

Do social spiders cooperate in predator defense and foraging without a web?

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Abstract Nearly all social spiders spin prey-capture webs, and many of the benefits proposed for sociality in spiders, such as cooperative prey capture and reduced silk costs, appear to depend on a mutually shared web. The social huntsman spider, *Delena cancerides* (Sparassidae), forms colonies under bark with no capture web, yet these spiders remain in tightly associated, long-lasting groups. To investigate how the absence of the web may or may not constrain social evolution in spiders, we observed *D. cancerides* colonies in the field and laboratory for possible cooperative defense and foraging benefits. We observed spiders' responses to three types of potential predators and to prey that were introduced into retreats. We recorded all natural prey capture over 447 h both inside and outside the retreats of field colonies. The colony's sole adult female was the primary defender of the colony and captured most prey introduced into the retreat. She shared prey with younger juveniles about half the time but never with older subadults. Spiders of all ages individually captured and consumed the vast majority of prey outside the retreat. Young spiders benefited directly from maternal defense and prey sharing in the retreat. However, active cooperation was rare, and older spiders gained no foraging benefit by remaining in their natal colony. *D. cancerides* does not share many of

the benefits of group living described in other web-building social spiders. We discuss other reasons why this species has evolved group living.

Keywords Cooperation · Sociality · Spiders · Foraging · Predator defense · Group living · Ecological constraints

Introduction

Sociality, including group living more generally, is a continuing conundrum in evolutionary biology (Alexander 1974; Krause and Ruxton 2002; Frank 2003). Group living carries with it automatic costs, such as increased competition and parasite transmission, and so organisms must derive substantial benefits from group living for it to evolve (Alexander 1974). As constraints are an inescapable feature of evolution (Gould 1980), whether sufficient benefits accrue for sociality to evolve and the nature of these benefits depend partly on the evolutionary history of the organism on which selection is acting.

Sociality is particularly rare in the spiders, suggesting that one or more features of their biology might limit social evolution. Here, we define “social” broadly to encompass any species in which individuals form long-term associations, including colonial species (e.g., the Araneid orb weaver *Metepeira incrassata*) and species without alloparental care (e.g., the Thomisid crab spider *Diaea ergandros*). All spiders are born grouped in both space and time within the egg sac; yet despite this, in over 99% of the 42,000+ identified spider species, individuals soon disperse to live solitarily (Avilés 1997; Whitehouse and Lubin 2005; Lubin and Bilde 2007; Platnick 2011). One reason that sociality is rare in the spiders may be that a prey-capture web is a critical preadaptation to spider sociality (Avilés 1997), and

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nonweb-building species comprise over half of all spiders (Blackledge et al. 2009). Most social spider species spin capture webs (Shear 1970), including species in families that do not typically build webs, such as the Lycosidae and the Oxyopidae (Brach 1976; Avilés 1994).

A survey of the literature on the benefits of group living proposed for spiders indicates that most benefits are contingent on a mutually shared web. Cooperative prey capture allows spiders to subdue prey that would otherwise be far too large for an individual spider (Buskirk 1981; Ward 1986; Jones and Parker 2002; Yip et al. 2008) and may even increase per capita food intake (Yip et al. 2008). Web vibrations caused by the prey struggling in the web act to simultaneously recruit multiple spiders (Burgess 1976), and additional web vibrations by other spiders facilitate hunting coordination (Krafft and Pasquet 1991). Thus, the web is crucial to cooperative prey capture in most of the social spiders. Even in the colonial spiders that do not cooperatively capture prey, orb-weaving spiders may benefit from increased prey capture success through the ricochet effect, by which insects become easier to capture after they have rebounded off an adjacent spider's web (Uetz 1989). Similarly, webs are closely associated with antipredator defense in the social spiders. Spiders in groups may be better defended from predators, either by early warnings communicated through the web (Hodge and Uetz 1992) or by silk that hinders predators from penetrating into the core of colonies (Rayor and Uetz 1990; Evans 1998; Henschel 1998). Finally, spiders benefit from cooperative web construction and reduced individual silk costs (Avilés 1997; Lubin and Bilde 2007).

Like all Sparassidae, the social huntsman spider, *Delena cancerides* Walckenaer, does not construct a web, making it one of only two known genera of social spiders that does not build capture webs (Rowell and Avilés 1995; Evans 1995). Instead, these spiders live exclusively in retreats under tree bark (Rowell and Avilés 1995). Colonies usually consist of a single female and her offspring, which may consist of up to five intermingled cohorts that range in age from newly emerged young to penultimate subadults (Rayor et al., in preparation). Bark retreats appear to be occupied for successive generations. Based on laboratory observations and collection data, this species does not form societies with multiple breeding females. However, offspring remain together with their mother and siblings until sexual maturity, and spiders require about 1 year to mature (personal observation). Therefore, spiders in these long-term societies should be subject to the inherent costs associated with any long-term group. Allozyme analyses have shown that most offspring are full or half siblings, though unrelated migrants have been detected in about half of collected colonies (Yip et al., in preparation). Spiders may, therefore, derive both direct and indirect benefits from

group living that outweigh its associated costs. Without a capture web, however, many of the benefits of group living ascribed to other social spiders might not apply to this species.

