Sexual cannibalism in spiders: mating and foraging strategy

Stefan ter Haar - s3132250
Supervisor: M. Dietz
Gedragsbiologie research
27-03-2020

Abstract

Sexual cannibalism is a common occurrence in spiders where females consume males before, during or after copulation. Sexual cannibalism has been proposed to function as part of female mating strategy through mate choice, which may be implemented via mate rejection pre-copulatory or control of male paternity post-copulatory. The chance of sexual cannibalism is positively related to the sexual size dimorphism between pairs, which may reflect male vulnerability to female cannibalism attempts. Hence, female mate choice may be indirect and based on male body size. Pre-copulatory cannibalism occurs infrequently so mate rejection may be a relatively unimportant part of female mate choice. Post-copulatory cannibalism may function to control copulation duration or to retain the ability to re-mate by preventing mate plugs, female genital mutilation and mate guarding, but evidence that supports this is scarce, and the role of relative sexual size dimorphism unclear. Sexual cannibalism may also function as a foraging strategy to gain food of high quality and increase female reproductive output. Yet most males are relatively small compared to females and males mostly consist of proteins whereas eggs mostly consist of lipids. Despite this, male consumption results in increased female fecundity in various ways in most, but not all, spider species. Cannibalistic females increased energy investment in eggs, possibly from their somatic reserves. Proteins may be required to allocate energy from female somatic reserves to their eggs. Therefore consumption of males, which are rich in protein, may result in enhanced fecundity of females.

Overall, sexual cannibalism appears to function both as mate choice and to gain a high quality meal in spider species. Hence, sexual cannibalism may have multiple functions in a spider, but it's functions probably vary in prevalence between spider species.

Table of contents

Introduction

Sexual conflict is the result of differences in optimal strategies between sexes. In many species optimal sexual strategies differ between males and females. Sexual conflict may result in the development of a number of traits in both males and females, which can sometimes be antagonistic in nature (*Perry & Rowe 2012*). For example, male water striders (*Gerris incognitus*) have developed genitals that can grasp females, but female water striders have developed abdomens that can repel males (*Perry & Rowe 2012*). Another example of sexual conflict are females attempting to avoid mating by faking their death, which has been observed in some arthropod species (*Khelifa 2017*). Sexual cannibalism, where one mate partner consumes the other mate partner(s), may be an extreme form of sexual conflict. It is especially common among arthropods, and within this phylum it is common among praying mantis and arachnids (*Wilder et al. 2009; Brown et al. 2016; Wilder & Rypstra 2008a*). Araneae are well known for sexual cannibalism, yet the frequency with which sexual cannibalism occurs varies considerably between species (*Wilder & Rypstra 2008a*). In spiders there is a positive relation between sexual size dimorphism and the frequency of cannibalism (*Wilder & Rypstra 2008a*). Sexual size dimorphism occurs in most spider species, and usually the female is larger than the male (*Elgar 1991; Prenter et al. 1998*). The size difference varies from moderate to extreme sexual size dimorphism between and within spider families (*Prenter et al. 1998; Elgar 1991; Wilder & Rypstra 2008a*). For example, female orb-weaving spiders (Araneidae) are generally about 2.42 times larger than males, but in some orb-weaving spider species females are over 10 times larger than males (*Prenter et al. 1998; Elgar 1991*). Usually females cannibalize males, though there are exceptions where males are larger and cannibalize females (*Prenter et al. 2006; Sentenská & Pekar 2013*).

Sexual cannibalism can occur before, during or after copulation and the potential costs and benefits of sexual cannibalism differ for both sexes for each of these moments (*Wilder et al. 2009*). Spider species often engage in both pre- and post-copulatory cannibalism (*Wilder et al. 2009*). Pre-copulatory cannibalism results in sexual conflict because it may be profitable for females, but males unequivocally do not profit from being cannibalized prior to copulation (*Wilder et al. 2009*). Male spiders generally approach females carefully and have developed numerous tactics to avoid or decrease the chance of being cannibalized, like waiting for the female to feed, wrapping the female in silk, sacrificing a leg for the female to feed on, etc. (*Prenter et al. 2006; Zhang et al. 2011; Neumann & Schneider 2020*). Females that engage in pre-copulatory cannibalism suffer the risk of remaining unmated, since mate availability may be relatively low in the wild (*Wilder et al. 2009*). Post-copulatory cannibalism could also be profitable for females and is without the risk of remaining unmated. It is also less costly for males since they have mated at least once (*Wilder et al. 2009*). So the timing of cannibalism is an important aspect in determining the costs and benefits of sexual cannibalism for males and females.

The question remains what the function of sexual cannibalism could be. Several hypotheses have been proposed that explain the function and possible costs and benefits. The most important hypotheses are the following: Hypothesis 1 states that sexual cannibalism has no function, but arises from a failure of females to discriminate between prey and conspecifics (*Kralj-Fišer et al. 2012*). However, females respond different to male spiders than to prey and males generally approach females carefully and display courting behaviour (*Elgar & Nash 1998*). Also, sexual cannibalism occurs regularly after mating (*Wilder et al. 2009; Wilder & Rypstra 2008b*). Thus is seems unlikely that females are unable to discriminate between prey and males, and hypothesis 1 has received little support in the literature.

Hypothesis 2 is comparable to hypothesis 1 in that it assumes that there is no specific function of sexual cannibalism. Hypothesis 2 states that sexual cannibalism is a mal-adaptation resulting from female foraging strategy (*Kralj-Fišer et al. 2012, 2016*). Females are often indiscriminate in their highly aggressive behaviour towards potential prey, which may be favourable as a juvenile. This aggression is hypothesized to 'spill over' to adult females due to genetic constraints or female

behaviour types, resulting in females being unable to differentiate their aggressiveness between prey and males. This is considered mal-adaptive because indiscriminate aggression can result in males being cannibalized and females remaining unmated. However, studies have found that despite consistent aggressiveness levels of females towards prey, females show no consistency in aggression towards conspecifics (*Kralj-Fišer et al. 2012, 2016*). Also, as stated above, females do respond different to approaching males than to prey (*Elgar & Nash 1988*). Hence hypothesis 2 also seems unlikely.

