

Sibling cannibalism in the false widow spider is dependent on spiderling density and the reliable availability of fresh prey

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Abstract

Adult female spiders lay batches of eggs in silken egg sacs, and after hatching, the spiderlings live for transient periods in their mother's web before dispersing. Sibling cannibalism is frequently observed among spiderlings of many species under conditions of food deprivation. Here, we conducted assays in small Petri dishes with different densities of newly hatched (second instar) spiderlings of the false widow spider, *Steatoda grossa*, using a split-clutch design. Prey (freshly killed fruit flies) availability was manipulated both numerically and temporally. Offspring from 10 different females were separated as siblings into densities of two, four, or eight spiderlings per Petri dish and these were provided with either 0 flies (starvation control), two flies, four flies, or eight flies that were replenished weekly or every 3 weeks. A further control was conducted with solitary spiderlings in Petri dishes deprived of flies. The number of surviving spiderlings per Petri dish was counted every 3 days until only one remained (or until death of the solitary spiderling). Our results show that the rate of cannibalism was lower with increasing spiderling density and when fresh flies were replenished more frequently, whereas the number of flies that were provided did not affect cannibalism. In *S. grossa*, juvenile cannibalism occurs primarily under conditions of extreme food limitation, although in synanthropic habitats where the spider is abundant, it may be an adaptive strategy owing to the potential scarcity of prey. Under certain conditions, cannibalism in spiderlings is adaptive by eliminating competitors and providing nutrient-rich food.

KEYWORDS

agonistic interactions, competition, intraspecific predation, starvation, *Steatoda grossa*

1 | INTRODUCTION

Group living, at least early during life, has been described in numerous arthropod taxa, including butterflies (Allen, 2010; Tullberg & Hunter, 1996), beetles (Costa et al., 2007; Deneubourg et al., 1990), harvestmen (Machado et al., 2000), scorpions (Pandey et al., 2021),

spiders (Lesne et al., 2016), and others. Laying eggs in batches can enhance fitness by allowing the mother to produce multiple offspring in a short period of time. This is especially important in organisms with short lifespans or those where the risk of mortality from predation is high. A gregarious lifestyle may reduce also predation risk through group defense, whereby multiple offspring are better

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able to ward off attackers than individuals (Gentry & Dyer, 2002; Hunter, 2000) or where numerous individuals provide a 'confusion effect' to natural enemies (Krakauer, 1995). Gregarious feeding may also be beneficial for herbivores in terms of overcoming plant defenses (Karbon & Agrawal, 2002) or for predators in subduing large prey (Griffiths, 1980). Under a given set of environmental conditions, egg desiccation in egg clutches can be reduced (Clark & Faeth, 1998), and small individuals feeding in close proximity with siblings are also often able to generate higher body temperatures than individuals feeding in isolation (Bryant et al., 2000; Fordyce, 2003; Fordyce & Nice, 2004). This leads to an increase in the metabolic rate and thus a reduction in the overall development time (Reader & Hochuli, 2003) which can benefit individual fitness in rapidly growing populations (Arendt, 2003; Gotthard, 2000) and facilitate the production of extra generations (Bryant et al., 2000).

Group living also confers costs that include higher levels of disease transmission amongst closely assembled individuals (Brown et al., 2001; Hochberg, 1991) and increased apparency to natural enemies (Ioannou et al., 2009; Sillen-Tullberg & Leimar, 1988). Moreover, among juveniles living together, there is an increase in the level of intraspecific competition for potentially limiting food resources such as plant tissues for herbivores and prey for predators (Fei et al., 2016; Krafft et al., 1986; Rohlf et al., 2005). Under food limitation, individual fitness is potentially compromised through contest competition, where some individuals monopolize remaining resources and others perish as a result or scramble competition, where limited resources are evenly spread among the population (Sharpe & Avilés, 2016). When resources are entirely depleted, however, individuals within a group may be forced to consume conspecifics, i.e., cannibalize, in order to survive. Cannibalism of conspecific individuals is adaptive under these circumstances in that it allows some individuals to survive rather than all individuals perishing from starvation (Simpson & Raubenheimer, 2012). Two forms of cannibalism can occur: the first involves cannibalism of genetically unrelated individuals, and the second involves the cannibalism of siblings or close kin, such as offspring (Fox, 1975; Osawa, 1989; Perry & Roitberg, 2005). Cannibalism has been recorded in over 1500 species of vertebrates and invertebrates (Polis, 1981).

