, 22 0.910	0.202, 22 0.367	0.340, 19 0.150	0.102, 24 0.560	0.105, 24 0.510	————

Figure 6.1   Hypothetical behavioral reaction norms for voracity across hetero-specific foraging contexts and mating contexts. Here voracity in either context is best predicted by the level of voracity that is optimal in that context.
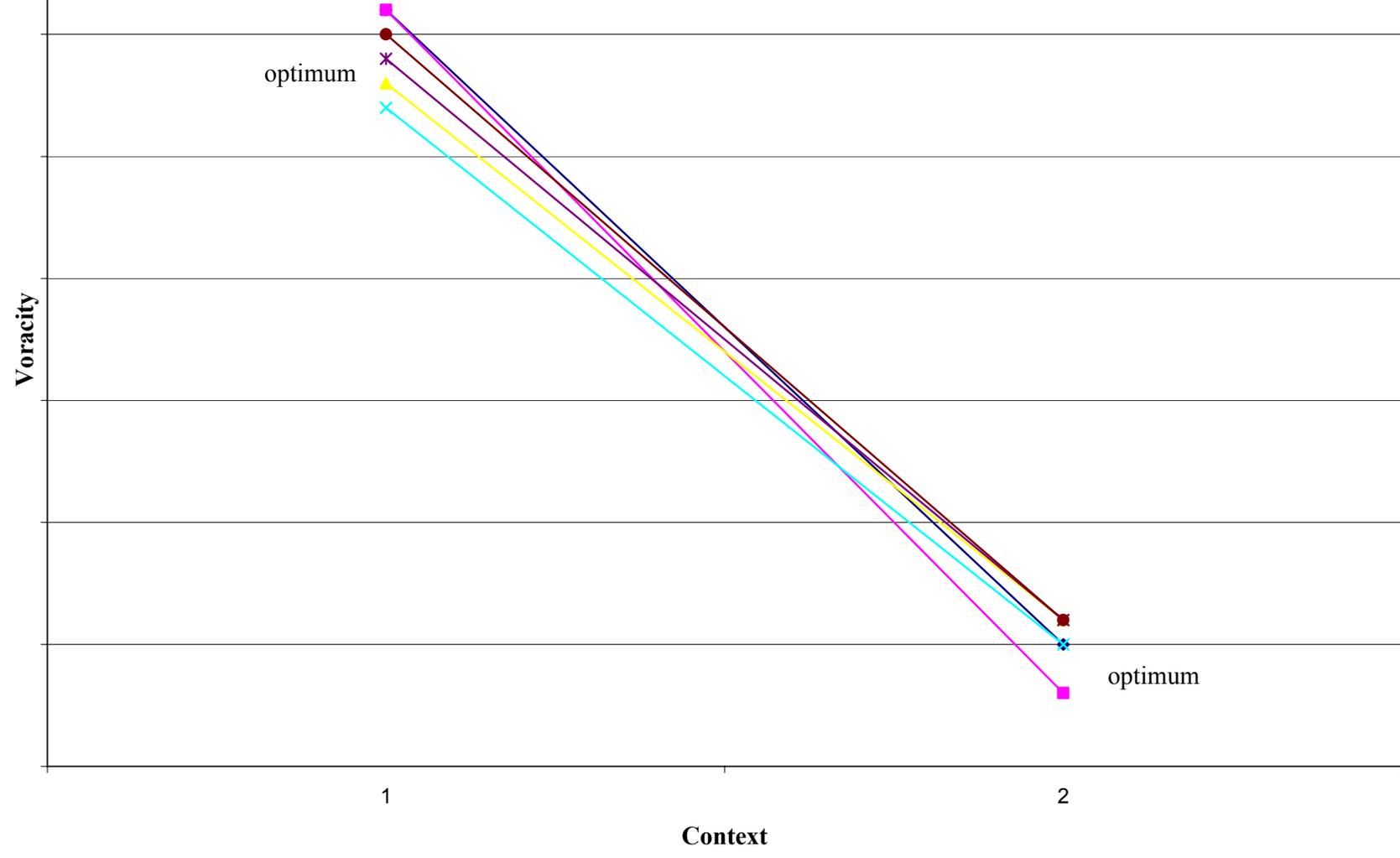
Figure 6.2   Hypothetical behavioral reaction norms for voracity across hetero-specific foraging contexts and mating contexts. Here, voracious expression is best predicted by the individual's voracity in other contexts.
