Ethology

The Interaction of Female Condition and Mating Status on Male-Male Aggression in a Wolf Spider

Chad D. Hoefler*, Gayatri Guhanarayan*, Matthew H. Persons† & Ann L. Rypstra‡

* Center for Animal Behavior and Department of Zoology, Miami University, Oxford, OH, USA
† Department of Biology, Susquehanna University, Selinsgrove, PA, USA
‡ Center for Animal Behavior and Department of Zoology, Miami University, Hamilton, OH, USA

Correspondence
Chad D. Hoefler, Department of Biology,
Arcadia University, Glenside, PA 19038, USA.
E-mail: hoeflerc@arcadia.edu

Received: July 29, 2008
Initial acceptance: October 23, 2008
Final acceptance: November 25, 2008
(D. Zeh)

doi: 10.1111/j.1439-0310.2009.01627.x

Abstract

Fighting behavior has been studied extensively with strong emphases on factors that independently determine winners and losers as well as how much effort an individual should invest in a given contest for a resource. Much less attention has been paid to how interacting qualities of disputed resources modulate aggression. In a laboratory study, we examined the interactive effects of female condition and mating status on dyadic male aggression in the wolf spider *Pardosa milvina*. We discovered that males exhibited significantly more aggressive behaviors when in the presence of virgin females in good condition and displayed lower and statistically similar levels of aggression when placed with virgin, poor condition females; mated, good condition females; mated, poor condition females; and no females. Because previous studies have suggested that virgin females alone should be highly prized because of putative first-mate sperm priority patterns, this study contributes to this body of literature by suggesting that diet history and body condition mitigate the reproductive advantages of mating with virgin females as indicated by levels of male-male aggression, but further investigation is needed.

Introduction

The evolution of fighting behavior has been extensively studied over a period of decades with a strong focus on male-male competition for resources. The development of game theory and the concept of evolutionarily stable strategies has helped clarify the logic of male contests (Maynard Smith & Price 1973; Maynard Smith 1974, 1982), and theorists and empiricists have identified many of the predictors of winners within contests (Parker 1974; Maynard Smith & Parker 1976; Parker & Rubenstein 1981; Austad 1983; Enquist & Leimar 1987; Dodson & Beck 1993; Hack et al. 1997; Hsu & Wolf 1999; Hoefler 2002; Lindström & Pampoulie 2005; Gherardi 2006). Males often compete over resources (e.g., potential mates, foraging areas, nest sites) that directly or indirectly affect fitness (Trivers 1972; Andersson 1994). However, intense male-male competition is expected when mating opportunities are limited and/or when females vary in quality and can be assessed based upon features that indicate potential reproductive success (Turner & Huntingford 1986; Andersson 1994).

Because agonistic contests can be metabolically costly and lead to risks of injury and/or predation (Huntingford & Turner 1987; Marden & Waage 1990; Hack 1997; Sneddon et al. 1999), it is expected that individuals will modulate their contest effort according to the competitive context; i.e. selection should favor individuals that adjust their fighting effort following resource value assessment (as well as their own fighting ability) (Parker 1974; Maynard Smith & Parker 1976; Parker & Stuart; Arnott & Elwood 2007, 2008). Game theory models demonstrate that fighting costs will increase with the value of the resource (e.g. Bishop et al. 1978; Enquist & Leimar 1987), thus we expect contestants to escalate to intense and/or costly fighting when competing for a highly valued resource such as a prospective mate (e.g. Buena & Walker 2008). In empirical studies, resource value assessment is typically inferred by quantifying variation in costs that animals are willing to pay (Arnott & Elwood 2008). Costs are usually estimated from vigor of specific behaviors (e.g. Briffa et al. 2000), injury (e.g. Austad 1983), contest duration (e.g. Thornhill 1984), and/or physiological changes (e.g. Prenter et al. 2006). Although many studies have considered a variety of factors (viz. differences in fighting ability, effects of resource value, ownership, etc.) that independently affect either the resolution of contests or levels of male-male aggression (e.g. Wells 1988; Bridge et al. 2000; Hoefler 2002; Guerra & Mason 2005; Lindström & Pampoulie 2005; Arnott & Elwood 2007; Goubault et al. 2007; Jonart et al. 2007; Mager et al. 2008), very few (e.g. Dick & Elwood 1990) have explored how interacting qualities of disputed resources affect aggression. Because the mediation of male-male aggression over disputed resources in natural contests is likely to be affected by multiple, interacting qualities that influence resource value, it is important to tease apart their effects in controlled studies.

