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Original Article

Sexual and nonsexual cannibalism have different effects on offspring performance in redback spiders

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Sexual cannibalism is often set apart from other forms of cannibalism; however, no studies have directly compared the fitness consequences of these 2 types of cannibalism. Here, we compared the consequences of cannibalism of a male by a female outside the context of mating (referred to as nonsexual cannibalism) and within the context of mating (referred to as sexual cannibalism) for the propensity to remate, fecundity, and offspring traits of female redback spiders *Latrodectus hasselti*. Although the timing of cannibalism relative to copulation is critical for male fitness, it is still unclear whether it can also influence female fitness, beyond the fertilization of eggs. Our results showed that sexual cannibalism and nonsexual cannibalism had different effects on offspring survival and growth. Sexually cannibalistic females produced offspring that survived better and grew faster than nonsexually cannibalistic or noncannibalistic females. By experimentally manipulating the quality of prey given to offspring, we showed that these effects were dependent on the spiderlings' diet quality. In particular, the effects of sexual cannibalism on offspring growth and survival were clearer when offspring were, respectively, fed a high-nutrient diet and a low-nutrient diet. However, sexual cannibalism did not increase offspring tolerance to starvation. Additionally, we did not find any effect of nonsexual cannibalism nor sexual cannibalism on female fecundity or subsequent sexual receptivity. As copulation duration did not account for these effects on offspring performance, our findings suggest that copulation occurring simultaneously with cannibalism plays an essential role in the fitness consequences of this behavior.

Key words: ***Latrodectus hasselti*, maternal effects, mating effort, offspring growth, offspring survival, paternal investment.**

INTRODUCTION

Cannibalism, the killing and consumption of individuals of the same species, occurs in a wide range of animals, from unicellular eukaryotes to primates (Fox 1975; Polis 1981; Elgar and Crespi 1992; Richardson et al. 2010). Cannibalism can take many forms including killing and consumption of eggs, juveniles, or members of the opposite sex. Sexual cannibalism, the killing and consumption of conspecific males by females during courtship, copulation, or immediately after copulation, has received particular attention because of its consequences for both male and female fitness (Elgar and Crespi 1992; Elgar and Schneider 2004). Interestingly, sexual cannibalism is often set apart from other types of cannibalism even though little is known about whether or not there are different consequences of the various types of cannibalism.

One hypothesis for cannibalism in general is that it is a foraging decision in which the consumer is seeking nutrients from the body of the victim (Fox 1975; Polis 1981; Newman and Elgar 1991; Elgar and Crespi 1992; Wise 2006; Barry et al. 2008). Cannibalism may also represent a form of competition in which cannibals reduce the number of other consumers competing for their food resources or the resources of their offspring (Fox 1975; Polis 1981; Elgar and Crespi 1992; Wise 2006). In addition to these 2 hypotheses proposed more generally for cannibalism, several hypotheses related to mate choice and sexual selection have been proposed for the occurrence and frequency of sexual cannibalism (Simmons and Parker 1989; Elgar and Schneider 2004; Prenter et al. 2006; Barry et al. 2008). In the evaluation of costs and benefits for both sexes, the occurrence of copulation is a critical factor. Precopulatory cannibalism is costly

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for males because it precludes copulation and, hence, any potential fitness gain (Newman and Elgar 1991; Elgar and Schneider 2004). Precopulatory cannibalism appears to be an extreme manifestation of sexual conflict: Males lose future opportunities for reproduction, but females can gain nutritional benefits (Schneider and Lubin 1998; Rabaneda-Bueno et al. 2008). In contrast, when cannibalism occurs during or after mating, it can be either a male or female adaptive strategy or both (Elgar and Schneider 2004). For instance, by cannibalizing, females may gain nutrients and increase their body mass, their body condition, or fecundity (Buskirk et al. 1984; Birkhead et al. 1988; Elgar and Nash 1988; Johnson 2005; Barry et al. 2008). In parallel, when males are able to copulate, sexual cannibalism can be an adaptive male strategy by giving cannibalized males advantages in sperm competition (mating effort) or by improving cannibalized males' offspring quality (paternal investment) (Simmons and Parker 1989; Elgar and Schneider 2004).

One species in which sexual cannibalism has been well studied is the Australian redback spider *Latrodectus hasselti* (Forster 1992; Andrade 1996, 1998; Andrade and Banta 2002; Andrade 2003; Snow and Andrade 2004; Andrade et al. 2005; Snow et al. 2006). In this species, sexual cannibalism appears to be a male-initiated strategy whereby males aid their own consumption by performing a "somersault" while copulating, positioning themselves above the female's chelicerae (Forster 1992; Andrade 1996). Despite the male's vulnerable posture, only 65% of matings involve cannibalism and the occurrence of cannibalism appears related to female hunger and discrimination among males (Forster 1992; Andrade 1996, 1998; Stoltz et al. 2008b). This male self-sacrifice behavior has been associated with 2 significant paternity advantages for cannibalized males when compared with uncannibalized males: an increased copulation duration, often linked to paternity (Andrade 1996; Snow and Andrade 2004), and a lower female receptivity to future suitors (Andrade 1996). These 2 advantages of sexual cannibalism combined with the high mortality risk for males during mate search in the field (Andrade 2003) may explain the selection of an extreme male investment in this monogynous mating system (Fromhage, Elgar, et al. 2005; Fromhage, Jacobs, et al. 2007; Miller 2007; Fromhage, McNamara, et al. 2008; Schneider and Fromhage 2010; Fromhage and Schneider 2012). Nevertheless, it is unclear whether it is the longer copulation, eating the male or both that contributes to the effects of sexual cannibalism on females. There is evidence in other arthropods that both eating nuptial gifts offered by males (in the case of redback spiders, their own bodies) and receiving manipulative seminal components can affect females (Koene and Ter Maat 2001; Sakaluk et al. 2006; Gwynne 2008). Whether the effects of sexual cannibalism on females result from the consumption of the male's body or from the transfer of seminal substances have considerable implications for the relative consequences of nonsexual and sexual cannibalism.