Hypothesis 3 states that sexual cannibalism functions as part of female mating strategy. This may operate via two pathways of the mate choice process. Sexual cannibalism may be used to reject males via pre-copulatory cannibalism, or used to control male paternity via post-copulatory cannibalism (*Prenter et al. 2006*). Female mate choice is common in many species of arthropods and an important driver behind many male traits across animal species (*Herberstein et al. 2017*). Hence female mate choice may be a likely explanation of the function of sexual cannibalism.

Lastly, hypotheses 4 states that females may consider males as a food item of high quality, and that sexual cannibalism is part of female foraging strategy and acts as a way for females to gain high quality food (*Wilder et al. 2009*). Consumption of high quality food is important to females, as this may increase female reproductive output. Sexual cannibalism can therefore be explained as a way to obtain food of high quality and to increase female reproductive output.

Hypotheses 1 and 2 have received little support and seem unlikely, therefore this thesis focusses on hypotheses 3 and 4. Multiple studies investigated these hypotheses and various, if not contradicting, results have been reported. In this thesis I review support for both hypotheses to determine which hypothesis is more likely to explain the functionality of sexual cannibalism.

Hypothesis 3: mating strategy

Female mate choice can be direct or indirect, the distinction being that direct choice reflects variation in female behaviour related to some variable trait(s) in males that indicates their quality, whereas indirect mate choice does not require active discrimination by females (*Prenter et al. 2006*). If mate choice is direct, females should attempt to cannibalize males of lower quality but not males of a higher quality, while if mate choice is indirect, females should behave similar towards all males, and males of higher quality would simply be better able to survive female cannibalisation attempts. Since both direct and indirect mate choice have been proposed to explain sexual cannibalism, it is important to study if females discriminate between males and based on what trait(s).

In spiders, male size is suggested to reflect quality (*Prenter et al. 2006*). Male body size may therefore influence the chance of being cannibalized. If females directly engage in mate choice and body size reflects mate quality, they should prefer to mate with males whose body size reflects high quality and reject males whose body size reflects low quality, and thus attempt to cannibalize rejected males. If females indirectly reject males based on body size, they are expected to not differ in their attempts to cannibalize males. The end result may be similar to direct mate choice, as lower quality males may be more vulnerable to female cannibalisation attempts and indirectly be rejected as a mate.

Yet, female body size may also influence the chance of males being cannibalized. Males may be more vulnerable to the cannibalisation attempts of a large sized female than to the cannibalisation attempts of an average sized female. Large sexual size dimorphism between the interacting pair could thus increase the chance of cannibalisation. It is therefore important to determine if females consistently reject low quality males or if this depends on the size difference between interacting pairs. If the latter case is true, it may also be the result of indirect mate choice, even if females do not attempt to cannibalize all males (*Prenter et al. 2006*). Hence, only if male body size independent of female body size influences the chance of cannibalisation would it be likely due to active discrimination of females, and therefore the result of direct mate choice. Only in this case sexual cannibalism is explained to function as a way to directly choose between mates.

Pre-copulatory cannibalism

Sexual cannibalism often occurs before and after copulation. Especially pre-copulatory cannibalisation has been suggested to function as direct mate choice, enabling females to reject low quality males. This may be especially important in spider species where females are monogamous. Post-copulatory cannibalism may also be used to discriminate between males, but since the male already copulated it may be unsuitable to fully reject a male. Therefore, if a mate is to be rejected, it should happen before copulation.

Four studies on sexual cannibalism have investigated effects of sexual size dimorphism on female aggressive and cannibalistic behaviour, albeit not always as the main subject of the study. Relatively small males (compared to female size) were more likely to be attacked and cannibalized than relatively large males in three of four species: *D. fimbriatus, P. pseudoannulata* and *H. radiata* (*Kralj-Fišer et al. 2016; Wu et al. 2013 Fernández-Montraveta et al. 2014; Table 1*). However, in *A. diadematus* small males were more likely to be cannibalized independent of female body size (*Elgar & Nash 1998*). Note that not all courting males were attacked, and not all males that were attacked were subsequently cannibalized (*Table 1*). Most of the attacked males managed to mate with the females that attacked them.

These results suggest that relatively small males are more often rejected as a mate than relatively large males. The discrimination appears to be indirect, since the size difference between an interacting male and female determined the chance of being cannibalized in most cases. Also, not all attacked males were cannibalized. This supports the hypothesis that mate rejection is based on male vulnerability, indicating that pre-copulatory cannibalism can function as indirect female mate choice.

Table 1: The effect of sexual size dimorphism on the frequency of pre- and post-copulatory attacks and cannibalism in different species. Sexual size dimorphism has been calculated with different methods, see references. *Kralj-Fišer 2016* had several mating trials, but only the 1st trial exclusively consisted of virgins. Other trials consisted both of virgins and mated females, but it is not clear in what ratio. Since mated females respond differently to courting males than virgins, only the results of the 1st trial are presented in this table.