In the Midwestern United States, the wolf spider *Pardosa milvina* (Hentz 1844) is commonly found in agricultural habitats often reaching high densities (Marshall et al. 2000, 2002). Adult males are attracted to an airborne female pheromone (Searcy et al. 1999), so there is some likelihood that several males could simultaneously be attracted to and compete for a single female. Female body condition has also been implicated as a quality that affects male behavior. Schlosser (2005) demonstrated that adult male *P. milvina* spend more time and move more slowly in areas containing cues from females in high body condition compared with females in poor condition. This is consistent with the idea that males value females differently and respond accordingly. The value of mating with an adult virgin female in good condition may be markedly high to entelegyne spiders like *P. milvina* because of the female's conduit spermathecal morphology hypothesized to result in a first mate sperm priority pattern (see Austad 1984).

In the current study, we explored the effects of two interacting resource characteristics simultaneously on the nature of contests in *P. milvina*. It was our specific aim to investigate the occurrence and nature of several male-male aggressive behaviors in experimental trials that involved a pair of males and an adult female who varied in body condition and mating status as well as in trials that only involve adult males. Furthermore, we explored the effects of differences in male body size (a measure of resource holding potential) as well as female body size (another potential measure of female value) on male-male aggression and predicted that most instances of aggression would occur between similarly sized males placed with large, virgin females in good condition. This prediction was made because similarly sized individuals may not be able to easily make an assessment about which opponent is superior. We also quantified the number of matings that occurred during trials and occurrences of cannibalism.

Methods

During the spring of 2005, we collected a mixture of adult and subadult male and female *P. milvina* from Miami University's Ecology Research Center (Oxford, Butler County, OH, USA) and raised subadults to maturity in the lab. We maintained spiders individually in 5.5-cm high × 5.5-cm diameter clear, cylindrical, plastic containers with a 2-cm layer of moistened peat moss as a substrate to minimize risks of desiccation. *Pardosa milvina* were maintained on a diet of two domestic crickets (2 mm; *Acheta domesticus*) twice a week for approx. 6 wk, and peat moss substrates were watered regularly. All immature individuals matured during this period. We removed egg sacs from adult females collected in the field that were produced in the lab and categorized them as mated. All females that molted to maturity in the laboratory were categorized as virgin. To create differences in female body condition, virgin and mated females were randomly assigned to either a good condition (well-fed) or poor condition (food-deprived) feeding regime. Good condition females were fed four 2-mm crickets twice a week and poor condition females were fed one 2-mm cricket twice a week. Females were maintained on their respective diets for 3 wk, which is known to create significant differences in body condition in *P. milvina* (Hoefler et al. 2008). Adult males were fed two 2-mm crickets twice a week throughout the experiment.

All test trials were conducted in cylindrical plastic arenas (8 cm high × 20.5 cm diameter) with Whatman® Filter Paper (Whatman, Inc. Florham Park, NJ, USA) covering the bottom. Some arenas were used more than once during the course of our experiment. We washed arenas thoroughly in warm soapy water and rinsed them with 95% ethanol to remove residual chemical cues from spiders. Trials involved five experimental treatments: virgin/good condition females (n = 21), virgin/poor condition females (n = 24), mated/good condition females (n = 20), mated/poor condition females (n = 19), and a control group involved no females (n = 19). If the trial involved an adult female *P. milvina*, she was placed in an arena for 60 min and allowed to deposit cues (e.g. silk, excreta and associated pheromones), because substrate-borne cues are important for eliciting male courtship behavior (Rypstra et al. 2003). Following this period, we placed arenas in an isolated booth under a Panasonic WV-CP470 video camera (Panasonic Corporation of North America, Secaucus, NJ, USA) located in an environmentally controlled room. The camera was connected to a Panasonic AG-1980 videocassette recorder located in a nearby laboratory room.

A randomly selected pair of males was placed in the arena and individually corralled under overturned glass vials (8 cm high × 2 cm diameter) at opposite ends of the arena for 5 min to give them a period to acclimate. After this period, we released males, and all three spiders were allowed to interact freely for 20 min. For control trials, we only placed males in arenas as described above and excluded females and female cues. We video recorded each trial for 20 min, and trials were conducted over a period of 10 d with the sequence of experimental groups run randomly. We later scored videos by recording the frequency and type of aggressive interactions between adult males, because these behaviors can be easily quantified, and the frequency of all or some of the more escalated aggressive activities can be considered an indication of the assessment of resource value. Non-contact aggressive behavior included *lunges*, which involved a male leaping towards the other, and *chases*, which took place when one male quickly ran after the other. Contact aggressive behavior involved *sparring*, which involved fast, repeated contact between males with the use of their forelegs (spider bodies did not come directly into contact), and *grappling*, which took place when males interlocked legs and attempted to pull one another towards the chelicerae (spider bodies came into contact). We also recorded if matings occurred.