Recent studies have provided new insights into our understanding of the evolution of sexual cannibalism. Most studies have failed to detect an overall increase in female fecundity after sexual cannibalism (Barry et al. 2008; Wilder et al. 2009). However, studies of other spider species have shown that there can be more subtle effects of cannibalism on fitness (Johnson 2001; Welke and Schneider 2012; Wu et al. 2013; Pruitt et al. 2014). More precisely, sexual cannibalism increases the probability that a female's egg sac will hatch in the fishing spider *Dolomedes triton* (Johnson 2001) and in the funnel-web spider *Agelenopsis pennsylvanica* (Berning et al. 2012; Pruitt et al. 2014). Furthermore, sexually cannibalistic females *Argiope bruennichi* and *Pardosa pseudoannulata* were shown to produce offspring with a prolonged survival time under starvation, compared with the offspring of noncannibalistic females (Welke and Schneider 2012; Wu et al. 2013). We investigated whether such subtle effects of cannibalism on offspring performance are found in *L. hasselti*. Additionally, Schneider and Elgar (2002) showed that females *Nephila plumipes* that attempted but that were prevented to cannibalize their mate gained more mass prior to oviposition and produced larger first clutches than noncannibalistic females. Such findings suggest that females of some species have variable life-history strategies and that sexual cannibalism can be a side effect of the increased foraging vigor displayed by females that matured at a smaller size. Thus, we tested whether the propensity of females to cannibalize their mate, rather than the act of cannibalism itself, was the critical variable explaining hypothetical differences in fitness between cannibalistic and noncannibalistic females.

We compared the consequences of sexual cannibalism and nonsexual cannibalism for the propensity to remate, fecundity, and offspring traits of female redback spiders, *L. hasselti*. We hypothesized that the copulation associated with sexual cannibalism was necessary for reduced female receptivity (Andrade 1996). Hence, we predicted that female receptivity after sexual cannibalism would be lower than receptivity in the nonsexual cannibalism and no-cannibalism treatments. Alternatively, if substances in the male body (e.g., hormones or other chemicals) rather than the ejaculate inhibit female remating, then we predict that both sexual and nonsexual cannibalism would be associated with reduced female receptivity. After the mating trials, we maintained females on constant diets until they produced eggs. We hypothesized that there would be no effect of cannibalism, regardless of whether it was sexual or nonsexual, on female fecundity because the male body is relatively small in this species (Andrade 1996; Barry et al. 2008). Finally, we quantified offspring survival and growth under 3 different diets: complete starvation, a low-nutrient diet, and a high-nutrient diet. We hypothesized that substances transferred either in the male ejaculate during cannibalism or through the male body could affect the survival and growth of a cannibalistic female's offspring. If compounds in the male body affect offspring traits, then we would predict that offspring growth and/or survival would be higher in both sexual and nonsexual cannibalism treatments relative to no cannibalism. Alternatively, if compounds in the ejaculate influence the effects of cannibalism on offspring traits, then we would predict higher survival and/or growth in the sexual cannibalism treatment relative to the no-cannibalism and nonsexual cannibalism treatments. Copulation may make a difference if some of these resources are transferred by the male through the ejaculate or utilized differently by the female if cannibalism and copulation occur simultaneously. We also manipulated the spiderlings' diet quality and expected it to influence the potential benefit of cannibalism in the sense that starving or nutrient-limited spiderlings might be the ones benefiting the most from their mother's cannibalistic behavior in terms of survival and growth (Welke and Schneider 2012; Wu et al. 2013).

METHODS

Study animals

Individual redback spiders were initially collected as mated adult females from Wentworth Park in Glebe (Sydney, New South Wales, Australia). They were housed individually in large cups (diameter: 11 cm, height: 10 cm) and reared in a temperature-controlled environment at 25 °C in a 13:11 h light:dark cycle. They were provided a diet of 1–3 locusts (*Locusta migratoria* or *Chorticetes terminifera*) per week until they produced eggs. After emerging from their egg sac, spiderlings were each placed into individual small cups (diameter: 4 cm, height: 4 cm) and fed 2–5 *Drosophila melanogaster* twice per week. Once females reached 5–8 mm in body length (i.e., fourth or fifth instar), they were moved into the larger cups and fed with 1 size-matched locust either once or twice per week until adulthood. Adult females were left unfed for 1–3 weeks between their final molt and the application of the treatments. Adult males were fed 5 flies twice per week.

In *L. hasselti*, after a 5-h long courtship, copulation typically begins with the male standing on the female's abdomen. The male inserts one of his paired copulatory organs (pedipalps) into one of the female's paired genital opening. A few seconds after palp insertion, the male raises his body into the air and quickly turns through 180° ("somersault"), landing with the dorsal surface of the abdomen above the female's mouthparts. Then, in most matings (65%), the female starts to consume the male while he is still transferring sperm (Forster 1992). Males that survive the wounds caused by the female typically withdraw their inserted pedipalp after 25 min and resume courtship in order to get access to a second copulation with the same female (Andrade et al. 2005). Indeed, redback matings can include 2 consecutive copulations as each of the paired male pedipalps can only inseminate one of the 2 female spermathecae (Andrade and Banta 2002). Thus, males that die after the first copulation (12.5% in the field; Andrade 1998) leave 1 female spermathecae empty and can lose 50% of their paternity to rival mates mating later on (Snow and Andrade 2005). In contrast, males able to make it through a second copulation can expect sperm precedence in each female reproductive tract after depositing sperm plugs (Snow et al. 2006).