The other spider genus with social species that lacks capture webs is *Diaea* (Thomisidae). Main (1988) and Evans (1998) studied the benefits of group living in *Diaea socialis* and *D. ergandros*, respectively, both of which form expandable retreats of silk and leaves. Evans (1998) found that, while *D. ergandros* spiders did not cooperate in defense against predators, they benefited from the barrier provided by their silk nest, which became larger and more protective as colony size increased. Sharing prey captured by the mother provided a considerable benefit to juveniles (Evans 1998). Spiders usually foraged individually near retreat entrances (Main 1988).

Here, we examine the benefits *D. cancerides* spiders derive from group living to answer two questions: (1) Has evolution circumvented the constraints imposed by the absence of both a capture web (spun by most other social spiders) and a silken nest (spun by all other social spiders, including *Diaea*), allowing these spiders to derive benefits of group living similar to other social spiders? (2) If not, what other benefits might have selected for group living in this species? We specifically examine cooperative defense and cooperative foraging, two benefits of group living that are important to a wide variety of social animals (e.g., Buskirk 1981; Macedonia and Evans 1993; Baird and Dill 1996; Breed et al. 2004; Yorzinski and Vehrencamp 2009). To accomplish this, we performed two sets of introduction experiments: (1) We introduced potential predators into field and laboratory retreats and recorded which spiders responded aggressively. (2) We introduced potential prey items into field retreats and recorded which spiders captured the prey and whether the prey was subsequently shared. In addition, we examined naturally occurring prey capture both inside and outside field retreats, recording the amount of prey captured in the presence of other spiders and whether spiders gained prey cooperatively. We employed a novel method for observing field colonies inside the retreat, allowing for observations that were both as unobtrusive and in as natural a setting as possible.

Because *D. cancerides* lacks a capture web to facilitate recruitment to predators or prey, we predicted active cooperation to be rare and for spiders to capture prey individually. However, based on laboratory observations, we expected prey sharing to provide an important component to the juvenile diet. As *D. cancerides* colonies typically contain multiple cohorts of different-aged spiders (Rayor et al., in preparation), we predicted the older siblings to maximize their inclusive fitness by sharing their prey and protecting the younger brood

Methods

Study organism and study sites

D. cancerides is endemic to Australia (Main 1962). Field observations were conducted at Mt. Ainslie, Canberra, Australia from 8 Oct. 2006 through 1 May 2007 and from 2 Feb. through 19 April 2008. Laboratory observations were conducted at Cornell University, Ithaca, NY, USA from 24 June until 11 July 2008. Colonies can consist of up to 300 individuals (Rowell and Avilés 1995), but the average colony size in this study is 22.6 individuals for field colonies and 27.0 for laboratory colonies. Most colonies have only one resident adult female, but two to three adult females are occasionally collected from the same retreat. Based on the condition of the cuticle (cuticle color and wear of cuticle hairs give an indication of spider age), these females are probably one older adult female that is the mother of one or two recently matured daughters. All but one field colony observed in this study had only a single adult female, presumed to be the mother of all the offspring. One colony was an orphaned colony, containing subadults and younger spiders, but no adult female. Female spiders have 10–11 instars, though males may have fewer. Because body size strongly correlates with prey size in spiders (Buskirk 1981), we divided immature spiders into two size categories: “juveniles” refer to spiders sixth instar and younger, while the readily sexed seventh to ninth instars are termed “subadults.” For analyses, adult males were grouped with subadults because both categories of spiders were similarly sized. The number of males was too few to compare analytically to subadults, but in the few trials with adult males, they behaved similarly to subadults (see the “Results” section and Figs. 2, 3, 4, 5). Colony demographics change not only over long periods of time but also from night to night, depending on the number of spiders that might be out foraging. Since not all tests were conducted simultaneously, colony demographics differ from test to test and are reported separately.