After each trial ended, we preserved all spiders in glass vials containing 70% ethanol and measured the length of each spider's left front tibia as well as the width of the carapace using a digital ocular micrometer mounted on a dissecting microscope. These measures were used as estimates of overall size. Using 2 sample t-tests, we tested if there was any difference in the size of male contestants. We also tested if there were differences in the sizes of males between treatments as well as the sizes of females between treatments via ANOVA. We compared the occurrence of male-male aggression using a contingency test as well as the frequencies of specific male aggressive behaviors via Kruskal–Wallis tests as data were not normally distributed. We also used the above morphometrics to explore the effect of female body size and body size differences (intrapair differences) between males on male-male aggressive behavior via simple linear regression analyses. All statistical analyses were performed using JMP™ 7.0 statistical software (SAS, Cary, NC, USA).

Results

Overall, males did not differ in size on the basis of tibia length [$t_{(204)} = 0.18$, $p = 0.87$, $N = 206$] or carapace width [$t_{(204)} = -0.09$, $p = 0.93$, $N = 206$). Similarly, males did not differ in size between treatments on the basis of tibia length [ANOVA, $F_{(4,201)} = 1.8$, $p = 0.13$, $N = 206$] or carapace width [ANOVA, $F_{(4,201)} = 0.06$, $p = 0.99$, $N = 206$]. Like males, between treatments, females did not differ in tibia length [ANOVA, $F_{(3,80)} = 0.25$, $p = 0.86$, $N = 84$] or carapace width [ANOVA, $F_{(3,80)} = 0.19$, $p = 0.9$, $N = 84$]. The interaction of female condition and mating status affected the occurrence of male-male aggression (i.e. whether a trial involved male-male aggression or not) (Contingency Test, $\chi^2{}_4 = 23.6$, $p < 0.0001$, $N = 103$). Trials with virgin/good condition females were the most likely to involve male-male aggression while trials with mated/poor condition females and control trials were the least likely (Fig. 1). There were significant differences between the frequencies of aggressive activities for all permutations of female types (Kruskal–Wallis tests; lunges, $\chi^2{}_4 = 37.5$, $p < 0.0001$; chases, $\chi^2{}_4 = 30.9$, $p < 0.0001$; sparring, $\chi^2{}_4 = 39.3$, $p < 0.0001$; grappling, $\chi^2{}_4 = 44.0$, $p < 0.0001$; $N = 103$) (Fig. 2). For the treatment involving virgin/good condition females, there were significantly more instances of all types of aggressive behavioral activities (non-parametric Tukey HSD (Honestly Significant Differences) (Honestly Significant Differences) test; $p < 0.05$). Other treatments did not differ for any activity (non-parametric Tukey HSD test; $p > 0.05$) (Fig. 2). There was no effect of size difference between males or absolute female size measured as tibia length or cephalothorax width on

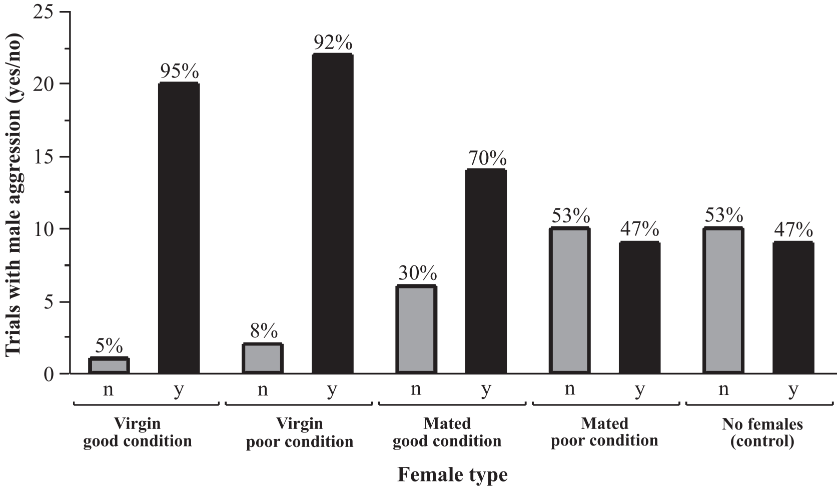

Fig. 1: The frequency and percentage of trials in which at least one instance of male-male aggression occurred. Black bars indicate trials with male-male aggression and grey bars indicate trials without.

