



Sexual cannibalism is associated with female behavioural type, hunger state and increased hatching success

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Precopulatory sexual cannibalism may represent the most extreme form of sexual conflict because it necessarily truncates the reproductive potential of the victim. Three of the most prominent mechanisms invoked to explain incidence of precopulatory sexual cannibalism are the 'adaptive foraging', 'aggressive spillover' and 'mate choice' hypotheses. These hypotheses argue that sexual cannibalism is either (1) the result of female choice, where females gauge the benefits of suitors as perspective mates versus prey, (2) a neutral (or deleterious) by-product of selection on aggressiveness in nonreproductive contexts, or (3) a mechanism by which females express their mating preferences, respectively. We tested the predictions of these hypotheses in the funnel-web spider *Agelenopsis pennsylvanica* using staged laboratory encounters. We then tracked numerous fitness proxies of cannibalistic versus noncannibalistic females to determine whether cannibalism was associated with increased female performance. We found that more aggressive females and those deprived of food were more likely to engage in precopulatory cannibalism. Cannibalism was not associated with male condition, male body size or female body size, nor with the mass of females' egg cases, the number of eggs therein, or the mass of individual eggs. In contrast, there was a positive association between the mass of the egg case and the number of offspring that emerged in cannibalistic females, but not in noncannibalistic females. Thus, offspring of cannibalistic mothers appear to have increased hatching success in heavier egg cases. This may represent a novel advantage associated with sexual cannibalism.

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Males and females rarely, if ever, enjoy identical optimal fitness strategies in the reproductive context. Instead, competing interests between sexes often lead to sexual conflict as males and females respond to divergent selective pressures (Rowe et al. 1994; Chapman et al. 2003). Sexual conflict is of particular interest to behavioural ecologists because it can lead to suboptimal performance for one or both sexes in the reproductive context and/or trigger evolutionary arms races, as each sex faces pressure to counter adaptations of the other (reviewed in Chapman et al. 2003). Sexual cannibalism, in which one sex (generally females) kills and consumes the other before, during, or after copulation, is an extreme form of sexual conflict and has been documented in a number of arthropods (e.g. Newman & Elgar 1991; Barry et al. 2008).

Precopulatory sexual cannibalism is an enigmatic behaviour that can entail great costs, particularly for males that risk death

before reproduction, but also for females that may squander mating opportunities and face fewer chances to reproduce. Thus, the mechanisms generating this behaviour are of general interest to sexual conflict theory. Several hypotheses have been proposed to explain sexual cannibalism. The 'adaptive foraging hypothesis' posits that females weigh the value of each male as either a prospective mate or prey item, and occasionally kill and consume males to gain direct nutritional benefits (Fromhage et al. 2003; Barry et al. 2008; Wilder & Rypstra 2008, 2010; Blamires 2011; Roggenbuck et al. 2011). In contrast, the 'aggressive spillover hypothesis' suggests that sexual cannibalism emerges as a by-product of selection for increased aggressiveness in other behavioural contexts (Arnqvist & Henriksson 1997; Johnson & Sih 2005, 2007; Pruitt & Riechert 2009). Or, in other words, it argues that sexual cannibalism could be a facet of aggressiveness in an overarching behavioural syndrome (Sih et al. 2004a, 2012), and selection favouring aggressiveness in one context can indirectly increase incidence of sexual cannibalism. Under these circumstances, sexual cannibalism threatens to sterilize highly aggressive females because they may cannibalize all of their potential suitors prior to mating (Riechert et al. 2001). This risk is further compounded by

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the finding that males in many systems tend to disfavour (and avoid) high-risk, aggressive females (Pruitt & Riechert 2009; Johnson et al. 2011). Finally, sexual cannibalism may merely represent an extreme form of mate choice (i.e. the 'mate choice hypothesis'), in which females attack undesired males (e.g. low-quality, unfamiliar) but allow preferred mates to copulate (Hebets 2003, 2007; Kralj-Fišer et al. 2012).

It is also possible, or even likely, that more than one of the aforementioned mechanisms could be at play in any system, since these hypotheses are not mutually exclusive. For instance, aggressive females might show greater incidence of sexual cannibalism than nonaggressive females, but both phenotypes might show increased probability of sexual cannibalism when they are presented with low-quality males. Moreover, more narrowly focused studies risk overlooking potential interactions among explanatory mechanisms. For example, nonaggressive females may adjust their behaviour depending on their hunger state, whereas aggressive females might show more fixed rates of sexual cannibalism (Dingemanse et al. 2010). Despite the possibility that multiple mechanisms could simultaneously impact sexual cannibalism rates, the majority of the recent papers on this topic have recovered support for only a single mechanism per system (e.g. Johnson & Sih 2005; Johnson et al. 2011; Kralj-Fišer et al. 2012). Thus, to date, very few studies that have found support for multiple mechanisms acting in concert in a unified test system (but see Roggenbuck et al. 2011).