Spiders (Araneae) habitually lay their eggs in clusters that are encased in silken sacs and generally undergo their first molt before eclosion (Trabalon et al., 2018). Some species are matrophagous and the mother allows her progeny to consume her (Kim et al., 2000), whereas mothers of some non-web-building spiders exhibit maternal care of egg sacs and newly hatched spiderlings (Horel & Gundermann, 1992; Ruhland et al., 2016). In most species, however, newly hatched spiderlings are left to fend for themselves and soon disperse from the natal web, although in some species they remain in association with their mother or mother's web for up to several weeks or even months. Here, they assist in capturing prey, which are shared among the brood (Jones & Parker, 2002), or scavenge on prey captured in their mother's web or even the webs of conspecifics (Jakob, 1991; Strickman et al., 1997).

Some spider taxa are synanthropic, living in close association with humans, and exploit structures such as cellars, greenhouses, or cupboards (Hänggi & Straub, 2016; Kobelt & Nentwig, 2008). A synanthropic lifestyle confers both benefits and costs (Hulme-Beaman et al., 2016). Organisms living in human environments may experience a reduced risk of predation or parasitism from invertebrate and vertebrate natural enemies, compared with organisms living in natural and semi-natural environments. On the other hand, reduced biological diversity found in human environments could lead to a higher risk of food deprivation and even starvation (Hulme-Beaman et al., 2016). For predatory arthropods, such as spiders, a scarcity of prey, or high spider densities living in close proximity, may increase the risk of cannibalism (Polis, 1981; Wise, 2006). Thus far, most studies of cannibalism in spiders have focused on sexual cannibalism, whereby the female consumes the male before, but more generally after, copulation (Arnqvist & Henriksson, 1997; Johnson & Sih, 2005; Schwartz et al., 2016; Segoli et al., 2008). However, cannibalism also sometimes occurs among juvenile spiders, including siblings, and has been suggested as a mechanism to regulate spider densities, or, when food supply is unpredictable, to prevent starvation of the entire brood (Mayntz & Toft, 2006; Modanu et al., 2014; Wagner & Wise, 1996).

Thus far, few studies have examined the multiple roles of spiderling density and prey density and/or availability on sibling cannibalism in spiders. Here, we examined the roles of these parameters on sibling cannibalism in the false widow spider *Steatoda grossa* Koch (Araneae: Theridiidae). This species is synanthropic and adult females lay egg sacs typically containing 50–250 eggs (Harvey, 2022). Juvenile spiderlings remain in the mother's web for up to several weeks after hatching before dispersing. Newly hatched spiderlings of different mothers were reared in small arenas at different densities and were either starved or fed with variable numbers of freshly killed (by freezing) fruit flies (*Drosophila melanogaster*) that were replenished weekly or only every 3 weeks. Spiderling mortality was determined until only one juvenile spider remained alive. The main aims of the study were to determine, (1) if spiderling density, fly density, and frequency of fly replenishment affected the time until one spiderling remained alive, and (2) the amount of variation in these parameters among different mothers. We hypothesize that spiderling density, food availability, and refreshment influence affect hunger level in *S. grossa* spiderlings and this in turn influences the decision to attack siblings.