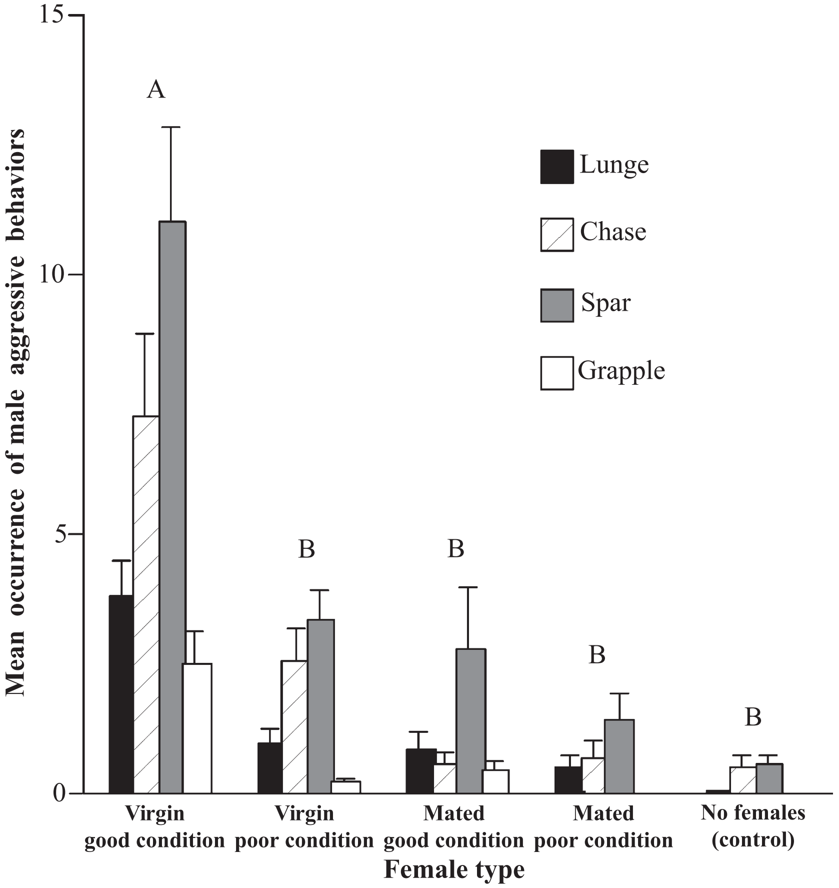

Fig. 2: The mean number of aggressive behaviors per treatment (+1 SE). Significant differences between groups are indicated by different letters (non-parametric Tukey HSD test).

the frequencies of male-male aggressive activities (linear regression; $p > 0.05$ for all analyses). Matings were most likely to occur with virgin/good condition females (n = 7; 33.3%). Only two (8.3%) virgin/poor condition females mated, one (5%) mated/good condition female mated, and no mated/poor condition females mated. Females killed three males during the course of trials: virgin/good condition females (n = 1; 4.8%), mated/good condition females (n = 1; 5%), mated/poor condition females (n = 1; 5.3%).

Discussion

Resource value, as indicated by female mating status and body condition, emerged as an important variable affecting the intensity of fighting behavior in male *P. milvina*. Males engaged in more costly encounters, as evidenced by acting more aggressively, performing more agonistic activities, when in the presence of virgin females in good body condition. This suggests that males can and do assess both of these qualities and use them to determine the degree to which they escalate fights. Arnott & Elwood (2007) recently reviewed studies on resource value assessment and provided a categorical framework into which studies can be placed, ranging from those failing to show resource assessment to those demonstrating very sophisticated assessment capabilities. In terms of this review, the present study provides a further example of both contestants gathering information about a resource, and adds to the existing literature by examining how two interacting aspects are evaluated in making a resource value assessment.