Retreat manipulation

To observe the defensive and foraging behaviors of spiders in the field, it was necessary to modify their retreats in such a way that allowed the retreat to be opened to observation with as little disturbance to the spiders as possible while maintaining the protective integrity of the bark. To this end, we constructed “retreat windows” in natural bark retreats. Two forms of retreat windows were used to view inside established colonies. Both forms of retreat windows involved cutting viewing holes in the external bark. To create retreat windows in occupied retreats in 2006/2007, holes were cut in the bark of 21 colony retreats using a

battery-powered rotary saw, and a thin (<0.5 mm) sheet of clear plastic was glued over the hole using polyepoxide. The piece of bark removed from the retreat was then reattached to the retreat with a string so that it covered the window and could be easily removed at night for viewing nocturnal activity within the colony (Fig. 1a). A thick fabric sheet between the cover and the window helped seal cracks from light and maintain a tight fit between window and cover. All retreats were given at least two windows, installed over at least 2 days, so that spiders could move to another portion of the retreat while each window was made. Window size varied and was dictated by the size of the bark that sheltered colonies (Fig. 1). In 2008, we collected 14 entire spider colonies along with their bark and moved them to the laboratory. A single, large window was cut into each piece of bark (Fig. 1b–d). An acrylic sheet (0.5 mm thick) was bolted to the bark, and the edges sealed with silicone sealant. Retreats were reattached to trees with hook and loop fasteners (Velcro), and the cover was attached with Velcro with a sheet of black fabric between the cover and window. Spiders from each colony were given colony-specific marks with Testors enamel paint applied to the carapace and sternum, fed, and returned to the field within 48 h of collection. The bark with the retreat window was reattached to the tree, and spiders were gently coaxed back into the retreat. To enhance retention of the spiders while they readjusted to the modified retreat, the entire retreat was enveloped in two to three layers of nylon tulle for at least 3 days. Both processes were clearly disruptive to spiders. Of 21 retreats given windows in 2006/2007, 10 were abandoned within 2 weeks. Of 14 retreats in 2008, 6 were abandoned within 3 days. However, colonies in which individuals remained together under the modified bark remained viable for months (some for over a year). We observed a total of 19 colonies that successfully remained under retreat windows.

While disruptive to the spiders, we believe that the retreat windows present an accurate representation of field behavior for two reasons. (1) We have also observed behavior on unmanipulated field retreats. In both manipulated and unmanipulated retreats, some portion of the colony leaves the retreat to forage at dusk and returns at dawn. While the precise percentage of the colony foraging is only known in manipulated retreats, the numbers of spiders seen leaving manipulated retreats are consistent with the numbers leaving unmanipulated retreats (average number of spiders leaving unmanipulated retreats, 3.33 ± 0.96 SE; average number of spiders leaving manipulated retreats, 3.98 ± 0.81 S.E; mean percentage of the colony leaving = $15\% \pm 14$ SD). All ages over second instar were seen leaving both types of retreats; though in both cases, most spiders were fourth to sixth instars. (2) Observations on the 19 manipulated colonies were taken 1–136 days after

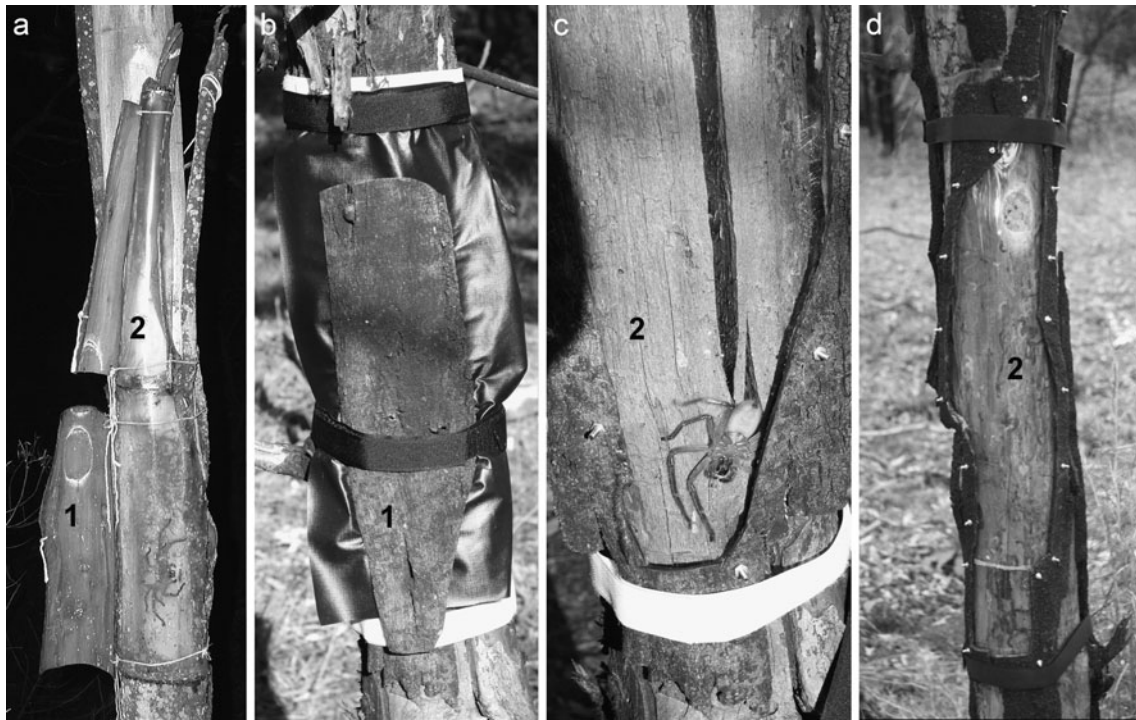


Fig. 1 Photographs of retreat windows in 2006/2007 (a) and in 2008 (b–d). The number 1 designates the bark cover, and the number 2 designates the clear plastic window for both types of retreat windows.