In our study, we use the funnel-web spider *Agelenopsis pennsylvanica* (Araneae, Agelenidae) to test among the various hypotheses commonly used to explain precopulatory sexual cannibalism. Funnel-web spiders of genus *Agelenopsis* have served as a long-standing model for behavioural syndromes research (Sih et al. 2004a, b). Several members of this genus show consistent individual differences in behaviour (termed 'behavioural types'; Hedrick & Riechert 1989; Riechert & Hedrick 1990), and many studies have documented correlations across functionally dissimilar contexts of behaviour (e.g. foraging, antipredator behaviour, locomotor tendencies; Riechert & Hedrick 1993; Riechert et al. 2001; Pruitt 2010; Pruitt & Husak 2010). Here we ask two questions. (1) What factors predict incidence of sexual cannibalism in *A. pennsylvanica* (e.g. female hunger state, female behavioural type, male quality)? (2) Is incidence of cannibalism associated with increased reproductive output for females? Identifying the correlates of sexual cannibalism is valuable because it can help elucidate the mechanisms driving this captivating sexual phenomenon. Additionally, documenting associations between cannibalism and females' reproductive output is particularly interesting, because data supporting such effects are still highly equivocal (e.g. Andrade 1996; Fromhage et al. 2003; Wilder & Rypstra 2010).

METHODS

Collection and Laboratory Maintenance

Spiders of genus *Agelenopsis* build funnel-webs that are composed of two parts: a nonsticky sensory sheet used to sense prey, and a funnel retreat. When foraging, spiders position themselves at the entrance to their funnel and use high-velocity movements to subdue prey that make contact with their webs (Riechert 1976; Pruitt & Husak 2010). Late-instar *A. pennsylvanica* were collected along urban hedgerows throughout Pittsburgh, Pennsylvania, U.S.A. Spiders were collected by dropping a cricket onto their sheet web and scooping up the spider as they initiated their prey capture sequence. Spiders were transported to the laboratory and housed in circular, transparent boxes (9 cm radius, 7.5 cm depth). Spiders were provided an ad libitum (1–6 prey items) diet of 2-

week-old crickets once a week. To provide water, spiders' webs were misted once per week using a spray bottle with tap water. All individuals were weighed and measured within 1 week of maturity. We measured cephalothorax length and width of spiders to the nearest 0.01 mm using Leica digital imaging software (LAS V3.8) and a stereo microscope (Leica M80). We estimated spiders' condition as the residuals of a linear regression of body mass on cephalothorax length (Jakob et al. 1996; but see Kotiaho 1999; Moya-Laraño et al. 2008).

Assessment of Female Aggressiveness: Latency of Attack

Virgin females were run through a latency of attack assay to determine their aggressiveness. Assays occurred in females' home containers, 3 days after a routine feeding. Trials were initiated by removing the lid to the females' containers. We provided 30 s of acclimation time before a single 2-week-old cricket was dropped centrally within the female's web. We recorded the time taken for females to make contact with the cricket, termed their 'latency of attack'. Latency of attack trials are a common measure of aggressiveness in spiders (Hedrick & Riechert 1989; Pruitt et al. 2008; Kralj-Fišer et al. 2012). To determine whether latency of attack was a repeatable measure for *A. pennsylvanica*, we ran females ($N = 132$) through a second test 2 weeks after their initial assay.

Food Deprivation Experiment

To assess the effect of females' hunger state on their probability of cannibalizing males, we varied the number of days that females went without food prior to being paired with a male. Females were paired 1, 3 or 5 days following a routine feeding. Females were randomly assigned to one of the three food deprivation treatments. Females paired 5 days after a routine feeding were predicted to be hungrier than females paired 3 days after a routine feeding, and so on.

Staged Male–Female Interactions

Male–female encounters were staged in females' home containers. Male–female pairings were determined randomly, and males were used in only a single mating event. Males were introduced into the females' containers using an open tipped syringe. The lids to females' containers were left ajar to provide males an escape route. We allowed the pair to interact for 6 h. After 6 h, all pairings had resulted in (1) successful copulation, (2) sexual cannibalism, or (3) the male having abandoned the female's web. We observed pairs during this time and noted all instances of sexual cannibalism. All instances of cannibalism were precopula and occurred shortly after males initiated their courtship sequence. After pairs were done mating (1–10 h later), we removed the male and returned him to his home container. In instances where the male was cannibalized ($N = 47$), we allowed the female 24 h to feed on her unsuccessful suitor before presenting her with a second male. Under no circumstances did females cannibalize two males consecutively; thus, data from females' second encounters were not used to predict incidence of sexual cannibalism, nor the effects of sexual cannibalism on females' reproductive output (detailed below). Females continued on their normal, weekly feeding schedules regardless of whether they cannibalized their first male.

Female Reproductive Output

To determine the impact of sexual cannibalism on females' reproductive output, we used four performance metrics. First, we weighed all mated females 1 week after their staged encounters

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