Family & species	Average sexual size dimorphism (Female / male)	Influence on chance of being attacked/ cannibalized	Pre-copulatory frequency of attacks and cannibalism	Post-copulatory frequency of attacks and cannibalism	virgin or mated	reference
Pisauridae: *Dolomedes fimbriatus*	marginal, no calculation reported	Sexual size dimorphism (weight)	Attacks: 52% Cannibalism: 10.3%	Attacks: 68.8% Cannibalism: 25 %	Both	*Kralj-Fišer et al. 2016*
Lycosidae: *Pardosa Pseudo-annulata*	Body length: 10.2 mm/7.26 mm = 1.40	mate size dimorphism	Attacks: 21.8% Cannibalism: 10.3%	Attacks: 62.1% Cannibalism: 27.6 %	Both	*Wu et al. 2013*
Lycosidae: *Hogna radiata*	centroid size: 2.07/ 1.74 = 1.19	absolute male body size & sexual size dimorphism	Attacks: - Cannibalism: 1.5%	Attacks : 50.8% Cannibalism: 24.6 %	Virgin	*Fernández-Montraveta et al. 2014*
Araneidae: *Araneus diadematus*	Mass: 4/1 = 4	Absolute male body size	Attacks: - Cannibalism: 25%	Attacks: - Cannibalism: 15.4%	Virgin	*Elgar & Nash 1988*

Yet, pre-copulatory cannibalism did not occur frequently in mating trials (*Table 1*), hence females may not be very selective. Frequency of pre-copulatory cannibalism may also be low because virgin females were used in most experiments, since there is evidence that mated females are more selective. Mated *H. helluo* females engaged more in pre-copulatory cannibalism while virgin *H. helluo* females engaged more in post-copulatory cannibalism (*Wilder & Rypstra 2012*). Similarly, in *D. fimbriatus* mated females were less likely to mate than virgin females, and mated *P. pseudoannulata* females did not mate again at all (*Kralj-Fišer et al. 2016; Wu et al. 2013*). This difference between virgin and mated females may be explained by a difference in optimal mating strategies. Virgin females may prioritize mating over mate selection and forgo pre-copulatory cannibalism to reduce the risk of remaining unmated, whereas mated females may prioritize mate quality and only re-mate if a male is of sufficient quality, thus engaging in pre-copulatory cannibalism more often than virgin females. There is evidence that prior exposure to potential mates and assessed mate availability influence the mating behaviour of both males and females. In *H. helluo*, females that were exposed to, but did not mate with, potential mates were more likely to mate with the next male encountered than females that were not exposed to mates prior to mating (*Wilder & Rypstra 2008b*). Hence, indirect mate choice via pre-copulatory cannibalism may only be a likely explanation if selection for mate quality is the optimal mating strategy. This probably occurs primarily in spider species where mate availability is high enough for females to avoid the risk of remaining unmated.

Post-copulatory cannibalism

Post-copulatory cannibalism generally occurs more frequently than pre-copulatory cannibalism (*Table 1*). This is especially true for *N. livida* and *H. radiata*, where 0% and 1.5% of the males were cannibalized pre-copulatory, but 47.1% and 24.6% of the males were cannibalized post-copulatory (*Kralj-Fišer et al. 2012; Fernández-Montraveta et al. 2014*). An exception is *A. diadematus*, where pre-

copulatory cannibalism occurred more frequently than post-copulatory cannibalism (*Table 1*). Hence in general, most cannibalism occurs post-copulatory.

Post-copulatory cannibalism could be an expression of female mate choice in several ways, if females are not monogamous. Firstly, it may act as a way to control the duration of copulation with a male. This may be beneficial, since increased copulation duration has been suggested to lead to increased sperm transfer and thus lead to increased paternity for males (*Prenter et al. 2006*). Hence cannibalism could be used to control the paternity of a mate and therefore be used to decrease the paternity of a low quality mate and increase paternity of a higher quality mate, without the danger of remaining unmated. Yet there is only controversial evidence for the suggestion that increased copulation leads to increased paternity (*Prenter et al. 2006*). Also, both increased and decreased copulation duration has been reported as an effect of post-copulatory cannibalism (*Prenter et al. 2006*). It is therefore unclear if post-copulatory cannibalism can actually function as mate choice by controlling copulation duration.

Secondly, post-copulatory cannibalism may control the amount of genital openings used. Female spiders generally have two genital openings and males generally have two pedipalps used for sperm transfer (*Uhl et al. 2010; Neumann & Schneider 2020; Mouginot et al. 2015; Appendix: Figure 1*). A relatively common characteristic of male pedipalps is the ability to partially break off during copulation, which can then act as mating plugs, thus preventing the female from mating with another male and securing paternity with varying effectiveness (*Neumann & Schneider 2020; Uhl et al. 2010; Kralj-Fišer et al. 2012*). Post-copulatory cannibalism may be used to avoid the insertion of a second male pedipalp and consequent mate plug, thus retaining one genital opening for a mate of higher quality. It is of course necessary for the female to engage in post-copulatory cannibalism at the right moment: after the first copulation but before the insertion of the second pedipalp. This may be achieved via cannibalisation after a certain time period. In *T. fenestrata* copulations where females attacked males were longer than copulations where females did not attack males, and copulation duration was positively correlated with the number of male copulations in a trial (*Neumann & Schneider 2020*). Yet smaller males copulated more often than larger males and more often copulated in both genital openings than larger males. This offers little support for the hypothesis that post-copulatory cannibalism functions as indirect mate selection for relative larger males. Moreover, not all species that engage in post-copulatory cannibalism possess mate plugs (*Table 2*).

Thirdly, in some species males guard the female after mating against other males to increase paternity, as is the case in *N. livida* and *T. fenestrata* (*Kralj-Fišer et al. 2012; Neumann & Schneider 2020*). It may be especially common in species where mate plugs have a lower effectiveness (*Welke & Schneider 2012; Kralj-Fišer et al. 2012*). If females have retained the possibility to mate again it may be unfavourable to be guarded by the previous mate, especially if that mate is of low quality. Hence post-copulatory cannibalism may also be used to avoid mate guarding.