Mating trials and treatment groups

Mating trials were conducted at 25 °C during the photophase, and video-recorded. We used virgin adult females aged between 1 and 3 weeks, and virgin males approximately 1 month after their final molt. One virgin male was presented to the female in her rearing cup and allowed to copulate with her once (i.e., 1 single insertion). To compare the effects of sexual cannibalism and nonsexual cannibalism, we used 3 distinct treatments. Females were randomly allocated to either the "no-cannibalism" treatment, the "sexual cannibalism" treatment, or the "nonsexual cannibalism" treatment.

In the nonsexual cannibalism treatment, we fed 1 adult male corpse to virgin females ($n = 16$) 3 days before the first mating trial. Males were killed by putting them in the freezer (approximately −20 °C) for 10 min. They were introduced into the female's web after warming to room temperature, and we used a modified electric toothbrush to perform vibrations around the male's body and draw the female's attention. As these females had not been fed since their final molt (i.e., for between 1 and 3 weeks), they all ate the introduced male. These females were given an oversized cricket 2 days before their mating trial so that they were satiated and unlikely to cannibalize their mate during mating (Andrade 1998). If the female attempted cannibalistic attacks during mating (8 of 14 successful matings), we prevented her from eating her mate by softly inserting a very thin paintbrush between her fangs and the male abdomen (Herberstein et al. 2010). Male web reduction behavior (Watson 1986; Forster 1995) during courtship made it easier not to touch the female's web with the paintbrush. In response, the female usually stopped eating the male or bit the paintbrush soft hairs without additional movements. No differences could be found in copulation duration between naturally noncannibalistic matings and matings whereby cannibalism was artificially prevented ($W = 197$, $P = 0.8$). Additional statistical analyses did not reveal any effect of the technique on studied variables (data not shown). Hence, disturbance due to our paintbrush technique seems negligible and is very unlikely to affect the results we present here.

In the sexual cannibalism treatment, females were not fed prior to mating trials and we allowed the occurrence of natural sexual cannibalism (during copulation) during the mating trial ($n = 29$). We included in this treatment only the females that copulated once (i.e., 1 single palp insertion) with the occurrence of cannibalism ($n = 16$ of the 29 trials). Females were fed 1 oversized cricket just after this mating event.

Finally, in the no-cannibalism treatment, females were fed 1 oversized cricket before the mating trial ($n = 19$) and prevented from cannibalizing during copulation (6 of 16 successful matings). As female propensity to cannibalize did not significantly affect any of the response variables tested (see Results for details), we also included females that were initially designed to be in the sexual cannibalism treatment and mated but did not cannibalize during their trial ($n = 9$). Hence, our control treatment included both females that were well fed during mating (as in the "nonsexual cannibalism" trials) and females that were hungry during mating and fed after the 2 trials (as in the "sexual cannibalism" trials). There were no significant differences in any of the response variables between control females that were fed before or after mating, and hence, they were all combined into the control treatment (data not shown).

Females that failed in copulating after 8 h of courtship were removed from the treatments ($n = 9$). Thus, the final sample sizes were as follows: sexual cannibalism treatment ($n = 16$), nonsexual cannibalism treatment ($n = 14$), and no-cannibalism treatment ($n = 25$).

During the first mating trial in which virgin females were presented with males for the first time, we allowed copulation to occur and recorded its duration and the occurrence of cannibalism. As the stereotyped somersault occurs a few seconds after pedipalp insertion (Forster 1992), we used it as a cue to observe the beginning of copulation. Matings where males were found dead (but not eaten) in the somersault posture with their palp still inserted ($n = 4$ of 55 matings) were not considered here, as true copulation duration could not be assessed. Such a death was diagnosed when no contraction of the inserted pedipalp could be observed under the microscope. These males may have been bitten by their mate without being totally consumed. To compare natural copulation duration between the no-cannibalism treatment and the sexual cannibalism treatment, we removed matings where copulation was artificially interrupted or disturbed when we failed in preventing cannibalism with the paintbrush and unintentionally caused the female to move ($n = 4$ of 41 matings).

Does the timing of cannibalism affect female sexual receptivity?

After copulation, each female was moved to a new large container where she built a new web. To assess remating probability, each mated female underwent a second trial. The second trial was performed within 1 week of the first trial and consisted of the assessment of female receptivity behavior to a new suitor, which was only allowed to climb on the female's abdomen for 15 min before being removed. That way, we made sure that the female had only been fertilized once by the first male. Because of limitations on the number of males available, some males ($n = 22$) that survived their first copulation (first trial) were reused for the receptivity assessment (second trial) with a different female. As experience may affect male mating behavior and especially courtship, we tested the effect of experience on our response variables through Mann–Whitney and Fisher's Exact tests (depending on the nature of the response variable).

Female receptivity was assessed by her behavior toward a new courting male. A receptive female usually stays quiescent during courtship with the abdomen lowered to enable access to the male (receptive posture), whereas a nonreceptive female tends to keep her abdomen close to the web, to move a lot, and to be aggressive by hitting the male with her front legs, sometimes making him fall from the web and cease courting (Forster 1992; Andrade 1996). Female willingness to remate was therefore measured via her posture (receptive or not), the occurrence of female front leg strikes at the male (at least 1 strike or no strikes), and the number of female movements on the web (i.e., number of displacements). We considered the occurrence of female leg strikes as a binomial variable rather considering its frequency because of the low frequency of this behavior. To compare the different response variables between the different treatments, we ran Fisher's Exact tests (posture and occurrence of leg strikes) and analyses of variance (number of displacements). All statistical analyses in the study were performed using R software version 3.0.1 (R Development Core Team 2013).

Does the consumption of a male result in female fecundity benefits?