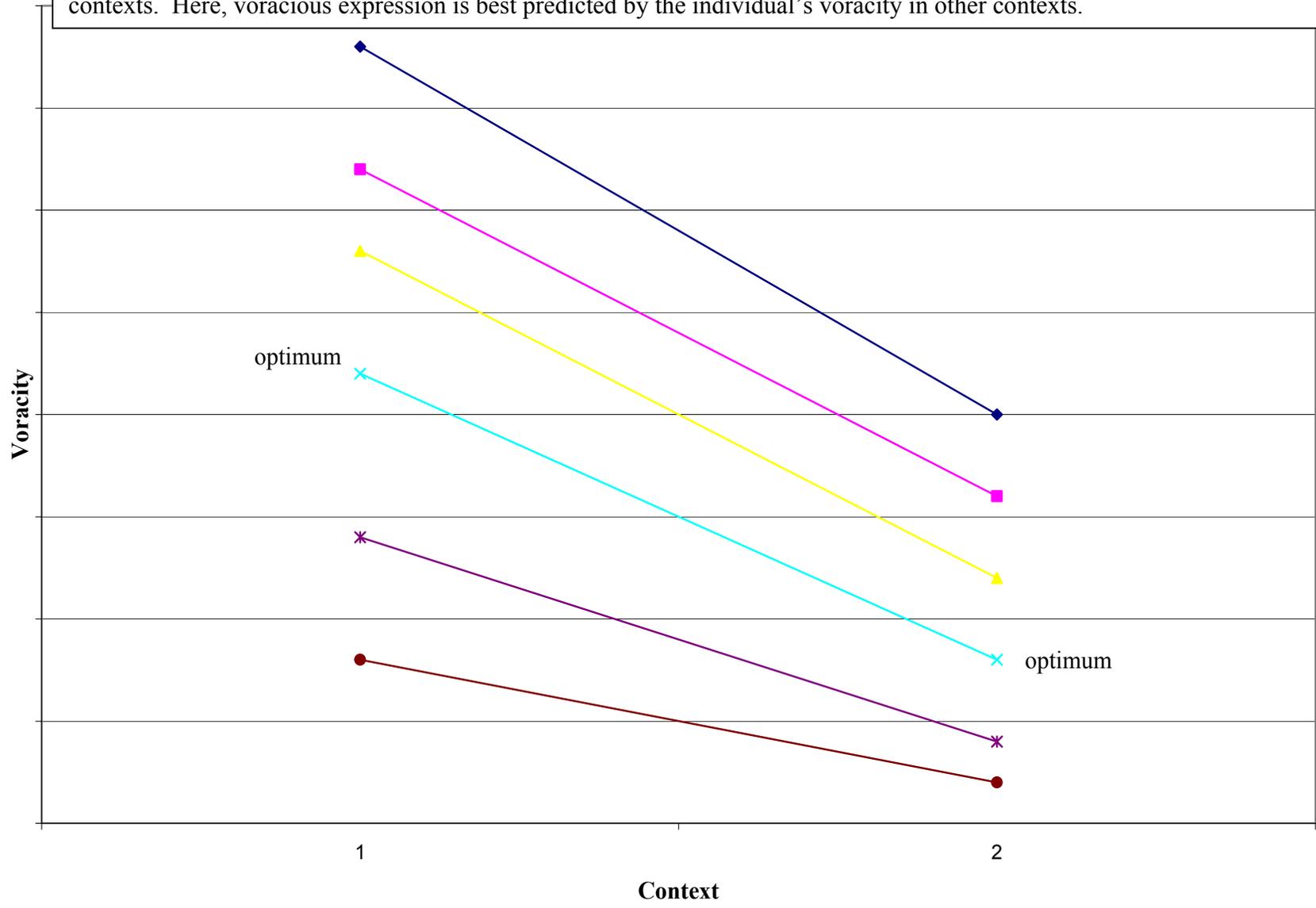
Figure 6.3   Multivariate path analysis depicting several alternative pathways to pre-SC.
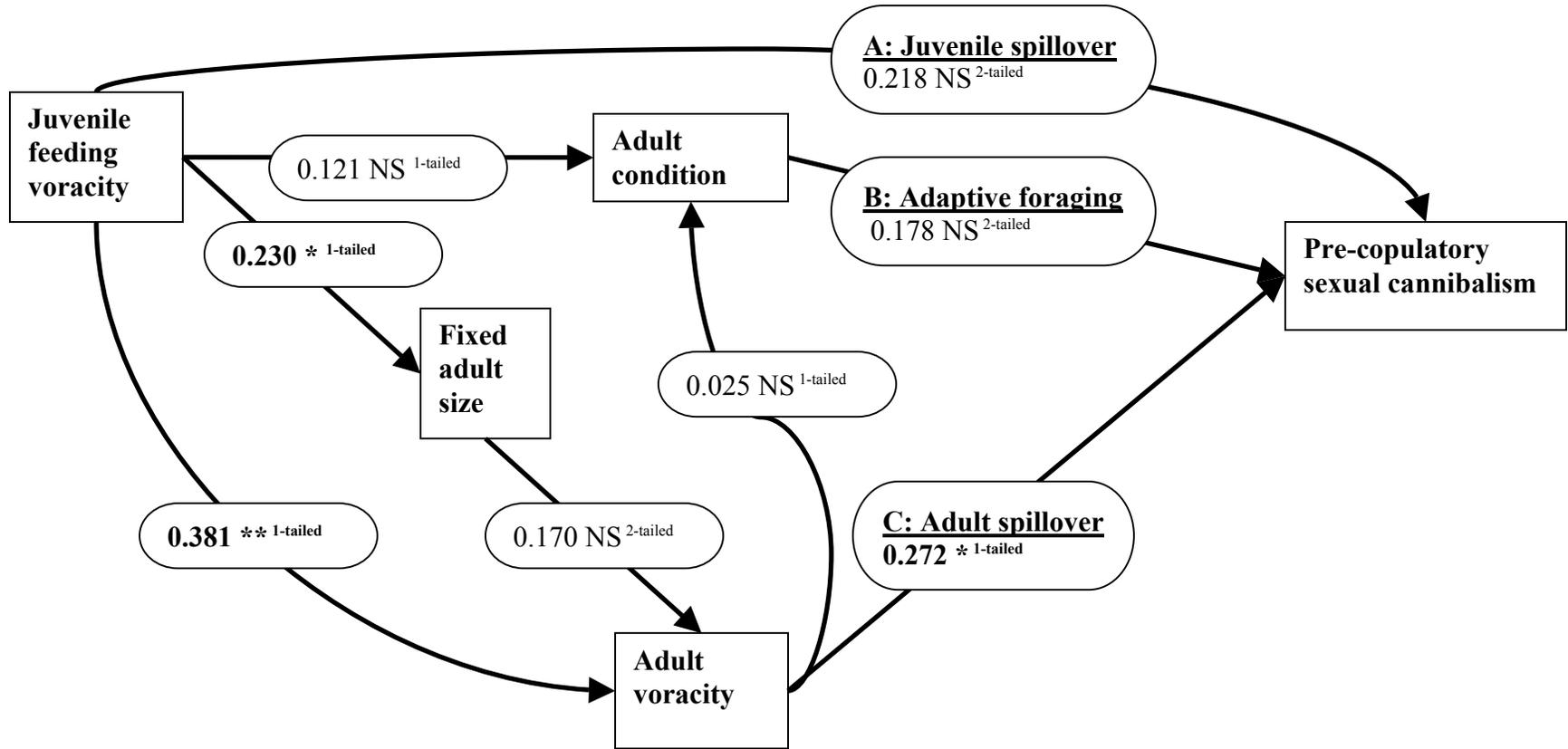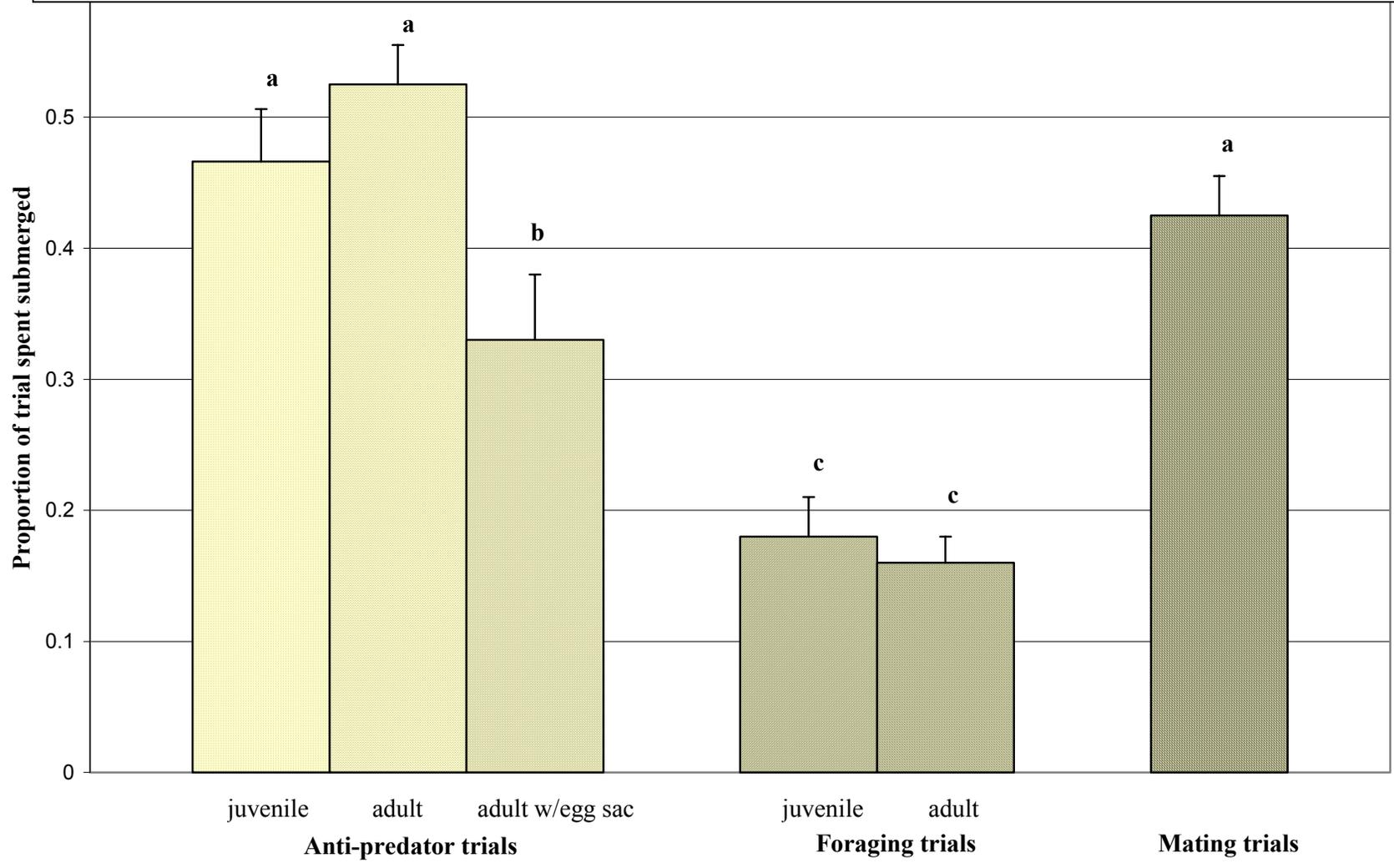
Figure 6.4   Proportion of time spent submerged by females in various ontogenetic and behavioral contexts. Note that significantly less time is spent submerged when prey and/or mates are available relative to time spent submerged in the absence of resource stimuli.