Bands of Velcro help hold the retreat window tightly onto the tree (b–d). Note the adult female and offspring in a and adult female in c

the retreat had been altered. There was no relationship between time postdisruption and the percentage of the colony leaving the retreat to forage (GLM with colony as a random effect, $t=0.31$, $p=0.76$, $n=31$), whether each age class of spider attacked the predator (logistic regression adult females: $\chi^2=0.01$, $p=0.91$, $n=34$; subadults: $\chi^2=1.54$, $p=0.22$, $n=19$; juveniles: $\chi^2=0.58$, $p=0.45$, $n=37$), or which age class of spider captured the introduced cricket (logistic regression, $\chi^2=1.04$, $df=2$, $p=0.59$, $n=24$). Given that manipulated colonies (1) showed minimal differences from unmanipulated colonies and (2) were consistent over time, there is no evidence to suggest that these spiders behaved differently than those in unmanipulated colonies.

Predator introductions and defense observations

Predation on *D. cancerides* spiders is not easily observed. However, spider numbers in colonies gradually decline over time and solitary individuals younger than the penultimate instar are rarely collected in the field (Rayor et al., in preparation), suggesting that mortality and predation may be common. Only three predation events have been directly observed: two instances of cannibalism (one inside and one outside the retreat) and one instance of an adult solitary huntsman spider (*Pediana regina*) capturing a fifth instar *D. cancerides* spider foraging outside the retreat. However, indirect evidence indicates that other

species of solitary huntsman spiders and ants are likely predators. The remains of dead *D. cancerides* spiders have been found in neighboring solitary huntsman retreats (Rayor, personal observation). Occasionally, when spiders escaped to the ground while being collected, they were attacked by large numbers of ants (unidentified species). Brown bulldog ants (*Myrmecia pyriformis*) were twice observed invading *D. cancerides* colonies. In one instance, the resident adult female survived with her offspring. In another instance, the retreat was found abandoned and filled with debris by the following observation and *M. pyriformis* ants were seen on or in the retreat for the following week. In another instance, a recently abandoned retreat was found with six dead *M. pyriformis* ants at the bottom and *M. pyriformis* ant heads have been found at the bottom of other *D. cancerides* retreats.

Because of these observations, we introduced *M. pyriformis* ants and three species of sympatric solitary huntsman as potential predators into retreats in the wild and in the laboratory and detailed the resulting behavior of the spiders. Nineteen *M. pyriformis* ants, 12 *P. regina* (Sparassidae) adult females, and 6 *Isopedella pessleri* (Sparassidae) males and females were collected on Mt. Ainslie and introduced into *D. cancerides* field colonies. Each colony was tested with one ant and one solitary huntsman, in a random order, and each trial was separated by at least 24 h. *P. regina* and *I. pessleri* adults are considerably smaller than an adult *D. cancerides*

(mean carapace length for *P. regina*=6.7 mm, Hirst 1989; *I. pessleri*=8.6 mm, Hirst 1993; *D. cancerides*=10.6 mm, Yip, unpublished data). To test how spiders might respond to a larger solitary huntsman, 14 large *Holconia flindersi* penultimate and adult spiders (mean carapace length of these laboratory animals=10.72 mm; unpublished data) from a laboratory population were introduced into laboratory colonies of *D. cancerides*. Three or more species of *Holconia* are found in much of *D. cancerides*' range in southeastern Australia, but not at our specific study sites in Canberra. Laboratory colonies were housed in glass terraria with clear acrylic sheets serving as retreats using the methods described in Yip et al. (2009). The *H. flindersi* spiders were offspring of animals collected in South Australia in 2006 and raised in the laboratory. Laboratory colonies of *D. cancerides* were collected from four sites across southern Australia: two in the Australian Capital Territory, one in New South Wales, and one in Victoria.