The first egg sacs laid by mated females were collected and weighed. Although the timing of feeding differed (i.e., before or after mating), all females were fed to satiation with crickets to standardize the amount of prey resources available for egg production. We randomly subsampled some females that produced egg sacs from the 3 treatment groups: "nonsexual cannibalism" ($n = 10$), "sexual cannibalism" ($n = 13$), and "no cannibalism" ($n = 12$). These mothers were weighed 3 weeks after mating (i.e., after they all produced an egg sac). Females did not receive any food during that period. Mothers were then frozen, photographed, and we measured their right front tibia–patella length, which is typically used to determine body size in web-building spiders (Schneider et al. 2005) using ImageJ software. As body size and body mass were correlated (see Results for details), we estimated body condition for each female as the residuals of the linear regression between tibia–patella length and body mass. Freshly hatched clutches were photographed, and the number of spiderlings was assessed using ImageJ software.

Data were tested for a normal distribution using Shapiro–Wilk normality tests. We used analyses of variance to compare the tested variables between the different treatments. We ran analyses of covariance to investigate the main factors influencing female fecundity (i.e., egg sac mass), namely the experimental cannibalistic group (categorical variable), body size, and body condition.

Does the occurrence of cannibalism or timing of cannibalism affect offspring performance?

As the nutritional composition of prey can vary widely in nature and can have a large effect on the growth of spiders (Toft and Wise 1999; Wilder 2013), spiderlings from the 3 experimental treatments were raised under 3 food treatments: "complete starvation," "low-nutrient," and "high-nutrient" diet (see details below). For each clutch, spiderlings ($n = 15$/clutch) were randomly chosen, weighed together to assess the average single spiderling weight, and then isolated into 3 treatment groups: starvation ($n = 5$/clutch), low-nutrient ($n = 5$/clutch), and high-nutrient ($n = 5$/clutch) diet. The spiderlings were individually placed in small containers (4-cm diameter, 4-cm height).

The high-nutrient treatment was achieved by feeding the spiderlings adult female *D. melanogaster* raised on enriched medium (Mayntz and Toft 2001). Enriched medium was prepared by mixing 2 parts of potato flake medium (Carolina© medium) to 1 part of ground dog food (Pedigree© Adult Complete Nutrition Dog Food; Mars Australia, North Ryde, Australia) made into a powder, by volume. The low-nutrient treatment was achieved by providing the same quantity of food, but the flies had been raised on the potato flake medium only. There were no differences in the dry mass or percent carbon content of flies raised on similar treatments in a previous study, but flies reared on the high-nutrient medium had higher nitrogen, lower carbon:nitrogen, lower lipid, higher protein, and lower lipid:protein than flies reared on the potato flake medium alone (Schmidt et al. 2012; Wilder 2013). We started feeding the spiderlings 1 week after emergence from the egg sac. They were given 2 female flies twice per week for the first 2 weeks, and then 3 female flies twice per week for the third and fourth weeks.

We checked all individuals daily for survival. We assessed the growth of individuals that survived 5 weeks after emergence from the egg sac in the low- and high-nutrient treatments by measuring their right front tibia–patella length (using ImageJ software) to determine body size (Schneider et al. 2005). As the spiderlings would have reached different instars after 5 weeks, observed differences in size are most likely to reflect differences in growth rate. Therefore, we also estimated the spiderlings' instars from the distribution of tibia–patella length: We sorted the spiderlings according to their patella–tibia length, plotted the resulting distribution, and assigned the spiderlings to different instars based on transitions in patella–tibia length (Supplementary Figure S1). We double-checked that these visible transitions corresponded to relevant phenotypic differences between the individuals of each group using photographs of individuals (e.g., differences in the color pattern).

To account for the relatedness of some individuals born to the same mother, we fitted mixed-effects Cox proportional-hazards models using the "coxme" package in R. We considered the mother ID as a random factor in the models and tested the effects of both the feeding treatment and the cannibalistic treatment of the mother on offspring survival.

We fitted linear mixed-effects models to test the effects of diet treatment, cannibalistic treatment, and their interaction on spiderling tibia–patella length (i.e., spiderlings size), followed by Tukey Honest Significant Difference (HSD) post hoc tests. Again, the mother ID was included as a random factor in the models. Finally, as the 5-week-old spiderlings' instar was a ordered categorical response variable, we fitted cumulative link mixed models using the function "clmm" in the "ordinal" package in R. While considering mother ID as a random factor in the models, we checked the effects of diet and mother cannibalism on the distribution of spiderlings' instars: How do these treatments affect the reaching of advanced instars after 5 weeks?

RESULTS

Copulation duration

Sexually cannibalized males (16.02 ± 1.19 min, $n = 15$) were found to copulate for significantly longer than noncannibalized males (10.34 ± 1.52 min, $n = 18$; $W = 207$, $P = 0.008$).

Does the timing of cannibalism affect female sexual receptivity?

Second males were always able to climb onto the female abdomen as the female always adopted a receptive posture. We analyzed the occurrence of female leg strikes at males and female activity level as indirect measures of receptivity. No difference could be detected between the 3 treatments in terms of leg strike occurrence (Fisher's Exact test, $P = 0.37$). In the sexually cannibalistic females, 7 out of 16 females (44%) showed at least 1 leg strike directed toward the male, whereas this proportion was 4 out of 11 (36%) and 6 out of 26 (23%), respectively, in the nonsexually cannibalistic and noncannibalistic females. Finally, the treatments did not differ when we considered the number of female movements during male courtship (sexual cannibalism: 2.88 ± 0.62 movements, $n = 16$; nonsexual cannibalism: 2.73 ± 0.49 movements, $n = 14$; no cannibalism: 1.83 ± 0.35 movements, $n = 25$). We ran an analysis of covariance with the number of movements as the dependent variable that included copulation duration during the first trial and cannibalistic treatment as explanatory variables. We found no significant effect of copulation duration ($P = 0.4$) or cannibalistic treatment ($P = 0.66$).