REFERENCES

CHAPTER 1

Andrade, M. C. B. (1996). Sexual selection for male sacrifice in the Australian redback spider. *Science* **271,** 70-73.

Arnqvist, G. (1992). Courtship behaviour and sexual cannibalism in the fishing spider, *Dolomedes fimbriatus* (Clerck) (Araneae: Pisauridae). *Journal of Arachnology* **20**.

Arnqvist, G. & Henrikkson, S. (1997). Sexual cannibalism in the fishing spider and a model for the evolution of sexual cannibalism based on genetic constraints. *Evolutionary Ecology* **11,** 255-273.

Choe, J. C. & Crespi, B. J. (1997). *The evolution of mating systems in insects and arachnids.* Cambridge University Press, Cambridge.

Crowley, P. H., Travers, S. E., Linton, M. C., Cohn, S. L., Sih, A. & Sargent, R. C. (1991). Mate density, predation risk, and the seasonal sequence of mate choices: a dynamic game. *The American Naturalist* **137,** 567-596.

Elgar, M. A. (1992). Sexual cannibalism in spiders and other invertebrates. In *Cannibalism: Ecology and Evolution among Diverse Taxa* (ed. M. A. Elgar and B. J. Crespi), pp. 128-155. Oxford University Press, Oxford.

Elgar, M. A. & Fahey, B. F. (1996). Sexual cannibalism, competition, and size dimorphism in the orb-weaving spider *Nephila plumipes* Latreille (Araneae: Araneoidea). *Behavioral Ecology* **7,** 195-198.

Elgar, M. A. & Nash, D. R. (1988). Sexual cannibalism in the garden spider *Araneus diadematus*. *Animal Behaviour* **36,** 1511-1517.

Johns, P. M. & Maxwell, M. R. (1997). Sexual cannibalism: who benefits? *Trends in Ecology and Evolution* **12,** 127-128.

Lima, S. L. (1998). Stress and decision making under the risk of predation: Recent developments from behavioral, reproductive, and ecological perspectives. *Stress and Behavior* **27,** 215-290.

Parker, G. A. (1979). Sexual selection and sexual conflict. In *Sexual Selection and Reproductive Competition in Insects* (ed. M. S. Blum and N. A. Blum), pp. 123-166. Academic Press, New York.

Rowe, L., Arnqvist, A., Sih, A. & Krupa, J. J. (1994). Sexual conflict and the evolutionary ecology of mating patterns: water striders as a model system. *Trends in Ecology and Evolution* **9,** 289-293.

Sakaluk, S. K. (1990). Sexual selection and predation: balancing reproductive and survival needs. In *Insect defenses* (ed. D. L. Evans and J. O. Schmidt), pp. 63-90. SUNY Press, Albany.

Sih, A. (1994). Predation risk and the evolutionary ecology of reproductive behavior. *Journal of Fish Biology* **45,** 111-130.

Vollrath, F. (1987). Growth, Foraging and Reproductive Success. In *Ecophysiology of Spiders* (ed. W. Nentwig), pp. 357-370. Springer-Verlag, Berlin.

Watson, P. J. (1998). Multi-male mating and female choice increase offspring growth in the spider *Neriene litigiosa* (Linyphiidae). *Animal Behaviour* **55,** 387-403.

Wojcicki, J.P. (1992). A description of the reproductive biology of the fishing spider *Dolomedes triton* (Walck.) (Aranea: Pisauridae) in central Alberta. M.S. Thesis, University of Alberta.

Zimmerman M, Spence JR, 1989. Prey use of the fishing spider *Dolomedes triton*: An important predator of the neuston community. *Oecologia*, **80**, 187-194.

Zimmerman M, Spence JR, 1992. Adult population dynamics and reproductive effort of the fishing spider *Dolomedes triton* (Araneae, Pisauridae) in central Alberta. *Canadian Journal of Zoology*, **70**, 2224-2233.

CHAPTER 2

Alexander, R. D., Marshall, D. C. & Cooley, J. R. (1997). Evolutionary perspectives on insect mating. In *The evolution of mating systems in insects and arachnids* (ed. J. C. Choe and B. J. Crespi), pp. 4-31. Cambridge University Press, Cambridge.

Anderrson, M. (1994). *Sexual selection*. Princeton University Press, Princeton.

Andrade, M. C. B. (1996). Sexual selection for male sacrifice in the Australian redback spider. *Science* **271,** 70-73.

Andrade, M. C. B. (1998). Female hunger can explain variation in cannibalism despite male sacrifice in redback spiders. *Behavioral Ecology* **9,** 35-42.

Arnqvist, G. (1992). Courtship behaviour and sexual cannibalism in the fishing spider, *Dolomedes fimbriatus* (Clerck) (Araneae: Pisauridae). *Journal of Arachnology* **20**.

Arnqvist, G. & Henrikkson, S. (1997). Sexual cannibalism in the fishing spider and a model for the evolution of sexual cannibalism based on genetic constraints. *Evolutionary Ecology* **11,** 255-273.

Austad, S. N. (1984). Evolution of Sperm Priority Patterns in Spiders. In *Sperm competition and the evolution of animal mating systems* (ed. R. L. Smith), pp. 223-250. Academic Press, Orlando.

Austad, S. N. & Thornhill, R. (1986). Female reproductive variation in a nuptial-feeding spider, *Pisaura mirabilis*. *Bulletin of the British Arachnologist Society* **7**.

Bakker, T. C. M. (1994). Evolution of aggressive behaviour in the threespine stickleback. In *The evolutionary biology of the threespine stickleback.* (ed. M. A. Bell and S. A. Foster), pp. 345-380. Oxford University Press, Oxford.

Basolo, A. L. (1990). Female preference predates the evolution of the sword in swordtail fish. *Science* **250,** 808-810.

Beck, M. W. & Connor, E. F. (1992). Factors affecting the reprtoductive success of the crab spider *Misumenoides formosipes*: The covariance between juvenile and adult traits. *Oecologia* **92,** 287-295.

Birkhead, T. R., Lee, K. E. & Young, P. (1988). Sexual cannibalism in the praying mantis *Hierodula membranacea*. *Behaviour* **106,** 112-118.

Bleckmann, H. & Barth, F. G. (1984). Sensory ecology of a semi-aquatic spider (*Dolomedes triton*). II. The release of predatory behaviour by water surface waves. *Behavioral Ecology & Sociobiology* **14,** 303-312.

Bleckmann, H. & Bender, M. (1987). Water surface waves generated by the male pisaurid spider *Dolomedes triton* (Walckenaer) during courtship behavior. *Journal of Arachnology* **15,** 363-369.

Breene, R. G. & Sweet, M. H. (1985). Evidence of insemination of multiple females by the male black widow spider, *Latrodectus mactans* (Araneae, Theridiidae). *Journal of Arachnology* **13,** 331-335.

Bristowe, W. S. (1958). *The World of Spiders*. Collins, London.

Brown, W. D. (1997). Female remating and the intensity of female choice in black-horned tree crickets, *Oecanthus nigricornis*. *Behavioral Ecology* **8,** 66-74.

Brown, W. D., Crespi, B. J. & Choe, J. C. (1997). Sexual conflict and the evolution of mating systems. In *The evolution of mating systems in insects and arachnids.* (ed. J. C. Choe and B. J. Crespi), pp. 352-377. Cambridge University Press, Cambridge.

Buskirk, R. E., Frohlich, C. & Ross, K. G. (1984). The natural selection of sexual cannibalism. *American Naturalist* **123,** 612-625.

Carico, J. E. (1973). The nearctic species of the genus *Dolomedes* (Araneae: Pisauridae). *Bulletin of the Museum of Comparative Zoology* **144,** 435-488.

Choe, J. C. & Crespi, B. J. (1997). *The evolution of mating systems in insects and arachnids.* Cambridge University Press, Cambridge.

Clark, D. L. & Uetz, G. W. (1992). Morph-independent mate selection in a dimorphic jumping spider: demonstration of movement bias in female choice using video-controlled courtship behavior. *Animal Behaviour* **43,** 247-254.

Clutton-Brock, T. H. & Parker, G. A. (1995). Sexual coercion in animal societies. *Animal Behaviour* **49**.

Crowley, P. H., Travers, S. E., Linton, M. C., Cohn, S. L., Sih, A. & Sargent, R. C. (1991). Mate density, predation risk, and the seasonal sequence of mate choices: a dynamic game. *The American Naturalist* **137,** 567-596.

Darwin, C. (1871). *Sexual selection and the descent of man.* Murray, London.

Davies, N.B. (1985). Cooperation and conflict among dunnocks, *Prunella modularis* in a variable mating system. *Animal Behaviour* **33,** 628-648.

Davies, N.B. (1989). Sexual conflict and the polygamy threshold. *Animal Behaviour* **38,** 226-234.

Dick, J. T. A. (1995). The cannibalistic behaviour of two *Gammarus* species (Crustacea: Amphipoda). *Journal of Zoology* **236,** 697-706.

Dodson, G., Morris, G. K. & Gwynne, D. T. (1983). Mating behavior in the primitive orthopteran genus *Cyphoderris* (Haglidae). In *Orthopteran mating systems: sexual competetion in a diverse group of insects.* (ed. D. T. Gwynne and G. K. Morris), pp. 305-318. Westview Press, Boulder.

Eberhard, W. G. (1996). *Female control: sexual selection by cryptic female choice.* Princeton University Press, Princeton.

Eberhard, W. G. (1997). Sexual selection bby cryptic female choice in insects and arachnids. In *The evolution of mating systems in insects and arachnids.* (ed. J. C. Choe and B. J. Crespi), pp. 32-57. Cambridge University Press, Cambridge.

Eberhard, W. G. (1998). Female roles in sperm competition. In *Sperm competition and sexual selection.* (ed. T. R. Birkhead and A. P. Moller). Academic Press, London.