Fourthly, post-copulatory cannibalism may be used to control the number of pedipalp insertions. In a number of species among diverse families, male pedipalps can damage and mutilate the genital structure of females (*Mouginot et al. 2015*). Whereas mating plugs often also result in males being unable to mate again, males that damage female genitalia do not sustain damage to their pedipalps, thus allowing males to mate again (*Nakata 2016*). Female genital mutilation is a highly effective means of securing paternity: females in *L. jeskovi* and *C. argenteoalba* sustained damage in 90% and almost 100% of the matings. Damage to the female genital structure by males prevented females from copulation with other males completely (*Mouginot et al. 2015; Nakata 2016*). Hence control of the number of insertions may be used to avoid genital mutilation and retain the possibility to mate again. However, in *L. jeskovi* and *C. argenteoalba* there was no difference in mating attempts between mutilated and non-mutilated females and males courted both mutilated and non-mutilated females (*Mouginot et al. 2015; Nakata 2016*). Mutilated females cannot copulate, therefore they should avoid mating and males should avoid mating with a mutilated female. Since both sexes

attempt to mate all the same, it suggests that both males and females fail to recognize the damage to the female genital structure, at least until the next mating attempt. Besides, observed cannibalism in *C. argenteoalba* was relatively low (3.3%) and took place after palpal insertions (*Nakata 2016*). Similarly, in L. *jeskovi* females allowed 4 palpal insertions on average, which almost always resulted in mutilation of the female genital structure (*Mouginot et al. 2015*). It is therefore unlikely that post-copulatory cannibalism is utilised by females to prevent genital mutilation in these species.

Table 2: occurrence of mate plugs for different spider species. If mate plugs were not reported in a species in the relevant study or in Uhl et al. 2010., it was assumed to be absent in that species. * In the species studied by Sentenská et al. 2020 males engage in cannibalism instead of females.

Family & species	Mate plugs	Source
Lycosidae: *Pardosa pseudoannulata*	No	*Wu et al. 2013*
Lycosidae: *Hogna radiata*	No	*Fernández-Montraveta et al. 2014*
Lycosidae: *Hogna helluo*	No	*Wilder & Rypstra 2012*
Pisauridae: *Dolomedes fimbriatus*	Possibly	*Kralj-Fišer et al. 2016*
Araneidae: *Araneus diadematus*	Yes	*Elgar & Nash 1988*
Araneidae: *Argiope bruennichi*	Yes	*Welke & Schneider* 2012
Araneidae: *Trichonephila fenestrata*	Yes	*Neumann & Schneider 2020*
Araneidae: *Nephilengys livida*	Yes	*Kralj-Fišer et al. 2012*
Gnaphosidae: *Latrodectus geometricus*	Yes	*Sentenská et al. 2020*

Hypothesis 4: foraging strategy

Increased female body size and mass generally result in increased fecundity. This suggests that female foraging strategy has a major effect on reproductive success. In spiders, female body mass usually continues to increase after mating, and females generally still forage after mating (*Elgar & Nash 1988; spence et al. 1996*). Female growth and development depends not only on the amount, but also on the quality of food consumed (*Toft 1999*). Given that food may only be limited available in the wild (*Wilder et al. 2009*), food quality may play an important role in the growth of females. The meal hypothesis states that males may be food of high quality and sexual cannibalism may be a way for the female to obtain this food. Sexual cannibalism may thus provide the female with nutritional benefits and increase her fecundity (*Wilder et al. 2009*). A trade-off may exist between mating and the timing of cannibalism for females, since cannibalism prior to mating can result in females remaining unmated. But pre-copulatory cannibalism requires fewer chases and physical interactions than post-copulatory cannibalism, suggesting that there is a higher chance of succeeding in capturing and cannibalizing a male pre-copulatory than post-copulatory (*Wilder & Rypstra 2012*). Therefore, if mating becomes less important to females, they may engage more in pre-copulatory cannibalism to obtain a meal. This has been observed in mated females and females with a lower body condition (*Wilder & Rypstra 2012; Wu et al. 2013*), which supports the hypothesis of a trade-off and suggests that females adjust the timing of cannibalism. Sexual cannibalism may therefore be part of the female foraging strategy.

Males might profit from being cannibalized, but only after copulation, via paternal material investment in the offspring (*Schwartz et al. 2016; Welke & Schneider*). This may play a role in species where males have obligatory deaths after copulation or evoke cannibalism by summersaulting into the female mouthparts (*Schwartz et al. 2014, 2016; Setenská et al. 2020*). Male sacrifice/compliance may be beneficial for males if the chance of re-mating is small and if paternity can be secured, for example via monopolisation of the female or if females are monogamous (*Welke & Schneider 2012; Wilder et al. 2009*).

The evidence for the hypothesis that males are a high quality meal and that cannibalistic females have increased fecundity compared to non-cannibalistic females is equivocal (Wilder et al. 2009; Welke & Schneider 2012). It has been proposed that males are a high quality meal because male bodies consist of similar nutrients as females (*Wilder et al. 2009; Wilder & Rypstra 2010*).

But cannibalistic *D. triton* females did not have increased clutch size or egg mass (Spence et al. 1996). Male *H. helluo* had a higher protein content compared to crickets, but females consumed only 51% of the male body while 72% of the cricket body was consumed, resulting in similar amounts of protein ingestion from both males and crickets (*Wilder & Rypstra 2010*). Moreover, crickets and insects had an almost 4 times higher lipid content than males. Therefore the lipid/protein ratio of crickets seems to match the nutritional demands of egg production better than the lipid/protein ratio of male spiders, because eggs generally have a high lipid content (*Wilder & Rypstra 2010*). This suggests that males are not a high quality food compared to the general prey of this species.