2 | MATERIALS AND METHODS

2.1 | Spider rearing

Steatoda grossa was maintained at $22 \pm 2^\circ\text{C}$ with a 16:8h light: dark photoperiod regime. Hundreds of male and female spiders were originally collected at numerous locations in Gelderland Province, The Netherlands, between late 2019 and throughout 2020, and thereafter were reared in Petri dishes (8 cm). Mature virgin females typically

weigh over 150mg and males between 10 and 40mg. Mature, virgin females were transferred to plastic boxes (8×8×10cm) and were mated with individual virgin males that were previously kept in small Petri dishes (8 cm). After ~15–20 days, mated females produce their first egg sacs. These were carefully removed from the boxes using dissection scissors and placed in Petri dishes (8 cm) until they were hatched after ~30 days. Newly hatched spiderlings were also placed individually into Petri dishes and were initially reared on freshly killed (by freezing) *D. melanogaster*. Later instar juveniles were fed with early and then progressively later instars of house crickets (*Acheta domestica*) as they matured. Fully grown virgin females were then removed from the dishes and individually placed into plastic boxes for several days and allowed to spin webs inside of them. At this point, the original procedure was repeated.

2.2 | Experimental protocol

All experiments were performed under the same conditions in which the spiders were reared. The cannibalism experiments with sibling spiderlings were conducted using a split-clutch protocol. The progeny of 10 unrelated adult females was used. Egg sacs from mated females in small Petri dishes were monitored daily for spiderling eclosion. Upon hatching, spiderlings are second instars (Figure 1) and the entire brood emerges from the egg sac over the course of a few hours. The treatments used in the experiments are depicted in Table 1. Newly hatched spiderlings were collected from Petri dishes and progeny from a single mother were separated into different densities of two, four, or eight spiderlings and placed with siblings into small Petri dishes (8 cm) under the following feeding treatments with freshly killed *D. melanogaster* flies: two, four, or eight flies that were refreshed once weekly or once every 3 weeks. The spiderlings take around 24h to settle into a Petri dish after being placed in them, and by this time they have constructed webs. Therefore, the feeding treatments only commenced 24h after the spiderlings were



FIGURE 1 Newly hatched second-instar spiderlings of *Steatoda grossa*, with more that will soon emerge from an egg sac.

TABLE 1 Feeding treatments with different numbers of frozen *Drosophila melanogaster* flies provided as fresh prey to newly hatched spiderlings of different densities (2, 4, and 8) of *Steatoda grossa* siblings in a split-clutch design.

Two sibling spiderlings	Four sibling spiderlings	Eight sibling spiderlings
2 spiderlings, 0 flies	4 spiderlings, 0 flies	8 spiderlings, 0 flies
2 spiderlings	4 spiderlings	8 spiderlings
2 fresh flies weekly	2 fresh flies weekly	2 fresh flies every 3 weeks
2 spiderlings	4 spiderlings	8 spiderlings
4 fresh flies weekly	4 fresh flies weekly	4 fresh flies every 3 weeks
2 spiderlings	4 spiderlings	8 spiderlings
8 fresh flies weekly	8 fresh flies weekly	8 fresh flies every 3 weeks

transferred. Freshly killed flies remain palatable for several days but thereafter desiccate. Spiderlings detecting the flies readily wrapped them in silk and proceeded to feed on them. For each adult female mother, 98 spiderlings (total) were necessary from each egg sac for all of the treatments to contain enough siblings, so any egg sacs producing less than 98 spiderlings were not used. Petri dishes were checked daily for spiderling mortality.

2.3 | Statistics

Data were analyzed using Cox regression survival analysis with the *survival* and *survminer* packages in R (R Core Team, 2022). Data were visualized using Kaplan–Meier survival curves. In the assays, sibling spiderlings were produced by different mothers. Survival data of control spiderlings that were maintained individually without food were analyzed with maternity (five mothers) as the only explanatory variable and time until death as response variable. Sibling density (two, four, or eight) and maternity (10 different mothers) were the explanatory variables in the models on cannibalism when spiderlings were starved. Spider density was included as a covariate and mother as a fixed term. In this analysis, the response variable was the duration until only one spiderling was still alive. Diet (two, four, or eight fruit flies) and feeding frequency (once a week, or once every 3 weeks) were included as additional explanatory variables when analyzing cannibalism when spiderlings were also fed fruit flies. To determine the effects of the other predictors, likelihood ratio tests were performed.