Elgar, M. A. (1991). Sexual cannibalism, size dimorphism and courtship behavior in orb-weaving spiders (Araneae). *Evolution* **45,** 444-448.

Elgar, M. A. (1992). Sexual cannibalism in spiders and other invertebrates. In *Cannibalism: Ecology and Evolution among Diverse Taxa* (ed. M. A. Elgar and B. J. Crespi), pp. 128-155. Oxford University Press, Oxford.

Elgar, M. A. (1998). Sperm competition and sexual selection in spiders and other arachnids. In *Sperm competition and sexual selection* (ed. T. R. Birkhead and A. P. Moller), pp. 307-339. Academic Press, London.

Elgar, M. A. & Fahey, B. F. (1996). Sexual cannibalism, competition, and size dimorphism in the orb-weaving spider *Nephila plumipes* Latreille (Araneae: Araneoidea). *Behavioral Ecology* **7,** 195-198.

Elgar, M. A. & Nash, D. R. (1988). Sexual cannibalism in the garden spider *Araneus diadematus*. *Animal Behaviour* **36,** 1511-1517.

Elgar, M. A., Schneider, J. M. & Herberstein, M. E. (2000). Female control of paternity in the sexually cannibalistic spider *Argiope keyserlingi*. *Proceedings of the Royal Society of London* **267,** 2439-2443.

Endler, J. A. (1992). Signals, signal conditions, and the direction of evolution. *American Naturalist* **139 (suppl),** S125-S153.

Fahey, B. & Elgar, M. (1997). Sexual cohabitation as mate-guarding in the leaf-curling spider *Phonognatha graeffei* Keyserling (Araneoidea, Araneae). *Behavioral Ecology & Sociobiology* **40,** 127-133.

Foelix, R. F. (1996). *Biology of Spiders*. Harvard University Press, Cambridge.

Forster, L. M. (1992). The stereotyped behaviour of sexual cannibalism in *Latrodectus hasselti* Thorell (Araneae: Theriidae), the Australian redback spider. *Australian Journal of Zoology* **40,** 1-11.

Gould, S. J. (1984). Only his wings remained. *Natural History* **93,** 10-18.

Greenstone, M. H. (1979). Spider feeding behaviour optimises dietary essential amino acid composition. *Nature* **282,** 501-503.

Gross, M. R. (1994). The evolution of behavioural ecology. *Trends in Ecology and Evolution* **9,** 358-360.

Gwynne, D. T. (1984). Courtship feeding increases female reproductive success in bushcrickets. *Nature* **307,** 361-363.

Gwynne, D. T. & Simmons, L. W. (1990). Experimental reversal of courtship roles in an insect. *Nature* **346,** 171-174.

Hawkes, K., Rogers, A. R. & Charnov, E. L. (1995). The males dilemma--increased offspring production is more paternity to steal. *Evolutionary Ecology* **9,** 662-677.

Hedrick, A. V. & Riechert, S. E. (1989). Genetically-based variation between two spider populations in foraging behavior. *Oecologia* **80,** 533-539.

Huntingford, F. A. (1976). The relationship between anti-predator behaviour and aggression among con-specifics in the three-spined stickleback. *Animal Behaviour* **24,** 245-260.

Herberstein, M.E., Schneider, J.M., & Elgar, M.A. 2002. Costs of courtship and mating in a sexually cannibalistic orb-web spider: female mating strategies and their consequences for males. *Behavioral Ecology & Sociobiology* **51(5),** 440-446.

Hurd, L. E., Eisenberg, R. M., Fagan, W. F., Tilmon, K. J., Snyder, W. E., Vandersall, K. S., Datz, S. G. & Welch, J. D. (1994). Cannibalism reverses male-biased sex ratio in adult mantids: female strategy against food limitation. *Oikos* **69,** 193-198.

Jackson, R. R. (1980). The mating strategy of *Phidippus johnsoni* (Araneae, Salticidae): II. Sperm competition and the function of copulation. *Journal of Arachnology* **8,** 217-240.

Jackson, R. R. & Hallas, S. E. A. (1986). Comparative biology of *Portia africana, P. albimana, P. fimbriata, P. labiata, and P. shultzi*, araneophagic, web-building jumping spiders (Araneae: Salticidae): utilisation of webs, predatory versatility, and intraspecific interactions. *New Zealand Journal of Zoology* **13,** 423-489.

Jackson, R.R. & Wilcox, R.S. (1993). Spider flexibly chooses aggressive mimicry signals for different prey by trial and error. *Behaviour* **127,** 21-36.

Jackson, R. R. & Pollard, S. D. (1997). Jumping spider mating strategies: sex among cannibals in and out of webs. In *The evolution of mating systems in insects and arachnids* (ed. J. C. Choe and B. J. Crespi), pp. 340-351. Cambridge University Press, Cambridge.

Johns, P. M. & Maxwell, M. R. (1997). Sexual cannibalism: who benefits? *Trends in Ecology and Evolution* **12,** 127-128.

Johnson, J. C., Ivy, T. M. & Sakaluk, S. K. (1999). Female remating propensity contingent on sexual cannibalism in sagebrush crickets, *Cyphoderris strepitans*: a mechanism of cryptic female choice. *Behavioral Ecology* **10,** 227-233.

Jones, D. (1983). *Spiders of Britain and northern Europe*. Hamlyn, London.

Knoflach, B. & Van Harten, A. (2000). Palpal loss, single palp copulation and obligatory mate consumption in *Tidarren cuneolatum* (Tullgren, 1910) (Araneae, Theridiidae). *Journal of Natural History* **34,** 1639-1659.

Kreiter, N. A. & Wise, D. H. (2001). Prey availability limits fecundity and influences the movement patterns of female fishing spiders. *Oecologia* **127(3),** 417-424.

Kynaston, S. E., McErlain-Ward, P. & Mill, P. J. (1994). Courtship, mating behavior and sexual cannibalism in the praying mantis, *Sphodromantis lineola*. *Animal Behaviour* **47,** 739-741.

Lima, S. L. (1998). Stress and decision making under the risk of predation: Recent developments from behavioral, reproductive, and ecological perspectives. *Stress and Behavior* **27,** 215-290.

Liske, E. & Davis, W. J. (1987). Courtship and mating behaviour of the Chinese praying mantis, *Tenodera aridifolia sinensis*. *Animal Behaviour* **35, ap,** 1524-1537.

Matsura, T. & Morooka, K. (1983). Influences of prey density on fecundity in a mantis *Paratenodera angustipennis* S. *Oecologia* **56,** 306-312.

Maxwell, M. R. (1999). The risk of cannibalism and male mating behavior in the Mediterranean praying mantid, *Iris oratoria*. *Behaviour* **136,** 205-219.

McClintock, W. & Uetz, G. (1996). Female choice and pre-existing bias: Visual cues during courtship in two Schizocosa wolf spiders (Araneae: Lycosidae). *Animal Behaviour* **52,** 167-181.

Newman, J. A. & Elgar, M. A. (1991). Sexual cannibalism in orb-weaving spiders: An economic model. *American Naturalist* **138,** 1372-1395.

Parker, G. A. (1979). Sexual selection and sexual conflict. In *Sexual Selection and Reproductive Competition in Insects* (ed. M. S. Blum and N. A. Blum), pp. 123-166. Academic Press, New York.

Parker, G.A. (1998). Sperm competition and the evolution of ejaculates: towards a theory base. In *Sperm competition and sexual selection* (ed. T. R. Birkhead and A. P. Moller), pp. 3-54, Academic Press, London.

Peretti, A. V., Acosta, L. E. & Benton, T. G. (1999). Sexual cannibalism in scorpions: fact or fiction? *Biological Journal of the Linnean Society* **68,** 485-496.

Platnick, N. (1971). The evolution of courtship behaviour in spiders. *Bulletin of the British Arachnological Society* **2,** 40-47.

Polis, G. A. (1981). The evolution and dynamics of intraspecific predation. *Annual Review of Ecology and Systematics* **12,** 225-251.

Prenter, J., Elwood, R. W. & Montgomery, W. I. (1994). Male exploitation of female predatory behaviour reduces sexual cannibalism in male autumn spiders, *Metellina segmentata. Animal Behaviour* **47,** 235-236.

Proctor, H. C. (1991). Courtship in the water mite *Neumania papillator*: males capitalize on female adaptations for predation. *Animal Behaviour* **42,** 589-598.

Real, L. & Caraco, T. (1986). Risk and foraging in stochastic environments. *Annual Review of Ecology and Systematics* **17,** 371-390.

Riechert, S. E. & Harp, J. M. (1987). Nutritional ecology of spiders. In *Nutritional ecology of insects, mites, spiders and related invertebrates.* (ed. F. Slansky and J. G. Rodriguez), pp. 645-672. Wiley, New York.