However, in many species, reproduction of cannibalistic females seem to be higher in one or more aspects than in non-cannibalistic females. Cannibalistic *H. radiata* females consumed the male almost completely and had heavier cocoons and more offspring, independent of female body size, condition or foraging rate (*Fernández-Montraveta et al. 2014*). However, spiderling size, weight and survival time did not differ between cannibalistic and non-cannibalistic females (*Fernández-Montraveta et al. 2014*).

A. keyserlingi females feeding on high protein–low energy prey or conspecific males with a similar nutritional composition, produced eggs with higher energy densities than females feeding on low protein–high energy prey. But there was no difference in egg sac energy content, clutch size and clutch and egg mass (*Blamires 2011*). Since egg energy content is an indirect indicator of development and survival of spiderlings, females that fed on high protein–low energy prey or males may have enhanced fecundity. The enhanced fecundity cannot be ascribed to females channelling

the nutrients from prey/males to the eggs however, since the energy density of the eggs was dissimilar to the low energy prey and males. Also, males were <10% of female body weight and thus too small to have provided nutrients for direct egg investment. Besides, females that invested in greater egg energy contents lost weight. This suggests that they had to appeal to their somatic reserves for the energy investment in eggs, but it may also reflect a deficiency in food consumption, or a combination of those two. It is further suggested that proteins may be required to relocate energy from somatic reserves to eggs, and the consumption of high protein prey might be a physiological trigger (*Blamires 2011*).

In *A. bruennichi,* polyandrous cannibalistic females had the largest clutch sizes, and females that were allowed to consume males laid heavier eggs in their second egg sacs (*Welke & Schneider 2012*). Furthermore, offspring of cannibalistic females survived longer in starvation in simulated overwintering conditions, with no effect of the amount of weight of males consumed.

In *D. tenebrosus*, where all males die during copulation and females usually cannibalize males, cannibalistic females had more and larger offspring than females who consumed a cricket post-copulatory (*Schwartz et al. 2016*). Offspring of cannibalistic females also survived significantly longer than offspring of non-cannibalistic or cricket consuming females. Females consumed 87% of the male's mass. Females in this study were well fed and the males were only 7-13% the body mass of females, so males were unlikely to largely contribute to the female energy budget (*Schwartz et al. 2016*).

Food quality may not only be determined by lipid and protein content, but also by nutrient composition. For example, in vertebrates a similar protein composition between food and its consumer is suggested to reflect food quality (*Welke & Schneider 2012*). If proteins are required to allocate energy from somatic reserves to invest in eggs, as suggested by Blamires (2011), and the required proteins have to consist of a certain composition which are readily available in male bodies, then cannibalistic females may have increased energy investment in eggs as a result of an increased uptake of such proteins.

Overall, in most studies females appear to gain some profit from cannibalizing males, mostly based on them having increased fecundity and/or offspring survival, even though the males have relatively little energetic value (*Blamires 2011; Welke & Schneider 2012; Schwartz et al. 2016*). The effects, however, vary considerably between studies, and sometimes contrasting effects of sexual cannibalism on female fecundity and spiderlings were found. For example, in *H. radiata* there was no difference is spiderling survival between cannibalistic and non-cannibalistic females, whereas spiderlings of cannibalistic females in *A. bruennichi* and *D. tenebrosus* had a longer survival than spiderlings of non-cannibalistic females (*Fernández-Montraveta et al. 2014; Welke & Schneider 2012; Schwartz et al. 2016*). This makes it difficult to reach a consensus on the quality of males as food and the general effect of sexual cannibalism on fecundity.

Discussion

Both mate choice and meal quality can partially explain the function of sexual cannibalism. Mate choice could be indirect and based on the relative body size difference between males and females. Pre-copulatory cannibalism can be used to reject relatively smaller males and happens more frequently in mated females than in virgin females. Post-copulatory cannibalism may also be used as a way to discriminate between males, but the evidence that supports this is scarce. It may still be part of female mating strategy, since it can function to retain the possibility to re-mate. Males may be a high quality meal for females and cannibalism can positively influence fecundity or spiderling survival, but not all studies support this. The studies that support the hypothesis report various effects on the number and mass of eggs and spiderlings and spiderling survival, which sometimes appear contradictory.

Most of the reviewed studies have investigated species of either wolf spiders (Lycosidae), nursery web spiders (Pisauridae) or orb-weaving spiders (Araneidae). Sexual cannibalism occurs in more families (*Wilder et al. 2009; Uhl et al. 2010*), and it is unclear if the results are representative for all Araneae. Spiders are a diverse group of species that exist in many habitats and have many different physiological traits (*Garrison et al. 2016; Wilder et al. 2009*). Ecological and phylogenetic factors are known to influence the occurrence of sexual cannibalism in spiders (*Wilder et al. 2009*). Factors influencing the occurrence of sexual cannibalism may therefore differ between spider families and species (*Wilder et al. 2009*). The function of sexual cannibalism may then also vary between spider families and species. Differences between families and species may thus be a reason why effects of sexual cannibalism appear so various or even contradictory. Wolf and nursery web spiders appear relatively similar in the general sexual size dimorphism and mating strategy and differ in these aspects from orb-weaving spiders (*Table 1; Table 2; Wilder et al. 2009*). Hence, sexual cannibalism may have a similar frequency and/or function in wolf and nursery web spiders, but a different frequency and/or function in orb-weaving spiders.

Family related differences - mate choice
Sexual cannibalism is usually less frequent in species with a lower sexual size dimorphism (*Wilder & Rypstra 2008a*). Wolf and nursery web spiders are generally moderate sexual size dimorphic (*Table 1*). Hence, sexual cannibalism could have a relatively low frequency in wolf and nursery web spiders. A lower frequency of sexual cannibalism can still be a strong selective force, however (*Prenter et al. 2006*). Yet, when considering that female wolf and nursery spiders often only mate once (*Jiao et al. 2011; Wu et al. 2013; Kralj-Fišer et al. 2016)* despite having the possibility to be polygamous (*Kralj-Fišer et al. 2016; Fernández-Montraveta et al. 2014*), that virgin females engage only infrequently in pre-copulatory cannibalism, and that most of the cannibalisation takes place post-copulatory, sexual cannibalism appears to be mostly irrelevant as mate choice.