Predator observations followed the following protocol: Predators were transported from the field or laboratory in plastic vials and then gently coaxed into the retreat entrances, which are usually restricted to one or two small openings by silk. While this does not present all spiders with an equal opportunity to encounter the predator, it presents a realistic scenario, as invertebrate predators, like the ones used in this study, almost certainly enter the retreat through these entrances. Predators and spiders were observed for 1 h or until the predator was killed. We recorded our observations in a hand-held tape recorder. To ensure that predators encountered as many spiders as possible, predators were not allowed to leave the retreat. Spiders were considered to have "contacted" a predator when they physically touched. Following contact, responses to the predator were classified as "ignore," defined as no action or slow movement away from the predator; "investigate," defined as tapping or following the predator without attacking the predator; "attack," defined as lunging, biting, or attempting to bite the predator; "retreat," defined as rapid movement away from the predator; and "kill." Attacks did not always result in mortality, but all spiders that "killed" were also considered to have "attacked."

Responses among age groups were compared using Kruskal–Wallis rank sum tests followed by Tukey–Kramer comparisons. For each trial, we scored whether individuals engaged in the behaviors defined above as yes/no. We calculated the percentage of individuals of a given age group engaging in a behavior and use these percentages as the unit of replication. The number of individuals in a given age group varied from trial to trial. Because percentages generated from trials with many individuals are a more reliable representation of spider behavior than percentages generated from only one or two individuals, data were

weighted by the number of individuals in each age group able to participate in a given behavior. For example, data comparing rates of contact were weighted by the total number of individuals in each age group in the colony, while data comparing rates of attacking were weighted by the number of individuals in each age group that contacted the predator.

Foraging observations

We examined possible benefits of group foraging in two ways in the field: observing natural prey capture and spiders' reactions to house crickets (*Acheta domesticus*) that were provided. Natural prey capture was observed both inside and outside the retreat. For prey capture inside the retreat, the 19 colonies with retreat windows were observed repeatedly over 68 nights for a total of 313 h. For prey capture outside the retreat, spiders seen leaving the 19 colonies with windows, plus an additional 2 colonies without windows, were tracked on foot over the same 68 nights for a total 134 h. We recorded all instances of spiders attacking or feeding on prey, including data on the approximate instar of the feeding spider, the approximate prey length, and the taxonomic order of the prey. We used the average weights of instars collected from the field (Yip, unpublished data) to estimate the weights of feeding spiders. Prey length and order were used to approximate prey mass using the methods of Sage (1982). We calculated the rates of prey capture inside and outside the retreat by dividing the total weight of prey captured by the number of spiders observed and by the hours of observation for each spider ("spider-hours"). All spiders within a given retreat were observed simultaneously. The number of spiders in the retreats varied from colony to colony and from one observation period to another. To calculate the total number of spider-hours inside the retreat, we multiplied the number of spiders in the retreat by the duration of the observation period. These were then summed over all observation periods for a total of 6,474 spider-hours inside the retreat. Most observations outside the retreat were on a single spider, but rarely two or three spiders were close enough to be observed simultaneously. The focus required to track a single individual made recording exact time intervals on secondary spiders impractical. Instead, the total mass of prey captured outside the retreat is divided by two spiders for a total of 268 spider-hours, creating a conservative estimate of prey capture outside the retreat.

Generally, we had only one observer in the field at a time, so only one colony or spider out foraging could be observed at a time. Observation time was divided between inside and outside the retreats using the following protocol: Observations began at one retreat 15 min prior to sunset each evening. The first spider leaving the retreat to forage

was then tracked on foot until it could no longer be sighted. The duration of tracking on an individual spider varied considerably, from 15 min to over 10 h. Subsequent spiders seen foraging outside were also tracked for prey capture until lost. When not tracking spiders outside the retreat, we opened retreat windows and observed spiders inside for any prey captured within the retreat.

To further examine the possibility of cooperative foraging, we introduced house crickets into colonies. Prey could be captured at the retreat in two ways. Prey might wander into the retreat or prey might alert spiders from outside the retreat entrance. To mimic these two situations, 18 crickets were placed inside the retreat. An additional 10 crickets were held (either manually or attached by sticky gum) at an entrance to the retreat of 10 colonies. The cricket's legs were allowed to scrape against the bark to cause vibrations, to which spiders might respond. We recorded the approximate age and sex of spiders that contacted, ignored, investigated, attacked, and killed the cricket (as defined in our predator observations) and whether the cricket was shared, and with which spiders, within 1 h of capture. As with the predator trials, all observations on prey capture were recorded with a tape recorder. We use the same analyses described under

predator observations to compare the behaviors of different age groups.

While house crickets are not part of *D. cancerides*' natural diet, their commercial availability allowed for easy replication of introductions, and spiders in the laboratory readily prey on them (Rayor, unpublished data). Crickets were adult and subadults (~2–2.5 cm). All colonies contained at least one spider large enough to capture the cricket on its own based on laboratory observations (either adult or subadult spiders).