We also tested whether the consumption of a male without copulation affected female receptivity in the first mating trial. Again, we did not find any significant differences when comparing receptivity factors during the first trial between the nonsexual cannibalism treatment and the 2 other treatments. All females adopted a receptive posture during male courtship. Two of 16 pairings (12.5%) did not copulate after 8 h of courtship in the nonsexual cannibalism treatment, 4 of 29 (13.8%) in the sexual cannibalism treatment, and 3 of 19 (15.8%) in the no-cannibalism treatment (Fisher's Exact test: $P = 1$). Six out of 14 females (42.9%) struck at their mate at least once in the nonsexual cannibalism treatment, 3 out of 25 in the no-cannibalism treatment (12%) and 4 out of 16 in the sexual cannibalism treatment (25%) ($P = 0.22$). Finally, the number of female movements did not differ either between females that ate a male before the first trial and those that did not (nonsexual cannibalism: 3.33 ± 0.65 movements, $n = 14$; no cannibalism: 2.16 ± 0.61 movements, $n = 25$; sexual cannibalism: 4.19 ± 0.9 movements, $n = 16$; $F = 2.17$, $P = 0.12$).

Additionally, we tested whether the female propensity to cannibalize during the first trial, rather than the act of cannibalism, could predict a subsequent lack of receptivity. Again, females that showed a willingness to cannibalize during the first trial but were either prevented or allowed to eat their mate did not show significantly more aggressive behaviors toward the male in the second trial. Results are presented in Supplementary Table S1. Finally, the reuse of some males for the receptivity trials was only found to affect the time to climb for the first time onto the female's abdomen—experienced males were significantly faster to climb onto the female's abdomen than virgin males (Supplementary Figure S2). Females showed significantly more aggressive behaviors (i.e., leg strikes) at these experienced males compared with virgin males (Fisher's Exact test: $P = 0.04$).

Does the consumption of a male result in female fecundity benefits?

Female body size was positively correlated to body mass ($r = 0.58$). No difference was found between cannibalistic and noncannibalistic matings in terms of female mass 3 weeks after mating, female front tibia–patella length (i.e., female size), female body condition, first egg sac mass, clutch size, and spiderling mass (Table 1). These response variables were also not affected by female propensity to cannibalize (Supplementary Table S2).

We ran analyses of covariance to test the effects of mother body size, mother body condition, and cannibalistic treatment on egg sac mass (i.e., fecundity). The model of best fit for egg sac mass was egg sac mass = female body size × female body condition (Supplementary Table S3). Adding the effect of the cannibalistic treatment did not improve the quality of the model (Akaike information criterion [AIC] = 211 vs. AIC = 207). Female body size and body condition were significant predictors of egg sac mass ($P = 0.04$ and $P = 0.01$, respectively).

Does the occurrence of cannibalism or timing of cannibalism in relation to copulation (i.e., sexual vs. nonsexual cannibalism) affect offspring survival?

Offspring survival results according to their feeding treatment and the cannibalistic treatment of their mother are shown in Figure 1 as Kaplan–Meier survival curves. When fitting mixed-effects Cox proportional-hazards models to account for repeated measures considering mother ID as a random factor, we compared the different models using log-likelihoods. The model of best fit (significant reduction in log-likelihood) is presented in Table 2 and includes the feeding treatment, the mother cannibalistic treatment, and their interaction. The mother cannibalistic treatment had a significant effect on offspring survival: sexual cannibalism significantly decreased the mortality risk of the offspring compared with offspring born of noncannibalistic mothers (reference level in the model). As expected, starvation strongly increased offspring

Table 1

A comparison of cannibalistic and noncannibalistic matings' effects on female's body features and fecundity

Factor	Sexual cannibalism			No cannibalism			Nonsexual cannibalism			Anova
	Mean	SE	*n*	Mean	SE	*n*	Mean	SE	*n*	*P*
Female mass (mg)	93.23	4.52	14	80.19	4.86	7	93.42	5.50	10	0.191
Female tibia/patella length (mm)	5.34	0.07	14	5.08	0.13	7	5.18	0.09	10	0.134
Female body condition index	0.08	0.07	14	−0.05	0.09	7	−0.08	0.08	10	0.288
First egg sac mass (mg)	76.60	6.39	14	68.92	5.37	7	69.77	5.38	10	0.614
Clutch size[a]	125	16	9	116	16	6	137	18	8	0.87
Spiderling mass[b] (mg)	0.42	0.04	13	0.28	0.05	7	0.37	0.05	10	0.146

Anova = analysis of variance; SE, standard error.

[a] Clutch size was only considered for fully hatched egg sacs.

[b] One egg sac did not hatch.