Male orb-weaving spiders may be vulnerable to cannibalisation regardless of the relative size difference between interacting pairs, since orb-weaving spiders generally have a large sexual size dimorphism, which may even result in a 100% success rate of female cannibalism attempts (*Kralj-Fišer et al. 2012*). Also, orb-weaving spiders generally have a more dangerous mating stance for males compared to wandering spiders (*Wilder et al.* 2009). Therefore, female orb-weaving spiders may be able to cannibalize males regardless of the relative size difference between interacting pairs. Hence, indirect mate choice based on body size may be an unlikely explanation for sexual cannibalism in orb-weaving spiders. Instead, sexual cannibalism may function for female orb-weaving spiders as a way to avoid monopolisation by males. Females of this family may profit from polygynous matings and are generally polygynous, but the occurrence of mating plugs, female genital mutilation and mate guarding limit the number of possible copulations and may result in monopolisation of females by males (*Welke & Schneider 2012; Kralj-Fišer et al. 2012; Neumann & Schneider 2020*). Hence, sexual cannibalism may still act as mate choice in female orb-weaving spiders by allowing monopolisation of high quality males, but is likely not based on male size.

Male mating strategy
If sexual cannibalism increases cannibalistic female's reproductive output compared to non-cannibalistic females, male sacrifice could be beneficial for males. An important requirement for this is that the increased female reproductive output outweighs the potential benefits for the male of mating with another female (*Schwartz et al. 2016*). This could be particularly true in species where females are monogamous or can be monopolized, or when the sex ratio is male biased (*Schwartz et al. 2016; Fromhage et al. 2005*). Yet male sacrifice occurs infrequently in spiders, and many male spiders attempt to avoid sexual cannibalism (*Schwartz et al. 2014; Neumann & Schneider 2020*), suggesting that it is usually more beneficial to attempt mating with another female. Male orb-weaving spiders may lose their ability to reproduce after mating with a female due to palpal damage, but often guard their female against other males, thus sacrifice may still not be beneficial for them (*Welke & Schneider 2012; Neumann & Schneider 2020*).

Foraging strategy
Overall, fecundity effects of sexual cannibalism appears to vary between species, but the variation does not seem to be related to differences between families. Sexual size dimorphism does not appear to influence the effect of sexual cannibalism on fecundity and cannibalistic females in nursery web and orb-weaving spiders had longer surviving offspring than non-cannibalistic females. Also, cannibalistic females usually had larger clutches than non-cannibalistic females in wolf, nursery and orb-weaving spiders (*Fernández-Montraveta et al. 2014; Schwartz et al. 2016; Welke & Schneider 2012*). Sexual cannibalism thus appears to enhance female reproductive output in wolf, nursery web and orb-weaving spiders, but it is unclear if males are food of high quality for females and how consumption of males contributes to enhanced female reproductive output.

In conclusion, sexual cannibalism appears to be able to function both as a mating and a foraging strategy is spiders, but the prevalence probably differs between families. Sexual cannibalism likely functions as a foraging strategy and has only a minor role as mate choice in wolf and nursery web spiders. In orb-weaving spiders sexual cannibalism may function both as mate choice and to gain a high quality meal, but is probably not influenced by the relative size difference between pairs.