Results

Predator introductions and defense observations

D. cancerides age groups varied in their responses toward predators (Figs. 2, 3, and 4). Adult females killed 23 (55%) of the 42 predators introduced into a colony with an adult female present. Thirty-two (63%) of 51 predator introductions were in colonies with subadults and/or adult males, but only once did a subadult successfully kill a predator. No juvenile killed a predator. These differences among age groups in killing predators were the result of differences in

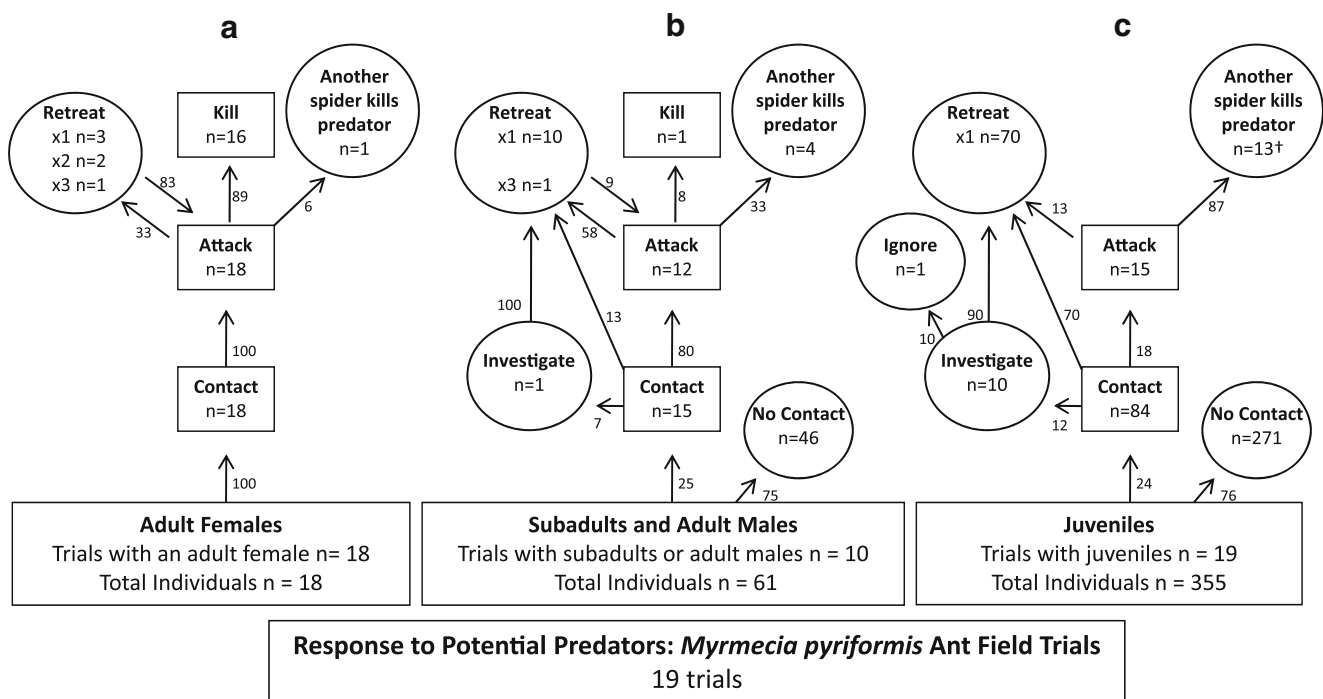


Fig. 2 A flowchart of **a** adult female, **b** subadult and adult male, and **c** juvenile behavior in response to the introduction of *M. pyriformis* ants into field colonies. *n* indicates the total number of spiders of that age group engaging in the behavior summed over all trials. Numbers adjacent to arrows indicate the percentage of spiders in the previous box moving down that behavioral path. The multiplier under “Retreat”

indicates the number of times a particular individual retreated from a single predator. Of the 61 subadult and adult male spiders, 5 were adult males. One adult male contacted the ant, attacked, then retreated. The dagger indicates that 13 juveniles were from a single exceptional trial (A86) in which multiple juveniles attacked an ant simultaneously (see the “Results” section)

