



# Male vulnerability explains the occurrence of sexual cannibalism in a moderately sexually dimorphic wolf spider



Carmen Fernández-Montraveta<sup>a,\*</sup>, José Miguel González<sup>a,b</sup>, Mariano Cuadrado<sup>b</sup>

<sup>a</sup> Departamento de Psicología Biológica y de la Salud, Universidad Autónoma de Madrid, Cantoblanco, 28049 Madrid, Spain

<sup>b</sup> Zoobotánico de Jerez, Madre Selva s/n, 11407 Jerez de la Frontera, Cádiz, Spain

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## ABSTRACT

Sexual cannibalism is a widespread phenomenon among a few animal taxa. Its occurrence is interpreted as female and/or male optimal reproductive decisions or as a non-adaptive side effect of selection for efficiently foraging females. In spite of the amount of research addressed at understanding its evolutionary origins, we lack accurate information about the proximate causes of sexual cannibalism. In a moderately sexually dimorphic wolf spider (*Hogna radiata*, Araneae, Lycosidae) we assessed the factors mediating the occurrence of sexual cannibalism and its fitness benefits to females. Sexual cannibalism was a rather common outcome of laboratory mating interactions, occurring in more than a quarter percent of courtship interactions involving virgin females. Sexual cannibalism mostly followed mating. Occurrence of sexual cannibalism depended on male vulnerability to female attacks: relatively smaller males were at higher risk of being attacked and older males were less likely to avoid female attacks. Sexual cannibalism had direct and positive effects on female fitness, as sexually cannibalistic females exhibited increased fecundity irrespective of their size, condition and foraging rate. Male consumption was almost complete and represented a relevant food intake to females. We interpret sexual cannibalism as a strategic foraging decision for *H. radiata* females that adjust their aggressive behaviour towards males so as to limit its potential costs.

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## 1. Introduction

Sexual cannibalism, a particular case of cannibalism in which individuals of one sex kill and consume their mates prior, during, or following mating (cf. Thornhill, 1976; Elgar, 1992), is a relatively widespread phenomenon among a few animal taxa, particularly insects and spiders (Birkhead et al., 1988; Edmunds, 1988; Elgar, 1991, 1992; Eggert and Sakaluk, 1994; Andrade, 1996; Barry et al., 2008). Most research on sexual cannibalism has been addressed to unravel its evolutionary origins, compared to the little attention given to its proximate causes (Foellmer and Khadka, 2013; Kralj-Fišer et al., 2013). Females are more often the sexually cannibalistic sex (but see Dick, 1995; Haddon, 1995; Cross et al., 2008; Aisenberg et al., 2009) and trade-offs of sexual cannibalism focus therefore on its benefits to females and

intersexual conflict (Elgar and Schneider, 2004). Fitness benefits of sexually cannibalistic females may relate to avoiding low-quality or non-preferred males (i.e., mate choice Elgar and Nash, 1988) or getting nutritional resources positively affecting their fecundity (Johnson, 2005; Rabaneda-Bueno et al., 2008). Supporting the view that sexual cannibalism entails reproductive costs to males, it is well known to drive the evolution of male strategies aimed at avoiding potentially risky sexual interactions (Elgar and Wedell, 1996; Johnson, 2001; Gaskett et al., 2004; Moya-Laraño et al., 2004; Fromhage and Schneider, 2005; Bilde et al., 2006; Gemeno and Claramunt, 2006; Lelito and Brown, 2006; Barry et al., 2009, 2010; Li et al., 2012). The only exception is post-mating sexual cannibalism in species in which males investment to their current sire compensates the cost of losing their reduced future mating opportunities (i.e., terminal investment Buskirk et al., 1984; Andrade, 1996, 2003). Sexual cannibalism also entails to females the risk of remaining unmated or having limited access to sperm (Arnqvist and Henriksson, 1997), and its occurrence is expected to depend on the relative value of the male as food compared to its value as a mate (i.e., optimal foraging, Newman and Elgar, 1991). Consequently, sexual cannibalism should be more likely shown by inseminated females or females experiencing high mate encounter

\* Corresponding author. Tel.: +34 913975034; fax: +34 913976441.

E-mail addresses: [carmen.montraveta@uam.es](mailto:carmen.montraveta@uam.es) (C. Fernández-Montraveta), [jmiguel.ge@gmail.com](mailto:jmiguel.ge@gmail.com) (J.M. González), [macuagu@cica.es](mailto:macuagu@cica.es) (M. Cuadrado).

rates (Johnson, 2005; Rabaneda-Bueno et al., 2008) or a limited access to food (Andrade, 1998; Barry et al., 2008).

The assumption that sexual cannibalism affects positively female fecundity has received inconsistent support (see Table 1); also female insemination status or feeding history do not always mediate its occurrence (e.g. Arnqvist and Henriksson, 1997, see also Table 1). Moreover, foraging by females does not necessarily affect their fitness (Spence et al., 1996; Arnqvist and Henriksson, 1997; Maxwell, 2000; Fromhage et al., 2003; Johnson and Sih, 2005, see Table 1). For example, cannibalistic females gain more mass than non-cannibalistic ones irrespective of whether or not they are allowed to effectively consume their mates (Schneider and Elgar, 2002), suggesting that sexual cannibalism is a side effect of female foraging efficiency and evolves indirectly from selection favouring more effectively foraging females (e.g., aggressive spillover hypothesis, Arnqvist and Henriksson, 1997). During development, effective foraging would lead to increased female size (Johnson and Sih, 2005), hence larger size becomes the proximate factor expected to mediate the occurrence of sexual cannibalism. Supporting this view, female size is well known to provide cannibalistic females direct physical advantages at restraining males (Elgar and Jones, 2008; Roggenbuck et al., 2011) and sexual cannibalism is far more common among extremely female-biased sexually dimorphic species (e.g., size dimorphism hypothesis, Wilder and Rypstra, 2008a,b; Wilder et al., 2009).