3 | RESULTS

We first determined survival of spiderlings that were maintained individually without food. The median survival of these control

spiderlings was 45.5 days (95% confidence interval 42–48 days). Here, maternity had no effect on offspring survival ($\chi^2 = 7.41$, $df = 4$, $p = .11$).

In the absence of food, the time until one spiderling was still alive depended on sibling density and maternity (Figure 2, Table 2). The median duration until only one spiderling was alive varied between 31 for two spiderlings and 39 days for eight spiderlings. When spiderlings were also given fruit flies as food, median survival until one spiderling was still alive varied between 27.5 days for two spiderlings and 50 days for eight spiderlings. Spiderling density significantly prolonged survival rate of the spiderlings also in the presence of additional food (Table 2, Figure 3a). Moreover, the frequency of food provisioning had a strong effect on survival probability, whereas the number of flies given each time did not (Table 2, Figure 3b,c). Both, in assays in which spiderlings were starved and in those in which spiderlings were provided with food, survival probability also depended on the female spider that had produced the spiderlings (maternity effect, Table 1). We reran the Cox regression model with feeding frequency with three levels (starved, fed once a week, or once every three weeks [$\chi^2 = 24.7$, $df = 2$, $p < .001$, $n = 210$]). Feeding spiders once every week increased survival by a factor of 2.4 compared to starved spiderlings, whereas feeding once every 3 weeks increased survival by a factor of 1.25 (Figure 4). However, the difference in survival rate between starved spiderlings and those fed once every 3 weeks was not statistically different (Log-rank test, $p = .29$).

4 | DISCUSSION

The results of this study show that cannibalistic behavior in sibling spiderlings of the false widow spider *S. grossa* was affected by both spider density (two, four, or eight siblings from the same brood) and the frequency of fly replenishment, but not by the number of fresh prey (freshly killed *D. melanogaster* flies) provided. Thus, spiderling

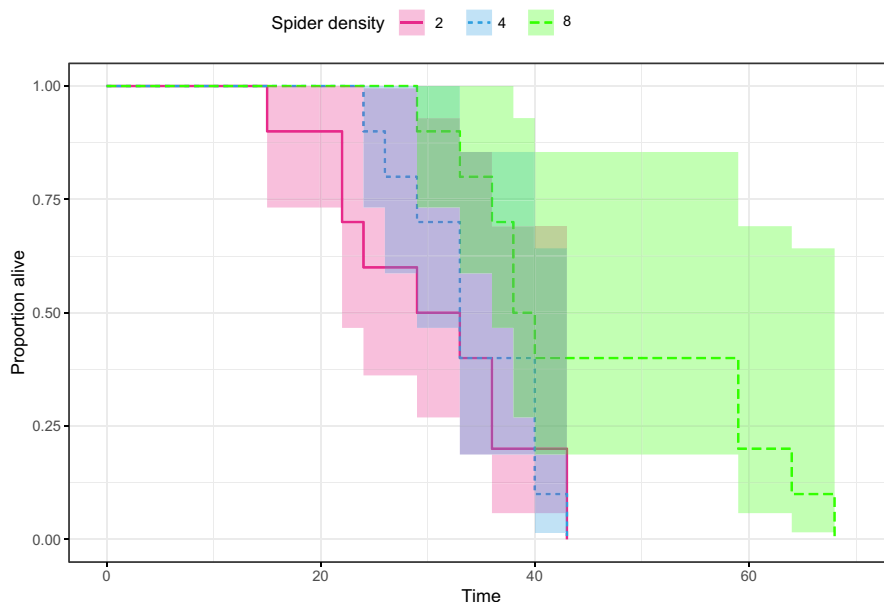


FIGURE 2 Survival probability of spiderlings until one spiderling was still alive when groups of spiderlings were maintained in Petri dishes at different densities (2 in red, 4 in green, or 8 in blue) without additional food with $n = 10$ per density treatment. The colored shading indicates 95% confidence intervals.

TABLE 2 Cox regression results on spiderling cannibalism.