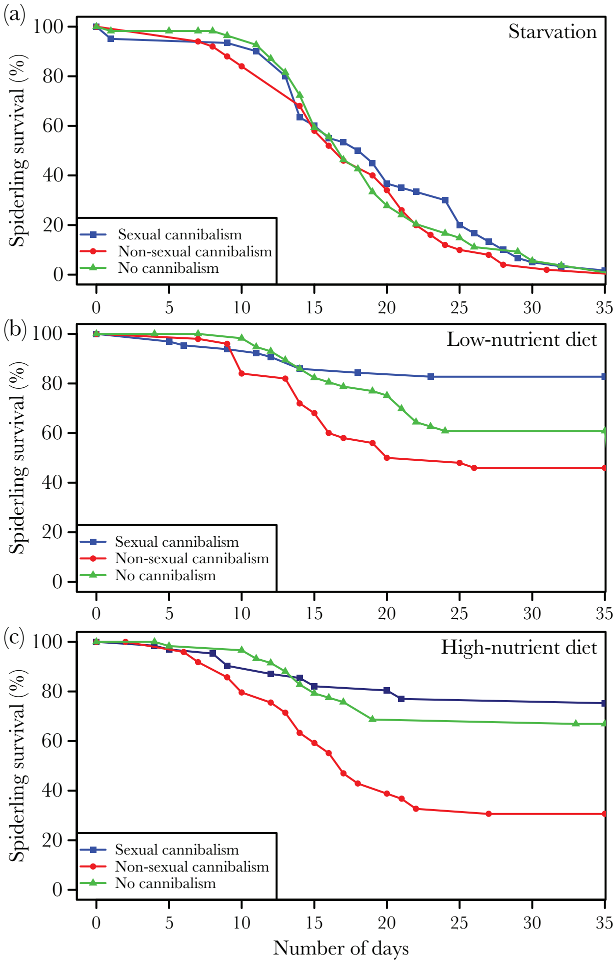

Figure 1

Comparison of survival of the offspring produced by sexually cannibalistic, nonsexually cannibalistic, and noncannibalistic females under starvation (a) and under the low-nutrient (b) and high-nutrient diet (c).

Table 2

Fitting of a mixed-effects Cox model to investigate the effects of diet (low or high nutrient) and cannibalistic treatment on 5-week-old spiderling survival

Covariables	Hazard rate coefficient	*z*	*P*
High-nutrient diet (H)	−0.25	−0.83	0.41
Starvation (S)	1.50	6.08	**<0.001**
Sexual cannibalism group (SC)	−1.12	−2.27	**0.02**
Nonsexual cannibalism group (NSC)	0.74	1.63	0.1
H:SC	0.81	1.62	0.11
S:SC	1.13	2.75	**0.006**
H:NSC	0.86	2.14	**0.03**
S:NSC	−0.42	−1.24	0.21

Mother ID is included as a random factor in the model. Reference levels for the spiderlings diet treatment and the maternal cannibalistic treatment are, respectively, “low-nutrient diet” and “no cannibalism.” Positive coefficient values indicate a higher death risk for the spiderlings. The bold values highlight *P* values that are <0.05.

mortality risk compared with offspring fed on a low-nutrient diet. Diet quality did not significantly affect offspring survival. The interaction between feeding treatment and cannibalistic treatment had a significant effect (comparison of models with or without the interaction term: $\chi^2 = 32.8$, $P < 0.001$). Interestingly, we found that nonsexual cannibalism had a negative effect on offspring survival under the high-nutrient diet (Figure 1, Table 2). The positive effect of sexual cannibalism was clearer under the low-nutrient diet. Adding the copulation duration of the mother did not significantly affect the log-likelihood of the model ($\chi^2 = 0.1$, $P = 0.76$). Thus, copulation duration did not influence offspring survival.

Does the occurrence of cannibalism or timing of cannibalism in relation to copulation (i.e., sexual vs. nonsexual cannibalism) affect offspring growth rate?

Five-week-old spiderling size according to their diet and the cannibalistic treatment of their mother is shown in Figure 2. The linear mixed model of best fit to explain 5-week-old spiderling size included the effect of the spiderling diet (low or high nutrient), the mother’s cannibalistic treatment, and their interaction (Table 3). The cannibalistic treatment of the mother tended to influence offspring size ($P = 0.06$). Tukey HSD post hoc tests revealed that sexually cannibalistic females had offspring that grew to a bigger size compared with those of noncannibalistic females. Spiderlings fed on the high-nutrient diet grew bigger in 5 weeks than spiderlings on the low-nutrient diet ($P < 0.001$). The interaction between diet treatment and cannibalistic treatment was also significant ($P = 0.009$), meaning that the amplitude of the effects of cannibalism on spiderling growth is mediated by the quality of the spiderling diet. In particular, post hoc comparisons revealed that there was no difference in the size of offspring of noncannibalistic offspring on high and low diets, but the sizes of offspring from both cannibalism treatments were higher on the high-quality diet than the low-quality diet (Figure 2). Adding the copulation duration experienced by the mother to the model did not improve its quality (AIC = 179 vs. AIC = 167.9). So we conclude that the mother copulation duration does not influence spiderling growth.

Size differences between treatments were consistent with differences in instar distributions (Figure 3). The cumulative link mixed model of best fit explaining the instars distribution is presented in Table 4. Diet quality did not influence offspring growth rate. Nonsexual cannibalism reduced offspring growth rate ($P = 0.03$). Interestingly, the positive effect of sexual cannibalism on growth rate was stronger in the high-nutrient treatment, whereas the negative effect of nonsexual cannibalism was clearer in the low-nutrient treatment.

DISCUSSION

Our results support the hypothesis that sexual cannibalism and nonsexual cannibalism have different effects on female fitness in *L. hasselti*, which is mostly mediated by different effects on offspring survival and growth. Females did not produce heavier egg sacs or more offspring in their first clutch when they fed on a male either outside or within the context of mating. We found no evidence that neither type of cannibalism affected subsequent female sexual receptivity. We found that sexual cannibalism in *L. hasselti* positively affected offspring survival when the spiderlings had access to food, compared with offspring born of noncannibalistic or nonsexually cannibalistic mothers. And we finally showed that sexual cannibalism also increased offspring growth rate when compared with nonsexual cannibalism. Sexual cannibalism has often been treated as a special case of cannibalism, and our results support this idea by showing that the effects of male consumption on offspring fitness

