



Sexual size dimorphism mediates the occurrence of state-dependent sexual cannibalism in a wolf spider

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Most research on sexual cannibalism has focused on factors influencing female motivation to engage in cannibalism. However, a critical factor that may mediate the actual occurrence of sexual cannibalism is male vulnerability to female attacks. We tested whether sexual size dimorphism (SSD) affected whether hungry females were successful in sexual cannibalism in a moderately size dimorphic wolf spider, *Hogna helluo*. Experimentally food-limited females cannibalized males more frequently than did well-fed females. However, in a correlational study, female body condition was only a significant predictor of the occurrence of sexual cannibalism if SSD was included in the model. Our results suggest that SSD is an important factor mediating the occurrence of sexual cannibalism in *H. helluo* by affecting male vulnerability to female attacks. Consideration of factors affecting male vulnerability to cannibalistic attacks by females may be critical to understanding the occurrence and evolution of sexual cannibalism.

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Although once thought to be primarily a cooperative endeavour (Darwin 1871; Mayr 1940; Lack 1968), recent views of mating interactions have emphasized the role of sexual conflict between males and females (Chapman et al. 2003; Arnqvist & Rowe 2005). This is especially apparent in species that engage in sexual cannibalism, the consumption of a male by a female in the context of mating (Elgar 1992; Elgar & Schneider 2004). Females gain a meal from consuming the male, but males lose all future reproductive success, which is a loss that is especially high if cannibalism occurs before mating (Elgar & Schneider 2004). In some species, sexual cannibalism appears highly derived and may be a form of male mating effort in which males sacrifice themselves to increase paternity (Sasaki & Iwahashi 1995; Andrade 1996; Foellmer & Fairbairn 2003; Andrade et al. 2005). However, for most species, males appear to resist being consumed by females and sexual cannibalism may essentially be a predator/prey

interaction (Bruce & Carico 1988; Fromhage & Schneider 2005; Lelito & Brown 2006).

In predator/prey interactions, two factors are important determinants of the outcome of predation: the motivation of the predator and the vulnerability of the prey (Polis et al. 1989; Rypstra & Samu 2005; Brose et al. 2006; Wise 2006). The same may be true for sexual cannibalism. A number of studies have documented that females may be more motivated to cannibalize males when males are abundant in the population (Newman & Elgar 1991; Johnson 2005a) or when females are food-limited (Liske & Davis 1987; Kynaston et al. 1994; Andrade 1998; Maxwell 2000; Schneider & Elgar 2001; Herberstein et al. 2002; Tsai & Dai 2003; Persons & Uetz 2005). However, female motivation to cannibalize a male is inconsequential if the female cannot capture the male. Males of some species have specialized adaptations to resist sexual cannibalism (binding the female with silk: Bristowe 1958; Bruce & Carico 1988; proportionately longer legs: Elgar et al. 1990; modifying the female web: Elgar 1991; mating while the female is feeding: Fromhage & Schneider 2005; nuptial gift: Bilde et al. 2006). On a broader scale, more general traits such as sexual size dimorphism may also affect male vulnerability. Size differences between predator and prey have long been known to affect the outcome of

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predatory interactions in a wide range of species (Polis 1981; Polis et al. 1989; Balfour et al. 2003; Rypstra & Samu 2005; reviewed in: Brose et al. 2006) and some studies have provided evidence that male or female size could affect the occurrence of sexual cannibalism (Elgar & Nash 1988; Persons & Uetz 2005; Johnson 2005b). However, few studies have simultaneously examined the role of female motivation and male vulnerability for the occurrence of sexual cannibalism.

The wolf spider *Hogna helluo* (Araneae, Lycosidae) is an ideal species in which to study the roles of female motivation and male vulnerability in sexual cannibalism. Sexual cannibalism occurs in over 30% of trials and can happen either before or after mating (Wilder & Rypstra 2007). Females appear food limited in nature and will readily attack insect prey, heterospecific spiders and conspecifics after only one week of starvation (Rypstra & Samu 2005; S. M. Wilder & A. L. Rypstra, unpublished data). In terms of vulnerability, males range in size from 65 to 100% of the size (i.e. carapace width) of females and vigorously attempt to escape from females after mating (Walker & Rypstra 2002; S. M. Wilder & A. L. Rypstra, unpublished data).