Predictor variable	χ^2	df	p-Value	Hazard rate
Starved spiderlings				
Sibling density	17.4	1	<.001	.83
Maternity	59.3	9	<.001	
Fed spiderlings				
Sibling density	17.0	1	<.001	.82
Diet	2.55	1	.11	
Frequency	19.8	1	<.001	1.54
Maternity	69.9	9	<.001	

Note: Mortality of sibling spiderlings maintained in different densities (2, 4, or 8) was recorded until one spiderling was still alive (= response variable). Spiderlings were starved or provided with fruit flies in different quantities, 2, 4, or 8 flies (= diet), at different frequencies (once every week, or once every 3 weeks). The unit of replication is a dish in which spiderlings were maintained with $n=10$ per density-diet-frequency combination (180 dishes in total for fed spiderlings and 30 for starved spiderlings). Spiderlings were produced by 10 different mothers and spiderlings in each dish were produced by the same mother. Maternity was included in the models as an additional explanatory factor. Cox regression models were run separately with data on starved and fed spiderlings. Statistics are based on likelihood ratio tests. Hazard rates are given for variables that were significant. Hazard rates <1 indicate a reduced instantaneous risk of dying with increasing values of the variable, while hazard rates >1 indicate an increased risk of dying with increasing values of the variable. Note that higher values of frequency mean that spiderlings are fed less frequently.

density and regularity of prey availability both affected the tendency of siblings to engage in cannibalism. Spiderlings were more reluctant to attack siblings at lower spider densities or if fresh prey were provided weekly, compared with every 3 weeks, suggesting that the perception of high larger numbers of competitors and hunger level are factors stimulating cannibalistic behavior. However, there was considerable temporal variation among the progeny of different female spiders to engage in cannibalism.

Cannibalism among spiderling sibs and non-sibs has been studied in only a few species of spiders. It has been argued that the genetic costs associated with eating close relatives should favor cannibalism of non-sibs, and this has been demonstrated in several spider species (Anthony, 2003; Beavis et al., 2007; Bilde & Lubin, 2001; Roberts et al., 2003). Importantly, kin recognition and kin discrimination are often based on the degree of asymmetry in the size of siblings, with increasing disparity in size among sibs making larger spiderlings more inclined to attack siblings (Johnson et al., 2016). For example, rates of cannibalism did not differ between similarly sized sib and non-sib spiderlings of the wolf spider, *Pardosa pseudoannulata*, but in both groups increased asymmetries in body size significantly influenced this parameter (Iida, 2003). When hungry spiderlings living together or in close proximity are similar in body size, they need to assess the risks and benefits of initiating cannibalism. Two hypotheses have been proposed to explain how hunger influences cannibalism. One posits that increasing hunger makes individual spiders weaker and thus makes them more susceptible victims to other spiders in

better physical condition (Petersen et al., 2010). The second is that increased hunger level pushes the willingness of individuals to take more risks and thus initiate cannibalism (Petersen et al., 2010). A significant cost of this is that an attack by a starved individual can also be fatal for the attacker. This could make individual spiderlings more reluctant to initiate cannibalism until some critical hunger threshold is exceeded. If successful, cannibalism confers several fitness-related benefits. First, it reduces numerical competition among spiderlings for access to future prey that is captured in the shared web (Wagner & Wise, 1996). Second, successful cannibalism allows individual spiderlings to grow larger than other spiderlings that do not cannibalize, also giving them a competitive edge for prey captured in the web (Hvam et al., 2005; Iida, 2003). Finally, the larger size enables cannibals to attack smaller spiderlings with less risk to their own survival. If non-spider prey remains scarce, then cannibals have a potentially ready supply of other conspecific spiderlings to utilize as food.