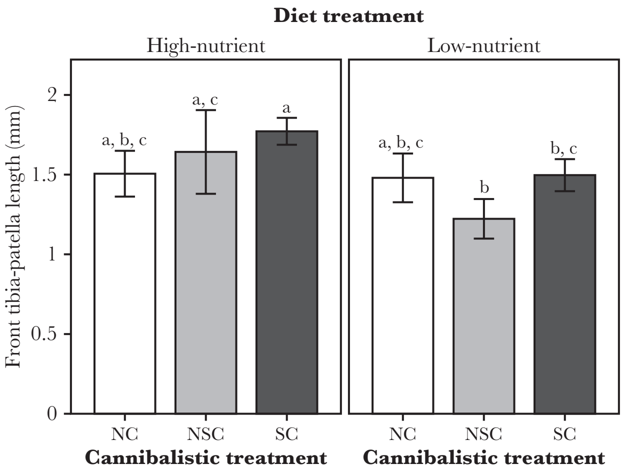

Figure 2

Comparison of mean (± 95% confidence interval) offspring's front tibia–patella length according to the mother's cannibalistic treatment under the 2 different diets. Mothers were from the sexual cannibalism treatment (SC), the no-cannibalism treatment (NC), and the nonsexual cannibalism treatment (NSC). Different lower case letters show significant differences between groups according to Tukey HSD post hoc tests ($P < 0.05$) after the mixed analysis of covariance described in Table 3.

Table 3

Results of the mixed model ANCOVA for the effects of diet (low or high nutrient) and cannibalistic treatment on 5-week-old spiderling body size

Source of variation	df	*F*	*P*	Post hoc tests (Tukey HSD)
Cannibalistic treatment	2	2.99	0.06	**SC–NC: *P* = 0.03** NSC–NC: *P* = 0.58 SC–NSC: *P* = 0.57
Diet	1	24.8	**<0.001**	**L–H: *P* < 0.001**
Cannibalism:diet	2	4.90	**0.009**	See Figure 2

Mother ID is included as a random factor in the model. The bold values highlight *P* values that are <0.05. ANCOVA, analysis of covariance; df, degrees of freedom.

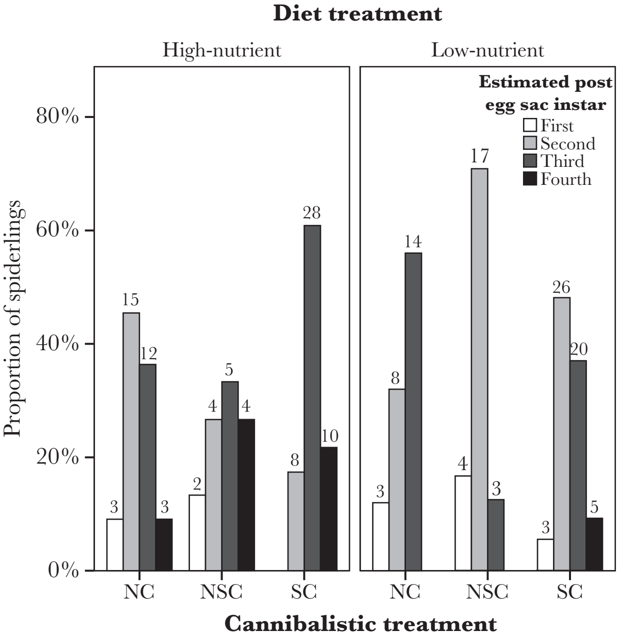

Figure 3

Proportion of 5-week-old spiderlings of a given estimated post egg sac instar according to the mother's cannibalistic treatment under the 2 different diets. Mothers were from the sexual cannibalism treatment (SC), the no-cannibalism treatment (NC), and the nonsexual cannibalism treatment (NSC). Figures written above each column gives the actual number of spiderlings in the given instar.

Table 4

Fitting of a cumulative link mixed model to investigate the effects of diet (low or high nutrient) and cannibalistic treatment on 5-week-old spiderling instar proportions

Variable	Coefficient	*Z*	*P*
High-nutrient diet (H)	−0.04	−0.08	0.94
Sexual cannibalism (SC)	0.002	0.004	0.99
Nonsexual cannibalism (NSC)	−1.63	−2.15	**0.03**
H:SC	1.68	2.46	**0.01**
H:NSC	2.50	2.74	**0.006**

Mother ID is included as a random factor in the model. Positive coefficient values indicate a higher probability of spiderlings in the advanced instars. Reference levels are "low-nutrient diet" and "no cannibalism." The bold values highlight *P* values that are <0.05.

(survival and growth) depend on whether the male is consumed during mating or outside the context of mating.

We were able to replicate some results from previous studies. First, sexually cannibalized males have access to a longer copulation compared with uncannibalized males (Andrade 1996; Snow and Andrade 2004). Additionally, males that already had a mating experience (in this case, 1 single insertion) were subsequently faster to climb onto the female's abdomen during courtship. This result is consistent with a previous study on redback spiders that showed that males that already had access to 1 or 2 insertions had shorter courtships compared with virgin males (Andrade and Banta 2002). In the present study, females exhibited more aggressive strikes toward males that already experienced 1 insertion with another female and that exhibited shorter courtships. Females were already showed to favor longer courtships in a previous study (Stoltz et al. 2008a).

A previous study on redback spiders found evidence that females decreased sexual receptivity after sexual cannibalism (Andrade 1996). We measured receptivity focusing on male abdomen mounting rather than the actual occurrence of copulation. Although abdomen mounting is required before copulation as suggested by our data from the first mating, it is not sufficient to guarantee a subsequent copulation. Most of our first trials where copulation did not occur still showed abdomen mounting. In this study, cannibalistic and noncannibalistic females all displayed the characteristic receptivity posture to second suitors and allowed them to mount the female abdomen. Additional receptivity factors (i.e., leg strikes and female activity level) were also not significantly different between the treatments. These results seem to go against Andrade's (1996) results, but unlike her study, we could not assess the actual remating probability of the female after cannibalism. Potential differences between our results may be because, in our study, females were tested for receptivity after receiving only 1 copulation. It is possible that females with 1 empty spermatheca may be more receptive than females with both spermathecae already inseminated. Repetition of this experiment with first males getting access to a full mating (i.e., 2 consecutive insertions) is needed to determine if the decrease in female receptivity after a cannibalistic mating is dependent on the number of insertions or if this phenomenon is context dependent.