Riechert, S. E. & Hedrick, A. V. (1993). A test for correlations among fitness-linked behavioural traits in the spider *Agelenopsis aperta* (Araneae: Agelenidae). *Animal Behaviour* **46,** 669-675.

Riechert, S. E. & Maynard-Smith, J. (1989). Genetic analyses of two behavioural traits linked to individual fitness in the desert spider *Agelenopsis aperta. Animal Behaviour* **37,** 624-637.

Robinson, M. H. (1982). Courtship and mating behavior in spiders. *Annual Review of Entomology* **27,** 1-20.

Robinson, M. H. & Robinson, B. (1980). Comparative studies of the courtship and mating behavior of tropical araneid spiders. *Pacific Insects Monographs* **36,** 1-218.

Roeder, K. D. (1935). An experimental analysis of the sexual behaviour of the praying mantis (*Mantis religiosa*). *Biological Bulletin* **69,** 203-220.

Rowe, L., Arnqvist, A., Sih, A. & Krupa, J. J. (1994). Sexual conflict and the evolutionary ecology of mating patterns: water striders as a model system. *Trends in Ecology and Evolution* **9,** 289-293.

Ryan, M. J. (1990). Sexual selection, sensory systems and sensory exploitation. *Oxford Surveys in Evolutionary Biology* **7,** 157-195.

Sakaluk, S. K. (1984). Male crickets feed females to ensure complete sperm transfer. *Science* **223,** 609-610.

Sakaluk, S. K. (1990). Sexual selection and predation: balancing reproductive and survival needs. In *Insect defenses* (ed. D. L. Evans and J. O. Schmidt), pp. 63-90. SUNY Press, Albany.

Sakaluk, S. K., Morris, G. K. & Snedden, W. A. (1987). Mating and its effect on acoustic signalling behavior in a primitive orthopteran, *Cyphoderris strepitans* (Haglidae): the cost of feeding females. *Behavioral Ecology and Sociobiology* **21,** 173-178.

Sasaki, T. & Iwahashi, O. (1995). Sexual cannibalism in an orb-weaving spider *Argiope aemula*. *Animal Behaviour* **49,** 1119-1121.

Schneider, J.M. & Elgar, M.A. (2001). Sexual cannibalism and sperm competition in the golden orb-web spider *Nephila plumipes* (Araneoidea): female and male perspectives. *Behavioral Ecology* **12 (5),** 547-552.

Schneider, J. M., Herberstein, M. E., Champion de Crespigny, F., Ramamurthy, S. & Elgar, M. A. (2000). Sperm competition and small size advantage for males of the golden orb-web spider *Nephila edulis*. *Journal of Evolutionary Biology* **13,** 939-946.

Schneider, J. M. & Lubin, Y. (1998). Intersexual conflict in spiders. *Oikos* **83,** 406-506.

Sih, A. (1994). Predation risk and the evolutionary ecology of reproductive behavior. *Journal of Fish Biology* **45,** 111-130.

Simmons, L. W. & Parker, G. A. (1989). Nuptial feeding in insects: mating effort versus paternal investment. *Ethology* **81,** 332-349.

Smith, R. L. (1984). *Sperm Competition and the Evolution of Animal Mating Systems*. Academic Press, Orlando.

Spence, J. R., Zimmerman, M. & Wojcicki, J. P. (1996). Effects of food limitation and sexual cannibalism on reproductive output of the fishing spider *Dolomedes triton* (Araneae: Pisauridae). *Oikos* **75,** 373-382.

Thornhill, R. (1976a). Sexual selection and nuptial feeding behavior in *Bittacus apicalis* (Insecta:Mecoptera). *The American Naturalist* **110,** 529-548.

Thornhill, R. (1976b). Sexual selection and paternal investment in insects. *American Naturalist* **110,** 153-163.

Thornhill, R. & Alcock, J. (1983). *The evolution of insect mating systems*. Harvard University Press, Cambridge.

Uetz, G. W. (1992). Foraging strategies of spiders. *Trends in Ecology and Evolution* **7,** 307-310.

Vahed, K. (1998). The function of nuptial feeding in insects--review of empirical studies. *Biological Reviews* **73,** 43-78.

Vollrath, F. (1980). Male body size and fitness in the web-building spider *Nephila clavipes*. *Zeit. Tierpsych* **53,** 61-78.

Vollrath, F. (1987). Growth, Foraging and Reproductive Success. In *Ecophysiology of Spiders* (ed. W. Nentwig), pp. 357-370. Springer-Verlag, Berlin.

Watson, P. J. (1998). Multi-male mating and female choice increase offspring growth in the spider *Neriene litigiosa* (Linyphiidae). *Animal Behaviour* **55,** 387-403.

Wiley, H. & Poston, J. (1996). Indirect mate choice, competition for mates, and coevolution of the sexes. *Evolution* **50,** 1371-1381.

Wise, D. (1983). An electron microscope study of the karyotypes of two wolf spiders. *Canadian Journal of Genetic Cytology* **25,** 161-168.

Zimmerman, M. & Spence, J. R. (1989). Prey use of the fishing spider *Dolomedes triton*: An important predator of the neuston community. *Oecologia* **80,** 187-194.

Zimmerman, M. & Spence, J. R. (1992). Adult population dynamics and reproductive effort of the fishing spider *Dolomedes triton* (Araneae, Pisauridae) in central Alberta. *Canadian Journal of Zoology* **70,** 2224-2233.

CHAPTER 3

Anderrson M, 1994. Sexual selection. Princeton: Princeton University Press.

Andrade MCB, 1996. Sexual selection for male sacrifice in the Australian redback spider. *Science*, **271**, 70-73.

Arnqvist G, 1992. Courtship Behavior and Sexual Cannibalism in the Semiaquatic Fishing Spider, *Dolomedes fimbriatus* (Clerck) (Araneae, Pisauridae). *Journal of Arachnology,* **20**, 222-226.

Arnqvist G, Henriksson S, 1997. Sexual cannibalism in the fishing spider and a model for the evolution of sexual cannibalism based on genetic constraints. *Evolutionary Ecology*, **11**, 255-273.

Barth FG, 1982. Spiders and vibratory signals: sensory reception and behavioral significance. In: Spider communication: mechanisms and ecological significance. (Ed. by Witt, P. N. & Rovner, J. S.), pp. 67-122. Princeton: Princeton University Press.

Bleckmann H, Barth FG, 1984. Sensory ecology of a semi-aquatic spider (*Dolomedes triton*). II. The release of predatory behaviour by water surface waves. *Behavioral Ecology & Sociobiology*, **14**, 303-312.

Bleckmann H, Lotz T, 1987. The vertebrate-catching behavior of the fishing spider *Dolomedes triton* (Araneae, Pisauridae). *Animal Behaviour*, **35**, 641-651.

Carico J. E. 1973. The nearctic species of the genus *Dolomedes* (Araneae: Pisauridae). Bulletin of the Museum of Comparative Zoology, 144, 435-488.

Elgar MA, 1991. Sexual Cannibalism, Size Dimorphism, and Courtship Behavior in Orb-weaving Spiders (Araneidae). *Evolution*, **45**, 444-448.

Elgar MA, 1992. Sexual cannibalism in spiders and other invertebrates. In: Cannibalism: Ecology and Evolution among Diverse Taxa (Ed. by Elgar, M. A. & Crespi, B. J.), pp. 128-155. Oxford: Oxford University Press.

Elgar MA, Fahey BF, 1996. Sexual cannibalism, competition, and size dimorphism in the orb-weaving spider *Nephila plumipes* Latreille (Araneae: Araneoidea). *Behavioral Ecology*, **7**, 195-198.

Elgar MA, Ghaffar N, Read AF, 1990. Sexual Dimorphism in Leg Length among Orb-Weaving Spiders - a Possible Role for Sexual Cannibalism. *Journal of Zoology,* **222**, 455-470.

Elgar MA, Nash DR, 1988. Sexual cannibalism in the garden spider *Araneus diadematus*. *Animal Behaviour*, **36**, 1511-1517.

Elgar MA, Schneider JM, Herberstein ME, 2000. Female control of paternity in the sexually cannibalistic spider *Argiope keyserlingi. Proceedings of the Royal Society of London Series B-Biological Sciences*, **267**, 2439-2443.

Fahey BF, Elgar MA, 1997. Sexual cohabitation as mate-guarding in the leaf-curling spider *Phonognatha graeffei* Keyserling (Araneoidea, Araneae). *Behavioral Ecology and Sociobiology*, **40**, 127-133.