We explored the relative roles of sexual size dimorphism and hunger on the occurrence of sexual cannibalism in the wolf spider *H. helluo*. We first investigated the role of hunger for sexual cannibalism by examining (1) whether females from the field were food limited and (2) whether experimentally food-limited females were more likely to engage in sexual cannibalism. Then, since one hypothesis for the occurrence of sexual cannibalism is that it is an artefact of artificial or stressful conditions in the laboratory (Elgar 1992), we conducted an experiment to test whether the arena conditions (i.e. substrate and duration of residence in the container) affected mating behaviour and sexual cannibalism of *H. helluo*. Finally, we conducted an experiment utilizing continuous variation in female hunger level and sexual size dimorphism to examine the relative importance of female motivation to cannibalize (i.e. body condition) and male vulnerability to female attacks (i.e. SSD) for the occurrence of sexual cannibalism. Given the moderate level of SSD in *H. helluo*, we predicted that both female body condition and SSD would be important determinants of the occurrence of sexual cannibalism.

METHODS

Study Species

The wolf spider *H. helluo* (females, ca. 300–800 mg; males, ca. 150–300 mg) is abundant in agricultural fields in the midwestern United States (Marshall et al. 2002). Unless indicated otherwise, individuals used in this study were laboratory-reared offspring of females collected in the agricultural fields at the Miami University Ecology Research Center (Oxford, Butler County, OH, U.S.A.). For individuals reared from egg to adulthood in the laboratory, recently hatched juveniles were placed in translucent plastic containers (8 cm diameter \times 5 cm high) with 1 cm of moist peat moss, 1 cm³ of potato and an active culture of the collembolan *Sinella curviseta* (Collembola, Entomobryidae), which served as a food source. Individuals were

switched to a diet of one or two appropriately sized domestic crickets (*Acheta domesticus*) once or twice per week after approximately 1 month on the Collembola diet and, when they reached 1 cm body length, were transferred to larger containers (11 cm diameter \times 8 cm high). We recorded the sex of each individual and the date when it reached maturity. Spiders were maintained in an environmental chamber at 25 °C and 70% humidity on a 13:11 h light:dark cycle.

Experiment 1: Food Limitation in the Field

We examined the effects of experimental food limitation on female body condition (Jakob et al. 1996) and compared the body condition of females captured in the field with females that were experimentally food limited in the laboratory. For the experimental food limitation, nine adult females were fed to satiation and then deprived of food for 3 months. The starvation period of 3 months was arbitrarily chosen but seems reasonable for this species given that the congener *Hogna lenta* (formerly *Lycosa lenta*) can survive starvation periods of over 6 months on average (Anderson 1974). Containers were checked weekly and water was added as needed to ensure that the peat substrate was moist. To examine the body condition of females in the field, we collected adult female *H. helluo* from within and around the agricultural fields at the Miami University Ecology Research Center in September 2004. Adult females were only collected from one habitat type (low grass) and only at one time period (September). Eleven females were collected by hand at night and immediately taken to the laboratory to be measured. Hydration levels of the females were not likely to have affected body condition as females were collected on a humid night in a field with abundant dew. Recent oviposition was also not likely to have resulted in low female body condition because female wolf spiders carry their eggsacs attached to their spinnerets for several weeks and none of the females that we collected were carrying eggsacs (Foelix 1996). Analysis of covariance with mass as a response and carapace width as a covariate was used to compare the body condition of adult female spiders before and after 3 months of starvation and to compare the body condition of adult females starved for 3 months in the laboratory with adult females captured from the field (Garcia-Berthou 2001). The ratio measure (mass/carapace width; Jakob et al. 1996) was used to present data on body condition.

Mating Trials Data Collection

Similar protocols for data collection were used for experiments 2–4. Before running the trials, we recorded the carapace width (to the nearest 0.01 mm with an ocular micrometer), mass (to the nearest 0.1 mg) and age (number of days since moulting to maturity) of males and females. Carapace width was used as a measure of size because this structure is fixed at maturity. Sexual size dimorphism was calculated as the ratio of female to male carapace widths; hence, a larger value indicates a greater

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