The aggressive spillover hypothesis was developed to explain instances of sexual cannibalism in which females undergo extreme insemination costs, i.e., pre-mating (Arnqvist and Henriksson, 1997). Such a maladaptive behaviour could evolve as part of a behavioural syndrome, meaning that females actually lack flexibility to properly adjust their aggressive behaviour across contexts (Arnqvist and Henriksson, 1997; Johnson and Sih, 2005; Foellmer and Khadka, 2013). The hypothesis hence requires that sexual cannibalism shows repeatability and consistent individual differences, a premise scarcely ever demonstrated (Kralj-Fišer et al., 2013). Evidences instead indicate a role of male behaviour as the proximate cause mediating the occurrence of sexual cannibalism; for example, male age affects the rate of sexual cannibalism in crab spiders (Morse and Hu, 2004), whereas relatively smaller spider males are at higher risk of being cannibalised in other cases (Elgar and Jones, 2008; Wilder and Rypstra, 2008b). The role of male behaviour and vulnerability in sexual cannibalism deserves further research.

*Hogna radiata* (Latreille, 1817) (Araneae, Lycosidae) is a European medium-sized wandering wolf spider. Wolf spiders are highly cannibalistic (Buddle et al., 2003; Wise, 2006), but show comparatively low rates of sexual cannibalism (Elgar, 1992; Elgar and Schneider, 2004). Wolf spiders are also only moderately sexually dimorphic (Vollrath and Parker, 1992), which could explain low rates of sexual cannibalism and predict potentially high nutritional benefits of feeding upon males. Therefore wolf spiders become particularly suitable models for testing the adaptive value and the proximate causes of sexual cannibalism (Wilder and Rypstra, 2010; Wu et al., 2013). *H. radiata* males are not sperm limited, but show a potentially polygynous mating system, whereas monandry is likely female-driven and inseminated females show a high rate of pre-mating sexual cannibalism (Fernández-Montraveta and Cuadrado, 2013). In this paper we tested the role of female size and male vulnerability in the occurrence of sexual cannibalism and its fitness benefits to females. If sexual cannibalism is part of a behavioural syndrome, it should depend on female size and foraging rate irrespective of male size and age (prediction 1), and positive effects of sexual cannibalism on female fitness should depend on female size or foraging (prediction 2). To test these predictions we measured the role of male size and age on the occurrence of sexual cannibalism and the effect of female foraging, size and condition on

the occurrence of sexual cannibalism and female fitness (growth, fecundity and time to reproduction).

## 2. Materials and methods

### 2.1. The species

*H. radiata* is a common medium-sized wandering wolf spider. The species inhabits a variety of terrestrial habitats that range from wet to arid sites dominated by grassy or scrubby vegetation. This is an annual species that matures early in summer and mates shortly afterwards. Males mature earlier than females but disappear from natural populations soon after the mating season. As in all wolf spiders so far studied, mating is rather long and includes the repeated and alternated insertion of both male reproductive bulbs into the female genital tract. Sexual size dimorphism is female biased, but females are only moderately larger than males (Fernández-Montraveta and Cuadrado, 2013). Females produce a cocoon (and spiderlings) that transport actively on their backs and the species is semelparous.

### 2.2. General procedures

*H. radiata* mating history cannot be properly assessed on an exclusively morphological basis, and we tested our predictions on laboratory-matured spiders. For mating trials, we captured spiders as immatures (cf. Foelix, 1996) during the late spring. We used headlamps to capture spiders by hand during field searching at night. Following capture, we transported the spiders to the laboratory (<10 km distance), where we maintained them in visually isolated individual 1 l plastic containers provided with sand and some small leaves to be used as refuge. We kept laboratory conditions in a natural light regime and  $25 \pm 2^\circ\text{C}$  ambient temperature, and sprayed water on the spider containers twice a week. We reared spiders on an almost monotypic diet (blowflies, occasionally supplemented with crickets) provided three times a week and noted the amount of preys that the spiders did consume. We kept the spiders in the laboratory until their natural death. Voucher specimens of spiders used in this study are deposited at the Universidad Autónoma de Madrid collection.

We checked spiders on a daily basis to assess their maturation date, which we established from the development of female and male external genitalia (the *epigynum* at the ventral side of the female opisthosoma and the *copulatory bulbs* at the distal male pedipalpal *tarsi*). We calculated the spider age as the number of days between maturation and trial. At maturation, we measured spider body mass (Mettler Toledo ABS54 electronic balance to the nearest 0.1 mg) and size. To reduce the observer bias we assessed the spider size from pictures instead of living specimens. We estimated the spider size from the centroid size (CS), calculated as the square root of the sum of the squared distances from a set of landmarks to their centroid. CS is used in Geometric Morphometrics as a size estimator because it is uncorrelated to shape (Corti, 1993; Rohlf, 1999; Slice, 2007). To calculate CS we digitised 15 landmarks on spiders' dorsal pictures, 14 on the prosoma and one on the distal opisthosoma.

### 2.3. Experimental set-up

As experimental arenas we used plastic cylinders (40 cm × 30 cm) fixed to an expanded polystyrene platform. Cylinders were filled half-full with sand, covered with a clean filter paper used as substrate and replaced between consecutive trials to avoid chemical contamination of the substrate. Two small pieces of cardboard (5 cm × 5 cm) on top of the substrate and close to the terrarium wall allowed the spider to find refuge. In mating trials we

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