Recommendations for further research
Many studies investigated effects on and of sexual cannibalism in spiders, but there appears to be a lack of studies that directly measured the fitness effects of sexual cannibalism, and especially the fitness effects of cannibalism over several generations. Studies on this subject are important, since they may serve to improve and support the hypotheses on, and our understanding of, the occurrence and functionality of sexual cannibalism in spiders. Furthermore, studies of sexual cannibalism in the field also appear to be scarce in literature. Mate and food availability may be limited and the proportion of mated spiders may be different in the field. These factors may vary throughout the mating season in the field. Since these factors can influence the behaviour of spiders, sexual cannibalism included, extrapolation of results gained from laboratory conditions to field conditions could be troublesome. Also, a bias in literature may exists towards certain spider families, like wolf and orb-weaving spiders, maybe because they are more common. Other families that engage in sexual cannibalism may thus be underrepresented in literature. To fully understand and represent the occurrence of sexual cannibalism these families should also be studied.
Despite several studies it is still unclear if or how male spiders are food of high quality for females. Isotopic signature has been used to investigate capital and income breeding in geese (*Gauthier et al. 2003*). Maybe isotopic signature can be used to study how the consumption of males influences female fecundity in spiders.
To summarize, future studies should mainly focus on investigating the fitness effects of sexual cannibalism. Also, there should be an increase in studies conducted in the field and of sexually cannibalistic spider families that may be underrepresented in literature. Lastly, isotopic signature may be a useful mechanism to investigate the effect of sexual cannibalism in spiders.
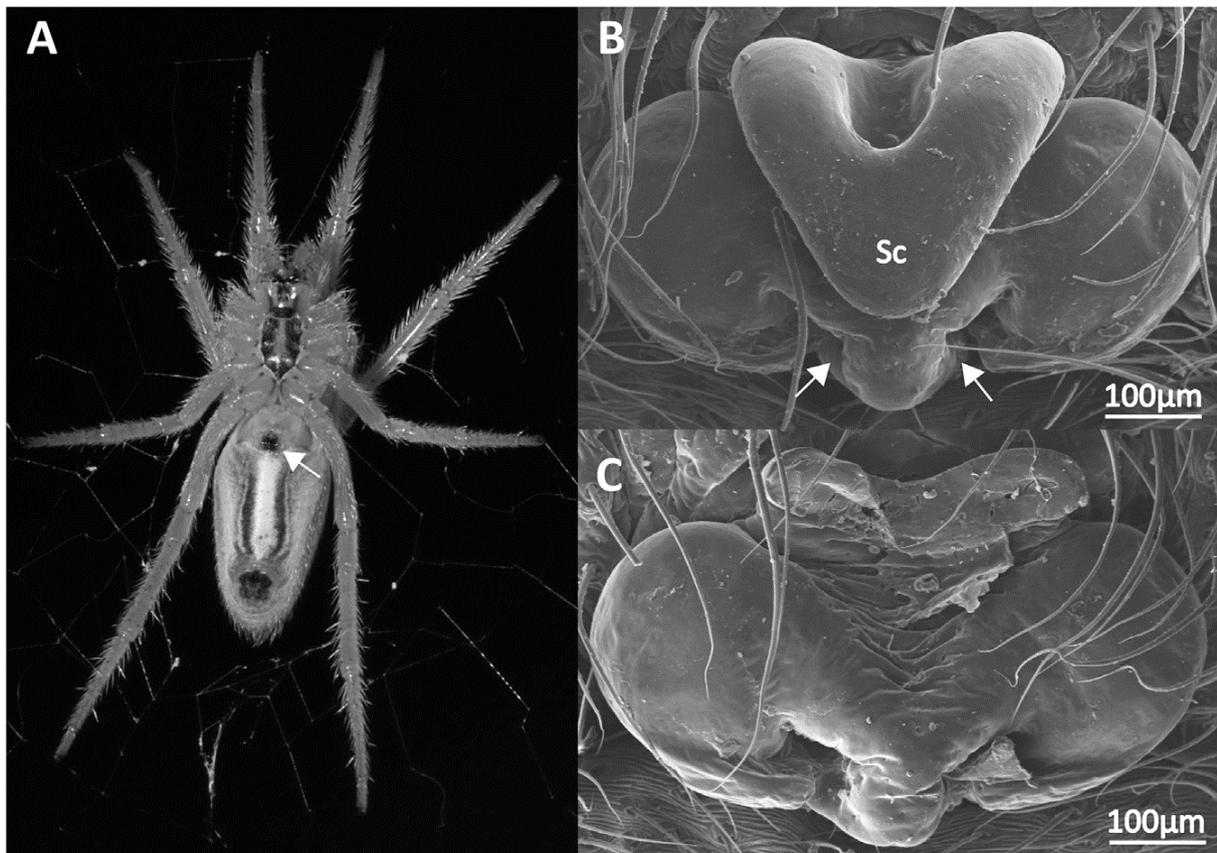
Figure 1: '(A) Macro-photograph of female Larinia jeskovi in her web in ventral view. Arrow points to external genitalia. (B and C) Scanning electron microscopic photographs of the external genitalia in ventral view with (B) an intact scapus (Sc) or (C) the scapus missing. Arrows point to copulatory openings. Scale bars, 100 mm.' Mouginot et al. 2015

References

Blamires, S. J. (2011). Nutritional implications for sexual cannibalism in a sexually dimorphic orb web spider. Austral Ecology, 36(4), 389–394. https://doi.org/10.1111/j.1442-9993.2010.02161.x

Brown, W. D., & Barry, K. L. (2016). Sexual cannibalism increases male material investment in offspring: Quantifying terminal reproductive effort in a praying mantis. Proceedings: Biological Sciences, 283(1833), 1–6.

Elgar, M. A., & Nash, D. R. (1988). Sexual cannibalism in the garden spider *Araneus diadematus*. Animal Behaviour, 36(5), 1511–1517. https://doi.org/10.1016/S0003-3472(88)80221-5

Fernández-Montraveta, C., González, J. M., & Cuadrado, M. (2014). Male vulnerability explains the occurrence of sexual cannibalism in a moderately sexually dimorphic wolf spider. Behavioural Processes, 105, 53–59. https://doi.org/10.1016/j.beproc.2014.03.002

Fromhage, L., Elgar, M. A., & Schneider, J. M. (2005). Faithful without care: The evolution of monogyny. Evolution, 59(7), 1400–1405.   https://doi.org/10.1554/04-680

Garrison, N. L., Rodriguez, J., Agnarsson, I., Coddington, J. A., Griswold, C. E., Hamilton, C. A., Hedin, M., Kocot, K. M., Ledford, J. M., & Bond, J. E. (2016). Spider phylogenomics: Untangling the spider tree of Life. PeerJ, 2016(2). https://doi.org/10.7717/peerj.1719

Gauthier, G., Bety, J., & Hobson, K. A. (2003). Are greater snow geese capital breeders ? New evidence from a stable-isotope model. Ecology, 84(12), 3250–3264.

Herberstein, M. E., Painting, C. J., & Holwell, G. I. (2017). Scramble competition polygyny in terrestrial arthropods. Advances in the study of behavior, 49, 237-295. https://doi.org/10.1016/bs.asb.2017.01.001

Jiao, X., Chen, Z., Wu, J., Du, H., Liu, F., Chen, J., & Li, D. (2011). Male remating and female fitness in the wolf spider *Pardosa astrigera*: The role of male mating history. Behavioral Ecology and Sociobiology, 65(2), 325–332. https://doi.org/10.1007/s00265-01

Khelifa, R. (2017). Faking death to avoid male coercion: Extreme sexual conflict resolution in a dragonfly. Ecology, 98(6), 1724–1726.