Freshly killed fruit flies provided to *S. grossa* spiderlings remain palatable for only a few days after being provided, and tended to desiccate quite rapidly. This may explain why the provisioning of fresh flies had the most significant effect on spiderling survival rates. In other species of spiders, hunger level among juveniles has been shown to strongly affect rates of cannibalism, with this parameter being more prevalent among solitary species than (sub)-social species (Mayntz & Toft, 2001, 2006; Roberts et al., 2003; Samu et al., 1999). Here, we noticed that some *S. grossa* spiderlings appeared to get better short-term access to flies than their sibs, with these 'winners' clearly gaining a later competitive edge over the 'losers'. The carcasses of cannibalized spiderlings were found in most treatments, with increasing visual asymmetry in the body size of spiderlings over time.

Thus far, the effects of starvation on spiderling physiology and survival have been little studied. Spiderlings habitually emerge as newly molted second instars with comparatively low levels of metabolic resources compared with adults (Vogelei & Greissl, 1989). *Steatoda grossa* spiderlings from several mothers that were reared individually from hatching without food and water lived an average of 45.5 days and as long as 80 days. Spiders are remarkably robust organisms, and many species can survive many months without food or water. For instance, starved adults of a cribellate spider *Filistata hibernalis*, and a wolf spider, *Lycosa lenta* lived an average of 276 and 208 days, respectively (Anderson, 1974), although duration of survival in another starved wolf spider, *Pardosa astrigera*, was much less (Tanaka & Itô, 1982). Food can remain in the spider gut for highly variable periods, leading to quite significant differences among individuals in their physiological responses to starvation and concomitant hunger level (Nakamura, 2012).

The combined effects of kin selection and physiological resilience may partially explain why some spiderlings are reticent to attack siblings, even when they are close to death. On the other hand, genetically based variation in behavioral traits reveals that more aggressive genotypes have a higher propensity to engage in cannibalism than more passive genotypes. In the western black widow, *Latrodectus hesperus*, there is strong genetic variation