Head G, 1995. Selection on Fecundity and Variation in the Degree of Sexual Size Dimorphism among Spider Species (Class Araneae). *Evolution*, **49**, 776-781.

Hormiga G, Scharff N, Coddington JA, 2000. The phylogenetic basis of sexual size dimorphism in orb-weaving spiders (Araneae, Orbiculariae). *Systematic Biology*, **49**, 435-462.

Newman JA, Elgar MA, 1991. Sexual Cannibalism in Orb-Weaving Spiders - an Economic-Model. *American Naturalist*, **138**, 1372-1395.

Prenter J, Elwood RW, Montgomery WI, 1998. No association between sexual size dimorphism and life histories in spiders. *Proceedings of the Royal Society of London Series B-Biological Sciences,* **265**, 57-62.

Prenter J, Elwood RW, Montgomery WI, 1999. Sexual size dimorphism and reproductive investment by female spiders: A comparative analysis. *Evolution*, *53*, 1987-1994.

Robinson MH, Robinson B, 1980. Comparative studies of the courtship and mating behavior of tropical araneid spiders. *Pacific Insects Monographs*, **36**, 1-218.

SAS Institute (1988). SAS/STAT User's Guide. Release 6.03 edn. Cary, North Carolina: SAS Institute.

Schneider JM, Elgar MA, 2002. Sexual cannibalism in *Nephila plumipes* as a consequence of female life history strategies. *Journal of Evolutionary Biology*, **15**, 84-91.

Thornhill R, Alcock J, 1983. The evolution of insect mating systems. Cambridge: Harvard University Press.

Vollrath F, 1987. Growth, Foraging and Reproductive Success. In: Ecophysiology of Spiders (Ed. by Nentwig W), pp. 357-370. Berlin: Springer-Verlag.

Vollrath F, Parker GA, 1992. Sexual Dimorphism and Distorted Sex-Ratios in Spiders. *Nature*, **360**, 156-159.

Vollrath F, Parker GA, 1997. Giant female or dwarf male spiders? Reply. *Nature*, **385**, 688-688.

Zimmerman M, Spence JR, 1989. Prey use of the fishing spider *Dolomedes triton*: An important predator of the neuston community. *Oecologia*, **80**, 187-194.

Zimmerman M, Spence JR, 1992. Adult population dynamics and reproductive effort of the fishing spider *Dolomedes triton* (Araneae, Pisauridae) in central Alberta. *Canadian Journal of Zoology*, **70**, 2224-2233.

CHAPTER 4

Andersson, M. 1994. *Sexual selection*. Princeton, New Jersey: Princeton University Press.

Andrade, M.C.B. 1996. Sexual selection for male sacrifice in the Australian redback spider. *Science*, **271**, 70-73.

Andrade, M.C.B. 1998. Female hunger can explain variation in cannibalism despite male sacrifice in redback spiders. *Behavioral Ecology*, **9**, 35-42.

Arnold, S.J. 1992. Constraints on phenotypic evolution. *American Naturalist*, **140**, S85-S107.

Arnqvist, G. 1992. Courtship behaviour and sexual cannibalism in the fishing spider, *Dolomedes fimbriatus* (Clerck) (Aranea: Pisauridae). *Journal of Arachnology*, **20**, 222-226.

Arnqvist, G. & Henriksson, S. 1997. Sexual cannibalism in the fishing spider and a model for the evolution of sexual cannibalism based on genetic constraints. *Evolutionary Ecology*, **11**, 255-273.

Bakker, T.C.M. 1994. Evolution of aggressive behaviour in the threespine stickleback. In: *The Evolutionary Biology of the Threespine Stickleback* (Ed. by M.A. Bell & S.A. Foster), pp. 345-380. Oxford: Oxford University Press.

Barth, F.G. 1982. Spiders and vibratory signals. Sensory reception and behavioral significance. In: *Spider communication. Mechanisms and ecological significance* (Ed. P. Witt & J.S. Rovner), Princeton NJ, Princeton University Press.

Bleckmann, H. & Barth, F.G. 1984. Sensory ecology of a semi-aquatic spider (*Dolomedes triton*). II. The release of predatory behaviour by water surface waves. *Behavioral Ecology & Sociobiology*, 14, 303-312.

Bleckmann, H. & Bender, M. 1987. Water surface waves generated by the male pisaurid spider *Dolomedes triton* (Walckenaer) during courtship behaviour. *Journal of Arachnology*, **15**, 363-369.

Bleckmann, H. & Lotz, T. 1987. The vertebrate-catching behaviour of the fishing spider *Dolomedes triton* (Araneae: Pisauridae). *Animal Behaviour*, **35**, 641-651.

Breene, R.G. & Sweet, M.H. 1985. Evidence of insemination of multiple females by the male black widow spider, *Latrodectus mactans* (Araneae: Theridiidae). *Journal of Arachnology*, **13**, 331-335.

Buskirk, R.E., Frohlich, C. & Ross, K.G. 1984. The natural selection of sexual cannibalism. *American Naturalist*, **123**, 612-625.

Carico, J.E. 1973. The nearctic species of the genus *Dolomedes* (Araneae: Pisauridae*). Bulletin of The Museum of Comparative Zoology*, **144**, 435-488.

Eberhard, W.G. 1998. Female roles in sperm competition. In: *Sperm competition and sexual selection* (Ed. by T.R. Birkhead & A.P. Moller), London: Academic Press.

Elgar, M.A. 1992. Sexual cannibalism in spiders and other invertebrates. In: *Cannibalism: Ecology and Evolution among Diverse Taxa* (Ed. by M.A. Elgar & B.J. Crespi), pp. 128-155. Oxford: Oxford University Press.

Elgar, M.A. 1998. Sperm competition and sexual selection in spiders and other arachnids. In: *Sperm competition and sexual selection* (Ed. by T.R. Birkhead & A.P. Moller), London: Academic Press.

Elgar, M.A. & Nash, D.R. 1988. Sexual cannibalism in the garden spider, *Araneus diadematus*. *Animal Behaviour*, **36**, 1511-1517.

Foelix, R.F. 1982. *Biology of Spiders*. Cambridge, MA: Harvard University Press.

Greenstone, M.H. 1979. Spider feeding behaviour optimises dietary essential amino acid composition. *Nature*, **282**, 501-503.

Gould, S.J. 1984. Only his wings remained. *Natural History*, **93**, 10-18.

Hedrick, A.V. & Riechert S.E. 1989. Genetically-based variation between two spider populations in foraging behavior. *Oecologia*, **80**, 533-539.

Houle, D. 1991. Genetic covariance of fitness correlates: What genetic correlations are made of and why it matters. *Evolution*, **45**, 630-648.

Huntingford, F.A. 1976. The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback. *Animal Behavior*, **24**, 245-260.

Jackson, R.R. 1980. Cannibalism as a factor in the mating strategy of the jumping spider *Phidippus johnsoni* (Araneae, Salticidae). *Bulletin of the British Arachnology Society*, **5**, 129-133.

Johns, P.M. & Maxwell, M.R. 1997. Sexual cannibalism: who benefits? *Trends in Ecology and Evolution*, **12**, 127-128.

Newman, J.A. & Elgar, M.A. (1991). Sexual cannibalism in orb-weaving spiders: An economic model. *American Naturalist*, **138**, 1372-1395.

Parker, G.A. 1979. Sexual selection and sexual conflict. In: *Sexual selection and reproductive competition in insects* (Ed. by M.S. Blum & N.A.Blum), pp. 123-166. Academic Press: New York.

Partridge, L. 1994. Genetic and nongenetic approaches to questions about sexual selection. In: *Quantitative genetic studies of behavioral evolution* (Ed. by C.R.B. Boake), pp. 126-141. Chicago: Chicago University Press.

Polis, G.A. 1981. The evolution and dynamics of intraspecific predation. *Annual Review of Ecology and Systematics*, **12**, 225-251.

Price, T. & Langen, T. 1992. Evolution of correlated characters. *Trends in Ecology and Evolution*, **7**, 307-310.

Riechert, S.E. & Harp, J.M. 1987. Nutritional ecology of spiders. In: *Nutritional ecology of insects, mites, spiders, and related invertebrates* (Ed. by F. Slansky & J.G. Rodriguez), pp. 645-672. New York: Wiley.

Riechert, S.E. & Hedrick, A.V. 1993. A test for correlations among fitness-linked behavioural traits in the spider *Agelenopsis aperta* (Araneae: Agelenidae). *Animal Behaviour*, **46**, 669-675.

SAS Institute 1988. *SAS/STAT user's guide*. release 6.03 edn. Cary, North Carolina: SAS Institute Inc.

Sih, A. 1992. Integrative approaches to the study of predation: general thoughts and a case study on sunfish and salamander larvae. *Annal Zool Fenn*, **29**, 183-198.