Our findings partly corroborate earlier findings demonstrating that males respond differently to females that have been raised on diets that generate relatively good and poor body conditions (Schlosser 2005). Males acted significantly more aggressively towards one another when in the presence of virgin females that were in good condition compared to all other types of females. Interestingly, males displayed a significantly lower and statistically equivalent level of aggressive behavior when in the presence of virgin/poor condition, mated/good condition, and mated/poor condition females as well as when no female was present. Taken together, these findings suggest that males are able to make some assessment of females, adjusting their level of contest effort, but may not discriminate between females that are not virgin and in good condition in terms of fighting. Levels of male-male aggression also suggest that females other than good condition virgins are not as valuable, although it is unknown how well male-male aggression accords with the reproductive success that could be achieved with females differing in quality. Male and female body size as measured by tibia length or cephalothorax width did not affect male-male aggression. The lack of an effect of female size on the frequencies of male aggressive behavioral activities was surprising given that a number of studies have found such an effect (Verrell 1986; Dick & Elwood 1990; Hack et al. 1997; Bridge et al. 2000).

Our discovery that males acted more aggressively towards one another in the presence of a virgin female in good condition supports the idea that wolf spiders have first male sperm priority. Austad (1984) predicted that because female entelegyne spiders, such as wolf spiders, have a conduit spermathecal morphology, a first-mate sperm priority pattern should result. Empirical studies have confirmed this hypothesis in some entelegyne species (e.g. Eberhard et al. 1993), and female *P. milvina* do mate repeatedly (A. L. Rypstra, pers. obs.). Therefore, male wolf spiders should benefit from male-male contests for females if they secure access to virgin females and their higher reproductive value. The behavior of male spiders in our study is partially consistent with this. As stated above, males exhibited greater levels of aggression when in the presence of good condition but not poor condition virgin females. Males were no more or no less aggressive when in the presence of virgin/poor condition, mated/good condition, and mated/poor condition females as they were when no female was present. Thus, putative sperm priority patterns and the mating status of females cannot, alone, explain the levels of aggression in our study. The effects of female reproductive status on male-male aggression appear to have been modulated by an interaction with condition. Female body condition and diet effects on reproductive success have been documented in numerous studies (e.g. Leather 1994; Meijer & Langer 1995; Kyneb & Toft 2006; Moreau et al. 2007; Warner et al. 2007) including those involving wolf spiders (e.g., Kessler 1971; Head 1995; Brown et al. 2003; Rickers et al. 2006). Thus, it is not surprising that the condition of adult female *P. milvina* influenced the competitiveness of male conspecifics because female condition can affect egg production and, therefore, their value to males. We expected males to act more aggressively towards one another in the presence of virgin females in good condition, as a male can expect to enhance fitness by mating with these types of females, and an increased motivation to fight can be a strategy that increases access to highly valued females. Other types of females elicited less aggression. This presumed reduction in value could be a result of decreased female receptivity (Norton & Uetz 2005), increased sperm competition (Parker 1970; Simmons 2001), increased risks of sexual cannibalism (Persons & Uetz 2005), and/or other factors that negatively impact lifetime reproductive success (Gaskett et al. 2004).

Although male-male aggression was common during trials, it did not result in conspicuous male injury (e.g. leg or pedipalp loss) or death. This was surprising since leg and pedipalp loss is common in *P. milvina* and occurs more frequently in males than females (Brautigam & Persons 2003; Lynam et al. 2006). For example, in natural populations of *P. milvina*, Bruseke et al. (2001) discovered that 16.4% of individuals were missing legs, and as the mating season progressed, this level increased to 32%. Although it was not our intent to directly quantify the costs of male-male aggression in the current study, it does not appear that males inflict significant physical injuries on rival males, but this is deserving of further investigation.

Compared to other experiments conducted with this species, a paucity of trials resulted in mating. Matings occurred in 33% of trials with virgin/good condition females, 8.3% of trials with virgin/poor condition females, 5% of trials with mated/good condition females, and 0% of trials with mated/poor condition females. In comparison, Rypstra et al. (2003) reported that *P. milvina* matings occurred 74% of the time when a single adult male was placed with an adult virgin female and 17% of the time when males were placed with mated females. This result suggests that interference from rival males affects mating success and may be common since this species is often found in very high densities (Marshall et al. 2000, 2002). Thus, socially imposed costs, which often takes the form of increased male aggression towards displaying males (Borgia 1995; Candolin 1997; Kotiaho 2001), may reduce male fitness directly from interference or via energetic costs. Male-male interference may also affect female willingness to mate. Rypstra et al. (2003) found that both virgin and mated females preferred males that courted at relatively high rates. If male courtship rate is reduced or interrupted by aggressive encounters with rival males, females may not be able to accurately assess males on the basis of courtship rate alone. However, assessment may still come from watching male-male contests (e.g. Chan et al. 2008).