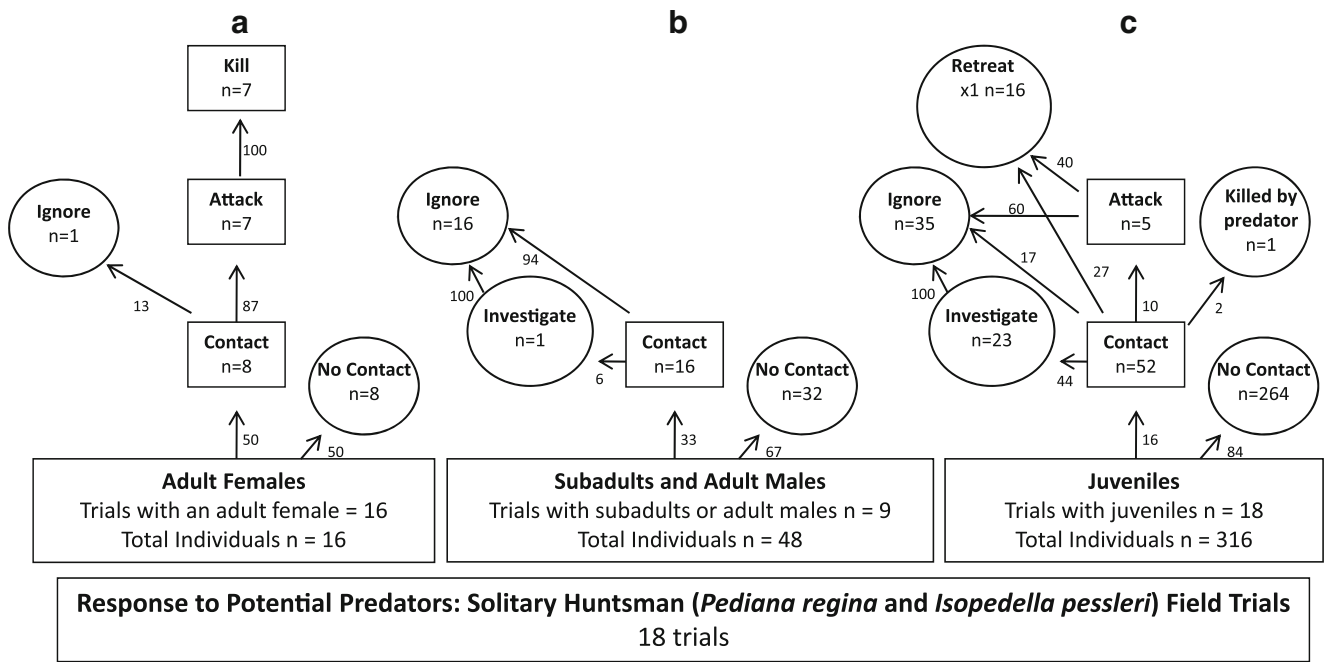


Fig. 3 A flowchart of **a** adult female, **b** subadult and adult male, and **c** juvenile behavior in response to the introduction of solitary huntsman spiders (either *P. regina* or *I. pessleri*) into field colonies. *n* indicates the total number of spiders of that age group engaging in the behavior summed over all trials. *Numbers adjacent to arrows* indicate the

percentage of spiders in the previous box moving down that behavioral path. The multiplier under “Retreat” indicates the number of times a particular individual retreated from a single predator. Of the 48 subadult and adult male spiders, 6 were adult males. Four adult males contacted the solitary huntsman and ignored it