Sih, A. & Gleeson, S. 1995. A limits-oriented approach to evolutionary ecology. *Trends in Ecology and Evolution*, **10**, 378-382.

Sih, A., L.B. Kats and E.F. Maurer. 2003. Behavioral correlations across situations and the evolution of antipredator behavior in a sunfish-salamander system. *Animal Behaviour*, **65,** 29-44.

Spence, J.R., Zimmerman, M. & Wojcicki, J.P. 1996. Effects of food limitation and sexual cannibalism on reproductive output of the fishing spider *Dolomedes triton* (Araneae: Pisauridae). *Oikos*, **75**, 373-382.

Thornhill, R. 1976. Sexual selection and paternal investment in insects. *American Naturalist*, **110**, 153-163.

Uetz, G.W. 1992. Foraging strategies of spiders. *Trends in Ecology and Evolution*, **7**, 307-310.

Wiley, H. & Poston, J. 1996. Indirect mate choice, competition for mates, and coevolution of the sexes. *Evolution*, **50 (4)**, 1371-1381.

Zimmerman, M. & Spence, J.R. 1989. Prey use of the fishing spider *Dolomedes triton*: An important predator of the neuston community. *Oecologia*, **80**, 187-194 .

Zimmerman, M. & Spence, J.R. 1992. Adult population dynamics and reproductive effort of the fishing spider *Dolomedes triton* (Araneae, Pisauridae) in central Alberta. *Canadian Journal of Zoology*, **70**, 2224-2233.

CHAPTER 5

Andrade, M. C. B. 1996. Sexual selection for male sacrifice in the Australian redback spider. *Science*, **271,** 70-72.

Andrade, M. C. B. 1998. Female hunger can explain variation in cannibalism despite male sacrifice in redback spiders. *Behavioral Ecology*, **9,** 35-42.

Arnqvist, G. 1992. Courtship Behavior and Sexual Cannibalism in the Semiaquatic Fishing Spider, Dolomedes-Fimbriatus (Clerck) (Araneae, Pisauridae). *Journal of Arachnology*, **20,** 222-226.

Arnqvist, G. & Henriksson, S. 1997. Sexual cannibalism in the fishing spider and a model for the evolution of sexual cannibalism based on genetic constraints. *Evolutionary Ecology*, **11,** 255-273.

Barth, F. G. 1982. Spiders and vibratory signals: sensory reception and behavioral significance. In: *Spider communication: mechanisms and ecological significance.* (Ed. by Witt, P. N. & Rovner, J. S.), pp. 67-122. Princeton: Princeton University Press.

Bleckmann, H. & Barth, F. G. 1984. Sensory ecology of a semi-aquatic spider (*Dolomedes triton*). II. The release of predatory behaviour by water surface waves. *Behavioral Ecology & Sociobiology*, **14,** 303-312.

Bleckmann, H. & Lotz, T. 1987. The vertebrate-catching behavior of the fishing spider *Dolomedes triton* (Araneae, Pisauridae). *Animal Behaviour*, **35,** 641-651.

Breene, R. G. & Sweet, M. H. 1985. Evidence of insemination of multiple females by the male black widow spider, *Latrodectus mactans* (Araneae, Theridiidae). *Journal of Arachnology*, **13,** 331-335.

Carico, J. E. 1973. The nearctic species of the genus *Dolomedes* (Araneae: Pisauridae). *Bulletin of the Museum of Comparative Zoology*, **144,** 435-488.

Elgar, M. A. 1991. Sexual Cannibalism, Size Dimorphism, and Courtship Behavior in Orb-Weaving Spiders (Araneidae). *Evolution*, **45,** 444-448.

Elgar, M. A. 1992. Sexual cannibalism in spiders and other invertebrates. In: *Cannibalism: Ecology and Evolution among Diverse Taxa* (Ed. by Elgar, M. A. & Crespi, B. J.), pp. 128-155. Oxford: Oxford University Press.

Elgar, M. A. & Nash, D. R. 1988. Sexual cannibalism in the garden spider *Araneus diadematus*. *Animal Behaviour*, **36,** 1511-1517.

Jackson, R. R. 1980. The mating strategy of *Phidippus johnsoni* (Araneae, Salticidae): II. Sperm competition and the function of copulation. *Journal of Arachnology*, **8,** 217-240.

Jackson, R. R. & Pollard, S. D. 1997. Jumping spider mating strategies: sex among cannibals in and out of webs. In: *The evolution of mating systems in insects and arachnids* (Ed. by Choe, J. C. & Crespi, B. J.), pp. 340-351. Cambridge: Cambridge University Press.

Krebs, J.R. & Davies, N.B. 1991. *Behavioural Ecology: an evolutionary approach.* 3rd edn. Oxford: Blackwell Scientific Publications.

Newman, J. A. & Elgar, M. A. 1991. Sexual Cannibalism in Orb-Weaving Spiders - an Economic-Model. *American Naturalist*, **138,** 1372-1395.

Rowe, L., Arnqvist, A., Sih, A. & Krupa, J. J. 1994. Sexual conflict and the evolutionary ecology of mating patterns: water striders as a model system. *Trends in Ecology and Evolution*, **9,** 289-293.

Schneider, J. M. & Elgar, M. A. 2002. Sexual cannibalism in Nephila plumipes as a consequence of female life history strategies. *Journal of Evolutionary Biology*, **15,** 84-91.

Spence, J. R., Zimmerman, M. & Wojcicki, J. P. 1996. Effects of food limitation and sexual cannibalism on reproductive output of the fishing spider *Dolomedes triton* (Araneae: Pisauridae). *Oikos*, **75,** 373-382.

Wojcicki, J.P. 1992. A description of the reproductive biology of the fishing spider *Dolomedes triton* (Walck.) (Araneae:Pisauridae) in central Alberta. M.S. Thesis, University of Alberta.

Zimmerman, M. & Spence, J. R. 1989. Prey use of the fishing spider *Dolomedes triton*: An important predator of the neuston community. *Oecologia*, **80,** 187-194.

Zimmerman, M. & Spence, J. R. 1992. Adult population dynamics and reproductive effort of the fishing spider *Dolomedes triton* (Araneae, Pisauridae) in central Alberta. *Canadian Journal of Zoology*, **70,** 2224-2233.

CHAPTER 6

Andrade, M. C. B. 1996. Sexual selection for male sacrifice in the Australian redback spider. *Science*, **271,** 70-72.

Arnqvist, G. 1992. Courtship Behavior and Sexual Cannibalism in the Semiaquatic Fishing Spider, Dolomedes-Fimbriatus (Clerck) (Araneae, Pisauridae). *Journal of Arachnology*, **20,** 222-226.

Arnqvist, G. & Henriksson, S. 1997. Sexual cannibalism in the fishing spider and a model for the evolution of sexual cannibalism based on genetic constraints. *Evolutionary Ecology*, **11,** 255-273.

Autumn, K., Ryan, M.J. & Wake, D.B. 2002. Integrating historical and mechanistic biology enhances the study of adaptation. *Quarterly Review of Biology*, **77(4),** 383-408.

Bakker, T.C.M. 1986. Aggressiveness in sticklebacks (*Gasterosteus aculeatus*): a behaviour-genetic study. *Behaviour*, **98,** 1-144.

Barth, F. G. 1982. Spiders and vibratory signals: sensory reception and behavioral significance. In: *Spider communication: mechanisms and ecological significance.* (Ed. by Witt, P. N. & Rovner, J. S.), pp. 67-122. Princeton: Princeton University Press.

Bishop, S. C. 1924. A revision of the Pisauridae of the United States. *Bulletin of the New York State Museum,* **252,** 1-140.

Bleckmann, H. & Barth, F. G. 1984. Sensory ecology of a semi-aquatic spider (*Dolomedes triton*). II. The release of predatory behaviour by water surface waves. *Behavioral Ecology & Sociobiology*, **14,** 303-312.

Bleckmann, H. & Lotz, T. 1987. The vertebrate-catching behavior of the fishing spider *Dolomedes triton* (Araneae, Pisauridae). *Animal Behaviour*, **35,** 641-651.

Carico, J. E. 1973. The nearctic species of the genus *Dolomedes* (Araneae: Pisauridae). *Bulletin of the Museum of Comparative Zoology*, **144,** 435-488.

Choe, J. C. & Crespi, B. J. 1997. *The evolution of mating systems in insects and arachnids.* Cambridge: Cambridge University Press.

Crowley, P. H., Travers, S. E., Linton, M. C., Cohn, S. L., Sih, A. & Sargent, R. C. 1991. Mate density, predation risk, and the seasonal sequence of mate choices: a dynamic game. *The American Naturalist*, **137,** 567-596.