In conclusion, our study provides support for assessment of multiple, interacting qualities of resource value that can modulate aggressive interactions between competing individuals. The interaction between female mating status and diet/condition mediated male-male aggression in the wolf spider *P. milvina*. Future studies should consider how females may adjust their signaling effort once mated and explore the fitness consequences of male-male aggression and matings with females varying in quality to improve our understanding of the evolution of mating behaviors in this common species of wolf spider.

Acknowledgements

The authors would like to thank Swathi Reddy and Montra Yazdani for spider care. Jennie Chen, Sam Evans, Ali Henry, Warwick Johnston, Dan Kozlowski, Steven Nagy, Sandra Rittman, Jason Schmidt, Kerri Wrinn, Brian Ulrich, and Rocklyn York offered helpful comments on the manuscript. This research was conducted with the support of NSF grants DBI 0216776 and DBI 0216947. Additional financial support was provided by Miami University's Summers Scholars program (to fund the participation of G. Guhanarayan), the Department of Zoology, Ecology Research Center, and Hamilton campus.

Literature Cited

Andersson, M. B. 1994: Sexual Selection. Princeton Univ. Press, Princeton, NJ.

Arnott, G. & Elwood, R. W. 2007: Fighting for shells: how private information about resource value changes hermit crab pre-fight displays and escalated fight behaviour. Proc. R. Soc. Lond. B Biol. Sci. **274**, 3011—3017.

Arnott, G. & Elwood, R. W. 2008: Information gathering and decision making about resource value in animal contests. Anim. Behav. **76**, 529—542.

Austad, S. N. 1983: A game theoretical interpretation of male combat in the bowl and doily spider, *Frontinella pyramitela* (Walckenaer). Anim. Behav. **31**, 59—73.

Austad, S. N. 1984: Evolution of sperm priority patterns in spiders. In: Sperm Competition and the Evolution of Animal Mating Systems (Smith, R. L., ed.). Academic Press, NY, pp. 223—249.

Bishop, D. T., Cannings, C. & Smith, J. M. 1978: War of attrition with random rewards. J. Theor. Biol. **74**, 377—388.

Borgia, G. 1995: Bower destruction and sexual competition in the satin bowerbird (*Ptilonorhyncus violaceus*). Behav. Ecol. Sociobiol. **18**, 91—100.

Brautigam, S. E. & Persons, M. H. 2003: The effect of limb loss on the courtship and mating behavior of the wolf spider *Pardosa milvina* (Araneae: Lycosidae). J. Insect Behav. **16**, 571—587.

Bridge, A. P., Elwood, R. W. & Dick, J. T. A. 2000: Imperfect assessment and limited information preclude optimal strategies in male-male fights in the orb-weaving spider *Metellina mengei*. Proc. R. Soc. Lond. B Biol. Sci. **267**, 273—279.

Briffa, M., Elwood, R. W. & Dick, J. T. A. 2000: Imperfect assessment and limited information preclude optimal strategies in male-male fights in the orb-weaving spider *Metellina mengei*. Proc. R. Soc. Lond. B Biol. Sci. **267**, 273—279.

Brown, C. A., Sanford, B. M. & Swerdon, R. R. 2003: Clutch size and offspring size in the wolf spider *Pirata sedentartus* (Araneae, Lycosidae). J. Arachnol. **31**, 285—296.

Bruseke, M. A., Rypstra, A. L., Walker, S. E. & Persons, M. H. 2001: Leg autotomy in the wolf spider *Pardosa milvina*: a common phenomenon with few apparent costs. Am. Midl. Nat. **146**, 153—160.

Buena, L. J. & Walker, S. W. 2008: Information asymmetry and aggressive behaviour in male house crickets, *Acheta domesticus*. Anim. Behav. **75**, 199—204.

Candolin, U. 1997: Predation risk affects courtship and attractiveness of competing threespine stickleback males. Behav. Ecol. Sociobiol. **41**, 81—87.

Chan, J. P. Y., Lau, P. R., Tham, A. J. & Li, D. 2008: The effects of male-male contests and female eavesdropping on female mate choice and male mating success in the jumping spider, *Thiania bhamoensis* (Araneae: Salticidae). Behav. Ecol. Sociobiol. **62**, 639—646.

Dick, J. T. A. & Elwood, R. W. 1990: Symmetrical assessment of female quality by male *Gammarus pulex* (Amphipoda) during struggles over precopula females. Anim. Behav. **40**, 877—883.

Dodson, G. N. & Beck, M. W. 1993: Pre-copulatory guarding of penultimate females by male crab spiders, *Misumenoides formosipes*. Anim. Behav. **46**, 951—959.