Kralj-Fišer, S., Schneider, J. M., Justinek, Z., Kalin, S., Matjaz, G., Pekár, S., & Kuntner, M. (2012). Mate quality, not aggressive spillover, explains sexual cannibalism in a size-dimorphic spider. Behavioral Ecology and Sociobiology, 66(1), 145–151. https://doi.org/10.1007/s00265-01

Kralj-Fišer, S., Čandek, K., Lokovšek, T., Čelik, T., Cheng, R. C., Elgar, M. A., & Kuntner, M. (2016). Mate choice and sexual size dimorphism, not personality, explain female aggression and sexual cannibalism in raft spiders. Animal Behaviour, 111, 49–55. https://doi.org/10.1016/j.anbehav.2015.10.013

Mouginot, P., Prügel, J., Thom, U., Steinhoff, P. O. M., Kupryjanowicz, J., & Uhl, G. (2015). Securing paternity by mutilating female genitalia in spiders. Current Biology, 25(22), 2980–2984. https://doi.org/10.1016/j.cub.2015.09.074

Nakata, K., & Ushimaru, A. (1999). Feeding experience affects web relocation and investment in web threads in an orb-web spider, *Cyclosa argenteoalba*. Animal Behaviour, 57(6), 1251–1255. https://doi.org/10.1006/anbe.1999.1105

Nakata, K. (2016). Female genital mutilation and monandry in an orb-web spider. Biology Letters, 12(2). https://doi.org/10.1098/rsbl.2015.0912

Neumann, R., & Schneider, J. M. (2020). Males sacrifice their legs to pacify aggressive females in a sexually cannibalistic spider. Animal Behaviour, 159, 59–67. https://doi.org/10.1016/j.anbehav.2019.11.003

Perry, J. C., & Rowe, L. (2012). Sexual conflict and antagonistic coevolution across water strider populations. Evolution, 66(2), 544–557.

Prenter, J., Elwood, R. W., & Montgomery, W. I. (1998). No association between sexual size dimorphism and life histories in spiders. Proceedings: Biological Sciences, 265(1390), 57–62. https://doi.org/10.1098/rspb.1998.0264

Prenter, J., MacNeil, C., & Elwood, R. W. (2006). Sexual cannibalism and mate choice. Animal Behaviour, 71(3), 481–490. https://doi.org/10.1016/j.anbehav.2005.05.011

Schwartz, S. K., Wagner, W. E., & Hebets, E. A. (2014). Obligate male death and sexual cannibalism in dark fishing spiders. Animal Behaviour, 93, 151–156. https://doi.org/10.1016/j.anbehav.2014.04.037

Schwartz, S. K., Wagner, W. E., & Hebets, E. A. (2016). Males can benefit from sexual cannibalism facilitated by self-sacrifice. Current Biology, 26(20), 2794–2799. https://doi.org/10.1016/j.cub.2016.08.010

Sentenská, L., & Pekár, S. (2013). Mate with the young , kill the old: Reversed sexual cannibalism and male mate choice in the spider *Micaria sociabilis* (Araneae : Gnaphosidae). Behavioral Ecology and Sociobiology, 67(7), 1131–1139.

Spence, J. R., Zimmermann, M., & Wojcicki, J. P. (1996). Effects of food limitation and sexual cannibalism on reproductive output of the nursery web spider *Dolomedes triton* (Araneae : Pisauridae). Oikos, 75(3), 373–382.

Toft, S. (1999). Prey choice and spider fitness. The Journal of Arachnology, 27(1), 301–307.

Uhl, G., Nessler, S. H., & Schneider, J. M. (2010). Securing paternity in spiders? A review on occurrence and effects of mating plugs and male genital mutilation. Genetica, 138(1), 75–104. https://doi.org/10.1007/s10709-009-9388-5

Welke, K. W., & Schneider, J. M. (2012). Sexual cannibalism benefits offspring survival. Animal Behaviour, 83(1), 201–207. https://doi.org/10.1016/j.anbehav.2011.10.027

Wilder, S. M., & Rypstra, A. L. (2008a). Sexual size dimorphism predicts the frequency of sexual cannibalism within and among species of spiders. American Naturalist, 172(3), 431–440. https://doi.org/10.1086/589518

Wilder, S. M., & Rypstra, A. L. (2008b). Prior encounters with the opposite sex affect male and female mating behavior in a wolf spider (Araneae, Lycosidae). Behavioral Ecology and Sociobiology, 62(11), 1813–1820. https://doi.org/10.1007/s00265-008-0610-8

Wilder, S. M., Rypstra, A. L., & Elgar, M. A. (2009). The importance of ecological and phylogenetic conditions for the occurrence and frequency of sexual cannibalism. Annual Review of Ecology, Evolution, and Systematics, 40, 21–39. https://doi.org/10.1146/annurev.ecolsys.l

Wilder, S. M., & Rypstra, A. L. (2010). Males make poor meals: A comparison of nutrient extraction during sexual cannibalism and predation. Oecologia, 162(3), 617–625. https://doi.org/10.1007/s00442-009-1518-3

Wilder S. M., & Rypstra A. L. (2012). Trade-off between pre-and postcopulatory sexual cannibalism in a wolf spider (Araneae, Lycosidae). Behavioral Ecology and Sociobiology, 66(2), 217–222. https://doi.org/10.1007/s00265-01

Wu, L., Zhang, H., He, T., Liu, Z., & Peng, Y. (2013). Factors influencing sexual cannibalism and its benefit to fecundity and offspring survival in the wolf spider *Pardosa pseudoannulata* (Araneae: Lycosidae). Behavioral Ecology and Sociobiology, 67(2), 205–212. https://doi.org/10.1007/s00265-012-1440-2

Zhang, S., Kuntner, M., & Li, D. (2011). Mate binding: Male adaptation to sexual conflict in the golden orb-web spider (Nephilidae: *Nephila pilipes*). Animal Behaviour, 82(6), 1299–1304. https://doi.org/10.1016/j.anbehav.2011.09.010