Elgar, M. A. 1992. Sexual cannibalism in spiders and other invertebrates. In: *Cannibalism: Ecology and Evolution among Diverse Taxa* (Ed. by Elgar, M. A. & Crespi, B. J.), pp. 128-155. Oxford: Oxford University Press.

Elgar, M. A. & Nash, D. R. 1988. Sexual cannibalism in the garden spider *Araneus diadematus*. *Animal Behaviour*, **36,** 1511-1517.

Elgar, M. A., Schneider, J. M. & Herberstein, M. E. 2000. Female control of paternity in the sexually cannibalistic spider Argiope keyserlingi. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **267,** 2439-2443.

Fahey, B. F. & Elgar, M. A. 1997. Sexual cohabitation as mate-guarding in the leaf-curling spider Phonognatha graeffei Keyserling (Araneoidea, Araneae). *Behavioral Ecology and Sociobiology*, **40,** 127-133.

Huntingford, F. A. 1976. The relationship between anti-predator behaviour and aggression among con-specifics in the three-spined stickleback. *Animal Behaviour*, **24,** 245-260.

Jackson, R. R. & Pollard, S. D. 1997. Jumping spider mating strategies: sex among cannibals in and out of webs. In: *The evolution of mating systems in insects and arachnids* (Ed. by Choe, J. C. & Crespi, B. J.), pp. 340-351. Cambridge: Cambridge University Press.

Johns, P. M. & Maxwell, M. R. 1997. Sexual cannibalism: who benefits? *Trends in Ecology and Evolution*, **12,** 127-128.

Ketterson, E.D. & Nolan, V. Jr. 1999. Adaptation, exaptation and constraint: a hormonal perspective. *American Naturalist, Supplement,* **154,** 4-25.

Kirkpatrick, M. & Ryan, M.J. 1991. The evolution of mating preferences and the paradox of the lek. *Nature,* **350,** 33-38.

Lima, S. L. 1998. Stress and decision making under the risk of predation: Recent developments from behavioral, reproductive, and ecological perspectives. *Stress and Behavior,* **27,** 215-290.

Maupin, J.L. & Riechert, S.E. 2001. Superfluous killing in spiders: a consequence of adaptation to food-limited environments. *Behavioural Ecology,* **12,** 569-576.

Newman, J. A. & Elgar, M. A. 1991. Sexual Cannibalism in Orb-Weaving Spiders - an Economic-Model. *American Naturalist,* **138,** 1372-1395.

Real, L. & Caraco, T. 1986. Risk and foraging in stochastic environments. *Annual Review of Ecology and Systematics,* **17,** 371-390.

Riechert, S. E. & Hedrick, A. V. 1993. A test for correlations among fitness-linked behavioural traits in the spider *Agelenopsis aperta* (Araneae: Agelenidae). *Animal Behaviour,* **46,** 669-675.

Riechert, S. E. & Maynard-Smith, J. 1989. Genetic analyses of two behavioural traits linked to individual fitness in the desert spider *Agelenopsis aperta. Animal Behaviour,* **37,** 624-637.

Rowe, L., Arnqvist, A., Sih, A. & Krupa, J. J. 1994. Sexual conflict and the evolutionary ecology of mating patterns: water striders as a model system. *Trends in Ecology and Evolution,* **9,** 289-293.

Ryan, M.J. & Rand, A.S. 1999. Phylogenetic influence on mating call preferences in female tungara frogs *Physalaemus pustulosus. Animal Behaviour,* **57,** 945-956.

Sakaluk, S. K. 1990. Sexual selection and predation: balancing reproductive and survival needs. In: *Insect defenses* (Ed. by Evans, D. L. & Schmidt, J. O.), pp. 63-90. Albany: SUNY Press.

Schneider, J. M. & Elgar, M. A. 2002. Sexual cannibalism in Nephila plumipes as a consequence of female life history strategies. *Journal of Evolutionary Biology,* **15,** 84-91.

Sih, A. 1994. Predation risk and the evolutionary ecology of reproductive behavior. *Journal of Fish Biology,* **45,** 111-130.

Sih, A., L.B. Kats and E.F. Maurer. 2003. Behavioral correlations across situations and the evolution of antipredator behavior in a sunfish-salamander system. *Animal Behaviour*, **65,** 29-44.

Sih, A., M. Lauer and JJ Krupa. 2002. Path analysis and the relative importance of amle female conflict, female choice and male-male competition in water striders. *Animal Behaviour*, **63,** 1079-1089.

Spence, J. R., Zimmerman, M. & Wojcicki, J. P. 1996. Effects of food limitation and sexual cannibalism on reproductive output of the fishing spider *Dolomedes triton* (Araneae: Pisauridae). *Oikos*, **75,** 373-382.

Wilson, D.S., Coleman, K., Clark, A.B. & Biederman, L. 1993. The shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): an ecological study of a psychological trait. *Journal of Comparative Psychology,* **107,** 250-260.

Zimmerman, M. & Spence, J. R. 1989. Prey use of the fishing spider *Dolomedes triton*: An important predator of the neuston community. *Oecologia*, **80,** 187-194.

Zimmerman, M. & Spence, J. R. 1992. Adult population dynamics and reproductive effort of the fishing spider *Dolomedes triton* (Araneae, Pisauridae) in central Alberta. *Canadian Journal of Zoology*, **70,** 2224-2233.

VITA

JAMES CHADWICK JOHNSON

EDUCATION

- M.S. Biological Sciences 1998, Illinois St. University, Normal, IL; Advisor: Scott Sakaluk
- B.A. Psychobiology 1990, Earlham College, Richmond, IN

PUBLICATIONS

Bell A, Davis J, DeBose J, Long S, Mabry K, Stankowich T, Watters J, Johnson JC 2002. Greatest hits in behavioral ecology. *Trends in Ecology and Evolution*, **17(6):** 296.

Ivy TM, Johnson JC, Sakaluk SK 1999. Hydration benefits to courtship feeding in crickets. *Proceedings of the Royal Society of London* **266:** 1523-1527.

Johnson JC (submitted to *Behavioral Ecology* 1-28-03) The role of male body size and sexual size dimorphism in mating interactions of a sexually cannibalistic fishing spider.

Johnson JC, Ivy TM, Sakaluk SK 1999. Female remating propensity contingent on sexual cannibalism in sagebrush crickets, *Cyphoderris strepitans*: a mechanism of cryptic female choice. *Behavioral Ecology* **10:** 227-233.

Johnson JC 1998. Post-copulatory female choice in sagebrush crickets (*Cyphoderris strepitans*). M.S. Thesis, Illinois State University.

Sih A, Bell A, Johnson JC, Ziemba R (Provisionally accepted *Quarterly Review of Biology*) Behavioral syndromes: an integrative overview.

Wu JC, Buchsbaum MS, Johnson JC, Hershey TG 1993. Magnetic resonance and PET imaging of the corpus callosum. *Jl. Aff. Disorders*, **28(1):** 15-25.

Wu JC, Gillin JC, Buchsbaum MS, Hershey TG, Johnson JC, Bunney WE 1992. Effect of sleep deprivation on brain metabolism of depressed patients. *Am. Jl Psych.*, **149(4):** 538-543.

Wu JC, Buchsbaum MS, Hershey TG, Hazlett E, Johnson JC 1991. PET in Generalized Anxiety Disorder. *Biol. Psych.*, **29:** 81-99.

JOURNALS REFEREED

American Midland Naturalist   *Animal Behaviour*   *Behaviour*

Behavioral Ecology   *Behavioral Ecology and Sociobiology*

Journal of Animal Ecology   *Ethology*

RESEARCH EXPERIENCE

- **Research Assistant** (2000-2003), Dr. Andrew Sih, University of California, Davis, CA
- **Research Assistant** (1996-1998), Dr. Scott K. Sakaluk, Illinois State University, Normal, IL
- **Research Assistant** (1995), Dr. David Westneat, University of Kentucky, Lexington, KY

GRANTS, FELLOWSHIPS AND HONORS

- National Science Foundation, Doctoral Dissertation Improvement Grant, 2002-2004
- Sigma Xi, Grant in Aid of Research, 2001
- University of Kentucky, Graduate School, Dissertation Enhancement Award, 2001
- Animal Behavior Society, Graduate Student Research Award, 2000
- National Science Foundation, Graduate Research Training (GRT) Fellowship, 1998-2000
- University of Kentucky, Graduate School, Graduate Student Development Award, 1999
- Illinois State University, Department of Biological Sciences:
    1. Outstanding M.S. student award, 1998
    2. Mockford Fellowship for outstanding student research, 1997