Eberhard, W. G., Guzmàn-Gòmez, S. & Catley, K. M. 1993: Correlation between spermathecal morphology and mating systems in spiders. Biol. J. Linn. Soc. **50**, 197—209.

Enquist, M. & Leimar, O. 1987: Evolution of fighting behavior: the effect of variation in resource value. J. Theor. Biol. **127**, 187—205.

Gaskett, A. C., Herberstein, M. E., Downes, B. J. & Elgar, M. A. 2004: Changes in male mate choice in a sexually cannibalistic orb-web spider (Araneae: Araneidae). Behavior **141**, 1197—1210.

Gherardi, F. 2006: Fighting behavior in hermit crabs: the combined effect of resource-holding potential and resource value in *Pagurus longicarpus*. Behav. Ecol. Sociobiol. **59**, 500—510.

Goubault, M., Cortesero, A. M., Poinsot, D., Wajnberg, E. & Boivin, G. 2007: Does host value influence female aggressiveness, contest outcome and fitness gain in parasitoids? Ethology **113**, 334—343.

Guerra, P. A. & Mason, A. C. 2005: Information on resource quality mediates aggression between male Madagascar hissing cockroaches, *Gromphadorhina portentosa* (Dictyoptera: Blaberidae). Ethology **111**, 626—637.

Hack, M. A. 1997: Assessment strategies in the contest of male crickets, *Acheta domesticus*. Anim. Behav. **53**, 733—747.

Hack, M. A., Thompson, D. J. & Fernandes, D. M. 1997: Fighting in males of the autumn spider, *Metellina segmentata*: effects of relative body size, prior residency and female value on contest outcome and duration. Ethology **103**, 488—498.

Head, G. 1995: Selection of fecundity and variation in the degree of sexual size dimorphoism among spider species (class Araneae). Evolution **49**, 776—781.

Hoefler, C. D. 2002: Is contest experience a trump card? The interaction of residency status, experience, and body size on fighting success in Misumenoides formosipes (Araneae: Thomisidae). J. Insect Behav. **15**, 779—790.

Hoefler, C. D., Persons, M. H. & Rypstra, A. L. 2008: Evolutionarily costly courtship displays in a wolf spider: a test of viability indicator theory. Behav. Ecol. (doi: 10.1093/beheco/arn055). **19**(5): 974—979.

Hsu, Y. & Wolf, L. L. 1999: The winner and loser effect: integrating multiple experience. Anim. Behav. **57**, 903—910.

Huntingford, F. A. & Turner, A. K. 1987: Animal Conflict. Chapman & Hall, London.

Jonart, L. M., Hill, G. E. & Badyaev, A. V. 2007: Fighting ability and motivation: determinants of dominance and contest strategies in females of a passerine bird. Anim. Behav. **74**, 1675—1681.

Kessler, A. 1971: Relation between egg production and food consumption in species of the genus *Pardosa* (Lycosidae, Araneae) under experimental conditions of food-abundance and food-shortage. Oecologia **8**, 93—109.

Kotiaho, J. S. 2001: Costs of sexual traits: a mismatch between theoretical considerations and empirical evidence. Biol. Rev. Camb. Philos. Soc. **76**, 365—376.

Kyneb, A. & Toft, S. 2006: Effects of maternal diet quality on offspring performance in the rove beetle *Tachyporus hypnorum*. Ecol. Entomol. **31**, 322—330.

Leather, S. R. 1994: Life history traits of insect herbivores in relation to host quality. In: Insect-Plant Interactions (Bernays, E. A., ed), Vol. 5. CRC Press, Boca Raton, FL. pp. 175—270.

Lindström, K. & Pampoulie, C. 2005: Effects of resource holding potential and resource value on tenure at nest sites in sand gobies. Behav. Ecol. **16**, 70—74.

Lynam, E. C., Owens, J. C. & Persons, M. H. 2006: The influence of pedipalp autonomy on the courtship and mating behavior of *Pardosa milvina* (Araneae: Lycosidae). J. Insect Behav. **19**, 63—75.

Mager, J. N. III, Walcot, C. & Piper, W. H. 2008: Nest platforms increase aggressive behavior in common loons. Naturwiessenschaften **95**, 141—147.

Marden, J. H. & Waage, J. K. 1990: Escalated damselfly territorial contests are energetic was of attrition. Anim. Behav. **65**, 453—462.

Marshall, S. D., Walker, S. E. & Rypstra, A. L. 2000: A test for differential colonization and competitive ability in two generalist predators. Ecology **81**, 3341—3349.