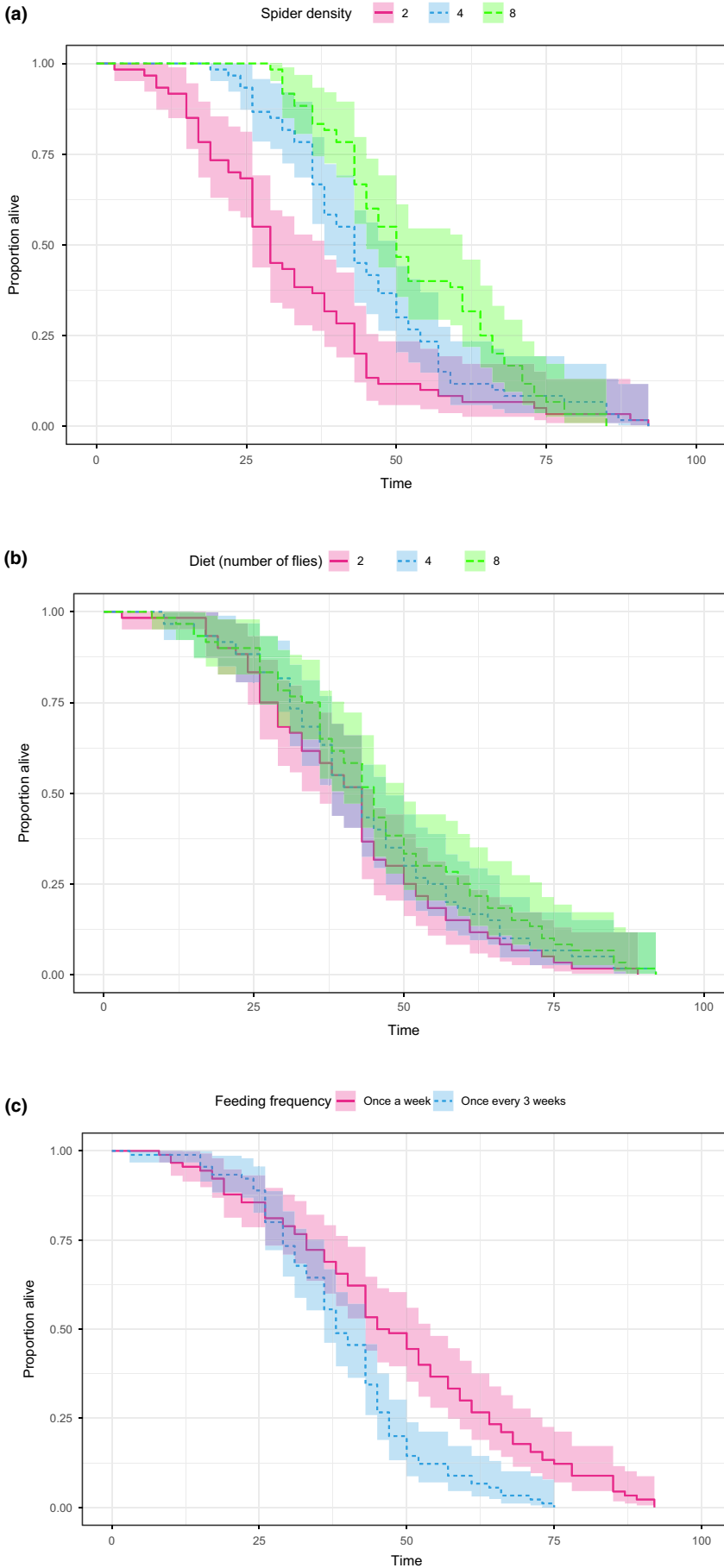
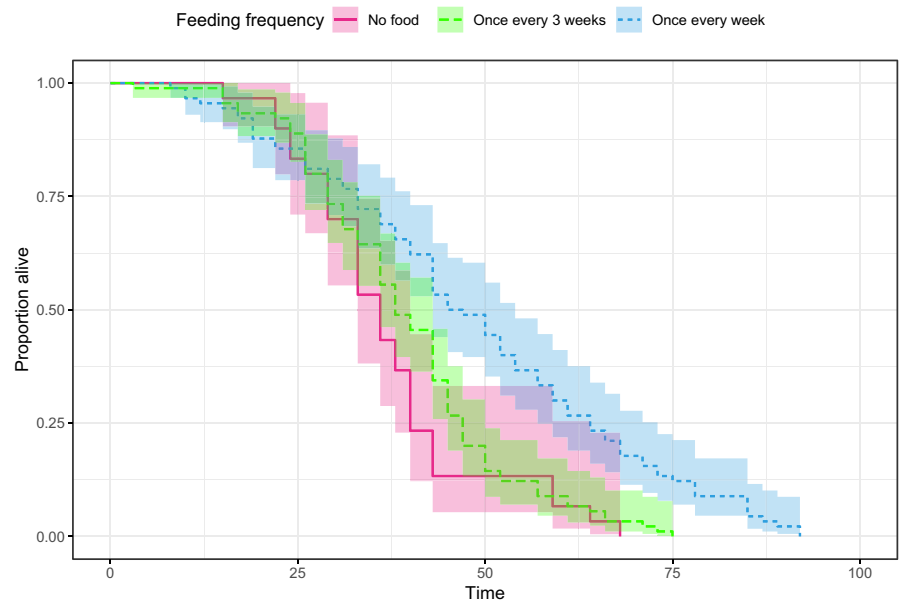


FIGURE 3 Survival probability of spiderlings until one spiderling was still alive when groups of spiderlings were maintained in Petri dishes at different densities with food provided in different amounts and at different frequencies. In (a) the effect of spiderling density is depicted, i.e., 2 (in red), 4 (in green), or 8 spiderlings (in blue) ignoring the effects of diet and frequency of food provisioning. In (b) the effect of diet is shown, i.e., whether spiderlings were given 2 (in red), 4 (in green), or 8 flies (in blue) ignoring the effects of spiderling density and frequency of food provisioning. In (c) the effect of frequency of food provisioning is depicted, i.e., once a week in red or once every 3 weeks in blue, ignoring the effects of diet and spiderling density. The colored shading indicates 95% confidence intervals. Total number of dishes is 180 with 10 dishes per treatment combination. Statistics are given in [Table 1](#).