We did not find any influence of either type of cannibalism on female fecundity measured as both egg sac mass and clutch size. These findings support a previous study on the effects of sexual cannibalism on fecundity in redback spiders (Andrade 1996). Studies on the potential benefits to fecundity provided by sexual cannibalism had different results depending on the study system (see Barry et al. 2008 for a review). The benefits of sexual cannibalism on fecundity were found in species with relatively large males (i.e., more nutritious), whereas studies on spider species exhibiting a high sexual size dimorphism (SSD; i.e., with the male representing less than 10% of the female mass) failed to show such an effect. Thus, in *L. hasselti*, it is not surprising that no effect of cannibalism could be found on fecundity as males represent a small relative quantity of food (1–2% of female body mass) (Newman and Elgar 1991; Wilder et al. 2009), and males may be a poor-quality meal (Wilder and Rypstra 2010). In a spider with similarly high SSD (*A. bruennichi*), there was also no effect of sexual cannibalism on egg sac mass for the first clutch of females, but there was a significant effect for the second clutch (Welke and Schneider 2012). This suggests that females may become nutritionally limited after laying their first egg sac and that cannibalism may only make a difference in second or subsequent egg sacs. Unfortunately, second egg sacs were not collected in the current study, and hence, we cannot completely rule out a potential effect of cannibalism on fecundity. However, first egg sacs could be more important to female reproductive success than subsequent sacs due to mortality risks for females or because offspring can be more developed by the end of the season.

Neither nonsexual nor sexual cannibalism affected offspring survival under complete starvation, whereas previous studies on other sexually cannibalistic spiders found that sexual cannibalism increased the survival time of starving offspring (Welke and Schneider 2012; Wu et al. 2013). However, nonsexual and sexual cannibalism had contrasting effects on survival and growth when the spiders were fed. Sexual cannibalism significantly reduced offspring death risk compared with offspring born of noncannibalistic mothers. Many studies report that prey nutrient content can dramatically affect spiders' survival and growth (Toft and Wise 1999; Mayntz and Toft 2001; Jespersen and Toft 2003; Mayntz et al. 2003; Wilder 2011, 2013). Our low-nutrient diet is more likely to reflect nutrient conditions in nature (Fagan et al. 2002; Denno and Fagan 2003; Fagan and Denno 2004; Matsumura et al. 2004; Wise 2006; Wilder 2011); however, spiders may sometimes experience higher nutrient conditions due to spatial and temporal variation in prey abundance (Henschel et al. 2001; Wilder 2011). Offspring born of a sexually cannibalistic mother displayed a higher growth rate compared with offspring born of nonsexually cannibalistic mothers. By increasing offspring performance, especially offspring survivorship in environments offering poor-quality food, sexual cannibalism may benefit male and female fitness. Interestingly, nonsexual cannibalism reduced offspring survival under the high-nutrient diet and offspring growth rate under the low-nutrient treatment. The lack of a benefit of cannibalism without mating may help explain why precopulatory cannibalism, which is common in some other spiders, is rare in this species (Forster 1992; Andrade 1996; Boisseau RP, personal observation). Female propensity to cannibalize can affect the results of cannibalism in some species (Schneider and Elgar 2002). As some of our females were prevented from actually eating their mate despite willing to, we tested it as the critical factor rather than the act of cannibalism itself for all our response variables. We found no effect, which suggests that propensity to cannibalize does not account for our results.

Our results suggest that the copulation simultaneously associated with sexual cannibalism plays an important role in the benefit of cannibalism for offspring survival and growth. Natural variation in copulation duration did not influence these effects on offspring survival and growth. Here, we show that copulation and cannibalism have to occur at the same time to result in benefits in terms of offspring performance. We may speculate that these effects may be due to an induced and increased investment in yolk density (Blamires 2011). Sexual cannibalism does not allow for an increased tolerance of the offspring to starvation but makes a difference when the spiderlings are fed, which suggests that these benefits do not involve energy reserves in eggs but, rather, could be some other type of dietary supplement or an epigenetic effect. As cannibalism alone did not result in improved offspring performance and as males are relatively small, it is very likely that this increased investment in offspring is permitted by maternal somatic reserves rather than a direct nutrient extraction from the cannibalized male body (Blamires 2011). Thus, we may suspect that such effects in the first clutch trade-off against fitness of offspring from later clutches. By inducing an increased female provisioning to her first egg sac, a cannibalized male may favor the first offspring of the female as a priority, which are more likely to be his. Whether this new effect is also beneficial to females is still unclear.

One potential explanation for the differences between sexual and nonsexual cannibalism treatments in offspring performance is that substances consumed from the male body during sexual cannibalism may affect the physiological changes in the female body associated with copulation. Indeed, copulation has been shown to result in a number of physiological changes to females such as the quick alteration of female pheromone production (pheromonostasis) (Stoltz et al. 2007; Thomas 2011). Thus, some chemicals from the male body may be able to manipulate how these physiological changes occur. Females that cannibalized a male several days before mating may have metabolized and cleared all compounds they consumed from the male body before the day of copulation. Further work is needed to explore the mechanism behind this phenomenon and the effect of sexual cannibalism on later egg sacs. More generally, additional studies are needed to test if different effects of sexual and nonsexual cannibalism on fitness are found broadly in other spider species.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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