Marshall, S. D., Pavuk, D. M. & Rypstra, A. L. 2002: A comparative study of phenology and daily activity patterns in the wolf spiders *Pardosa milvina* and *Hogna helluo* in soybean agroecosystems in southwestern Ohio (Araneae, Lycosidae). J. Arachnol. **30**, 503—510.

Maynard Smith, J. 1974: The theory of games and the evolution of animal conflicts. J. Theor. Biol. **47**, 209—221.

Maynard Smith, J. 1982: Evolution and the Theory of Games. Cambridge Univ. Press, Cambridge.

Maynard Smith, J. & Parker, G. A. 1976: The logic of animal contests. Anim. Behav. **24**, 159—175.

Maynard Smith, J. & Price, G. R. 1973: The logic of animal conflict. Nature **246**, 15—18.

Meijer, T. & Langer, U. 1995: Food availability and egg-laying of captive European starlings. Condor **97**, 718—728.

Moreau, J., Thierry, D., Troussard, J. P. & Benrey, B. 2007: Grape variety affects female but also male reproductive success in wild European grapevine moths. Ecol. Entomol. **32**, 747—753.

Norton, S. & Uetz, G. W. 2005: Mating frequency in Schizocosa ocreata (Hentz) wolf spiders: evidence for a mating system with female monandry and male polygyny. J. Arachnol. **33**, 16—24.

Parker, G. A. 1970: Sperm competition and its evolutionary consequences in the insects. Biol. Rev. **45**, 525—582.

Parker, G. A. 1974: Assessment strategy and evolution of fighting behaviour. J. Theor. Biol. **47**, 223—243.

Parker, G. A. & Rubenstein, D. I. 1981: Role assessment, reserve strategy and the acquisition of information in asymmetric animal contests. Anim. Behav. **29**, 221—240.

Persons, M. H. & Uetz, G. W. 2005: Sexual cannibalism and mate choice decisions in wolf spiders: influence of male size and secondary sexual characters. Anim. Behav. **69**, 83—94.

Prenter, J., Elwood, R. W. & Taylor, P. W. 2006: Self-assessment by males during energetically costly contests over precopula females in amphipods. Anim. Behav. **72**, 861—868.

Rickers, S., Langel, R. & Scheu, S. 2006: Dietary routing of nutrients from prey to offspring in a generalist predator: effects of prey quality. Funct. Ecol. **20**, 124—131.

Rypstra, A. L., Weig, C., Walker, S. E. & Persons, M. H. 2003: Mutual mate assessment in wolf spiders: differences in the cues used by males and females. Ethology **109**, 315—325.

Schlosser, A. M. 2005: The effects of female body condition, female cue and predator cue presence on the locomotive and reproductive behavior of the male wolf spider *Pardosa milvina* (Araneae; Lycosidae). MS thesis. Miami Univ., Oxford, OH, USA.

Searcy, L. E., Rypstra, A. L. & Persons, M. E. 1999: Airborne chemical communication in the wolf spider *Pardosa milvina*. J. Chem. Ecol. **25**, 2527—2533.

Simmons, L. W. 2001: Sperm Competition and Its Evolutionary Consequences in the Insects. Princeton Univ. Press, Princeton, NJ.

Sneddon, L. U., Taylor, A. C. & Huntingford, F. A. 1999: Metabolic consequences of agonistic behavior: crab fights in declining oxygen tensions. Anim. Behav. **57**, 353—363.

Thornhill, R. 1984: Fighting and assessment in *Harpobittacus* scorpionflies. Evolution **38**, 204—214.

Trivers, R. L. 1972: Parental investment and sexual selection. In: Sexual Selection and the Descent of Man 1871—1971 (Campbell, B. ed.). Chicago: Aldine, pp. 136—179.

Turner, G. F. & Huntingford, F. A. 1986: A problem for game theory analysis: assessment and intention in male mouthbrooder contest. Anim. Behav. **34**, 961—970.

Verrell, P. A. 1986: Wrestling in the red-spotted newt (*Notophthalmus viridescens*): resource value and contestant asymmetry determine contest duration and outcome. Anim. Behav. **34**, 398—402.

Warner, D. A., Lovern, M. B. & Shine, R. 2007: Maternal nutrition affects reproductive output and sex allocation in a lizard with environmental sex determination. Proc. R. Soc. Lond. B Biol. Sci. **274**, 883—890.

Wells, M. S. 1988: Effects of body size and resource value on fighting behaviour in a jumping spider. Anim. Behav. **36**, 321—326.