FIGURE 4 Survival probability of spiderlings until one spiderling was still alive when groups of spiderlings were maintained in Petri dishes at different densities and were provided with food (fruit flies) once every 3 weeks (green), once a week (blue), or not all (red). The colored shading indicates 95% confidence intervals. Total number of dishes was 210 with 90 dishes for each of the treatments with food and 30 without food provisioning.



among spiderlings of different mothers in their tendency to cannibalize siblings during the group-living phase. Spiderlings of some widow mothers cannibalized siblings within 2 days of hatching but spiderlings of unrelated mothers waited as long as 3 weeks after hatching to cannibalize siblings (Johnson et al., 2010). Sokolowski and colleagues (Fitzpatrick et al., 2007; Sokolowski et al., 1986) described genetic-based polymorphisms in foraging behavior ('rovers' and 'sitters') of *Drosophila melanogaster* (fruit fly) larvae among different fly populations based on resource availability in variable habitats. As far as we know, however, the factors underpinning variation in levels of aggression and cannibalistic behavior among sibling offspring of the same mother has, thus far, not been studied in spiders or other arthropods.

Thus far, most studies on cannibalism in spiders have focused on sexual or filial cannibalism, with less attention paid to cannibalism among juveniles (Wise, 2006). Moreover, research has focused on biotic factors affecting cannibalism that are linked with prey availability, hunger level, intraspecific competition for prey, the quality of prey, and size asymmetry among juveniles (Wise, 2006). Cannibalism can also be triggered by other biotic factors, such as habitat heterogeneity. For example, more complex small-scale habitats in laboratory arenas reduced spiderling cannibalism in the wolf spider *Pardosa palustris* (Rickers & Scheu, 2005). Alternatively, in the absence of other prey, habitat complexity had no effect on cannibalism in another lycosid, *Schizocosa ocreata* (Wagner & Wise, 1996). The influence of abiotic factors on cannibalism in spiders has received less attention. Metabolic activity in ectotherms increases with temperature, and this in turn could accelerate hunger level, as has been shown in insects and other arthropods (Bailey, 1989; Romey & Rossman, 1995; Scharf, 2016). In *L. hesperus*, siblings were consistently more cannibalistic when maintained at higher (33°C) than lower (27°C) temperatures (de Tranaltes et al., 2022). In a warming, world, extreme temperature events are increasing in intensity and frequency, and the effects of temperature on behavioral shifts

in traits like cannibalism in spiders are clearly worthy of further investigation.

Cannibalism has, thus far, been described in almost every group of vertebrate and invertebrate taxa in ecosystems across the biosphere (Fouilloux et al., 2019). Clearly, cannibalism can play a vitally important role in the structure and functioning of communities by regulating the abundance of individuals within populations (Wise, 2006). Despite this, it remains an enigmatic and largely unexplored phenomenon in many organisms, including spiders. Thus far, cannibalism has been studied in only a relatively small number of spider species, primarily wolf spiders (Lycosidae) and widows (Theridiidae). Given that, as of 2022, some 50,356 species of spiders have been described from 132 families (World Spider Catalog, 2023), it is clear that vast gaps remain in our knowledge of many traits, including cannibalism, in these fascinating arthropods. Spiders consume an estimated 400–800 million tons of biomass as prey every year (Nyffeler & Birkhofer, 2017), highlighting their importance and biological control agents and in regulating the abundance of other arthropods. Given the propensity of many spiders to engage in cannibalism or even to use other spiders as preferred prey, it would be interesting to quantify cannibalism in spiders and to determine how this affects their development, reproduction, and fitness.

AUTHOR CONTRIBUTIONS

Jeffrey A. Harvey: Conceptualization; investigation; writing – original draft; writing – review and editing; supervision. **Robin Steegh:** Investigation; writing – review and editing. **Yuting Dong:** Investigation; writing – review and editing. **Rieta Gols:** Writing – original draft; writing – review and editing; visualization; formal analysis.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

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DATA AVAILABILITY STATEMENT

Raw data of the study are provided as [supporting information](#).

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