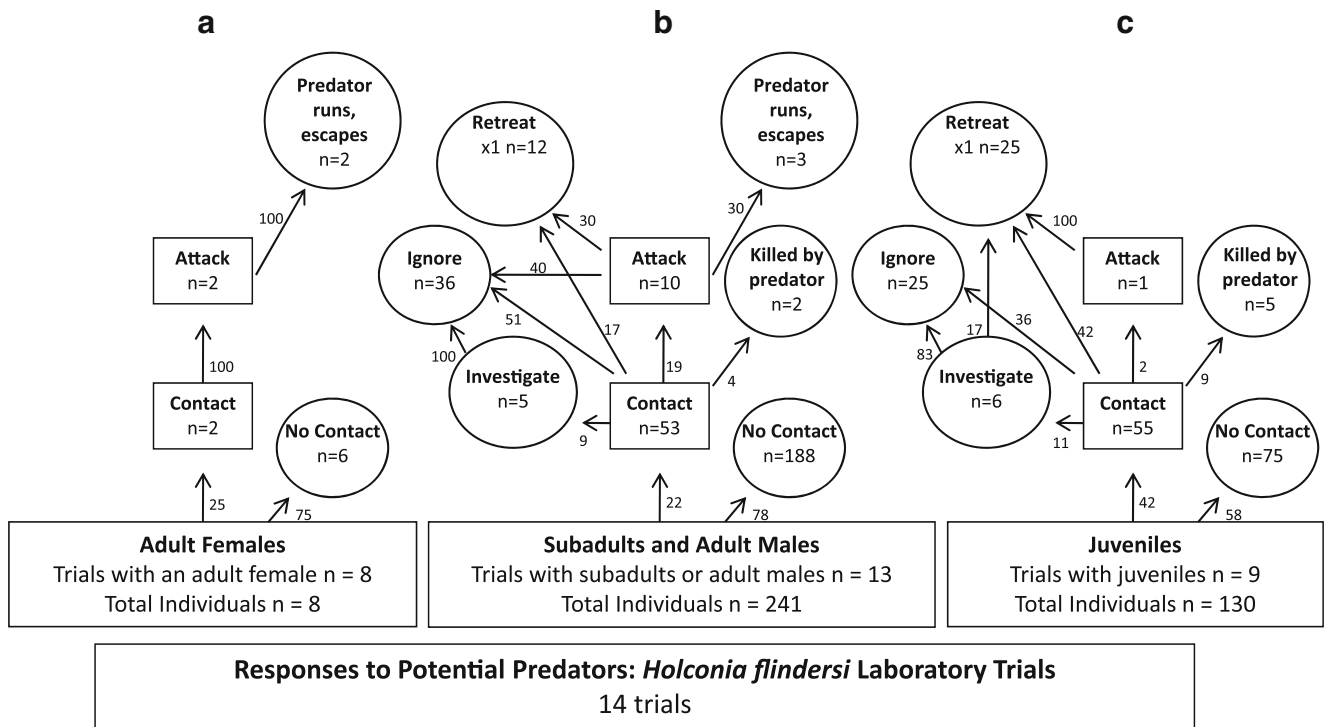


Fig. 4 A flowchart of **a** adult female, **b** subadult and adult male, and **c** juvenile behavior in response to the introduction of solitary huntsman spiders (*H. flindersi*) into laboratory colonies. *n* indicates the total number of spiders of that age group engaging in the behavior summed over all trials. *Numbers adjacent to arrows* indicate the

percentage of spiders in the previous box moving down that behavioral path. The multiplier under “Retreat” indicates the number of times a particular individual retreated from a single predator. Of the 241 subadult and adult male spiders, 79 were adult males. Six adult males contacted the solitary huntsman. Five ignored the predator, and one investigated it before ignoring it

their probability of contacting, their propensity to attack, and their capacity to kill predators.

Adult females were more likely to contact *M. pyriformis* ants than subadults/males or juveniles (Kruskal–Wallis rank sum test followed by Tukey–Kramer comparison: $\chi^2=26.74$, $df=2$, $p<0.0001$, $n=47$). There were no other significant differences in the rate of contact among age groups for other predators.

After initial contact, adult females were the most aggressive age group and attacked predators in all but one case. Subadults and adult males attacked *M. pyriformis* ants if directly threatened ($n=12$ instances over 4 trials), but they uniformly ignored the small *P. regina* and *I. pessleri* huntsman. They occasionally attacked the larger *H. flindersi* huntsman but most often ignored them. A small number of juveniles (third to sixth instars) attacked all predator types ($n=21$ instances over 7 trials), but were more likely to investigate, ignore, or retreat from predators (Figs. 2, 3, and 4). Adult females were more likely than subadults/males and juveniles to follow contact with an attack against both the small solitary huntsman (Kruskal–Wallis rank sum test followed by Tukey–Kramer comparison: $\chi^2=15.39$, $df=2$, $p=0.0005$, $n=25$) and the larger *H. flindersi* (Kruskal–Wallis rank sum test followed by Tukey–Kramer comparison: $\chi^2=9.69$, $df=2$, $p=0.0079$, $n=21$). Both adult females and subadults/males were more likely than juveniles to attack *M. pyriformis* ants following contact (Kruskal–Wallis rank sum test followed by Tukey–Kramer comparison: $\chi^2=23.68$, $df=2$, $p<0.0001$, $n=38$).

Once they attacked potential predators, adult females were the most effective at killing them. They not only overpowered the predators more easily, but were also more tenacious in their attacks. When encountering the formidable *M. pyriformis* ants, adult females sometimes retreated, but reengaged the ant until they killed it (Fig. 2a). Only one adult female, after engaging the ant and retreating twice, failed to kill the ant during the observation period. By contrast, after the initial attack subadults (and the single adult male that contacted the ant) usually ran and avoided future contact with the ant (Fig. 2b). This resulted in attacks by adult females killing more ants than attacks by subadults/males (Kruskal–Wallis rank sum test: $\chi^2=7.26$, $df=1$, $p=0.007$, $n=22$). Attacks by juveniles were ineffective at killing predators. Their lighter bites appeared to not pierce the cuticle, as no hemolymph was ever seen to bead from a wound caused by a juvenile. Instead, bites sometimes caused the predators to flinch or startled them into running. Unlike field trials, no spider successfully killed an *H. flindersi* spider due to the latter's size and speed (Fig. 4).

Multiple spiders cooperating in the defense against predators was very rare. In all trials, spiders running away from the predator precipitated other spiders to run or adjust

their position. However, there was no obvious evidence that spiders recruited nestmates to attack the predator, nor was there indication that spiders running in response to sibling contact moved to a particular safe location away from the predator, near the mother, or in tighter areas under the bark. Of all predator introductions, only one predator (an ant) was attacked simultaneously by multiple individuals for more than a few seconds. It was attacked by all spiders it contacted, (12 fourth to fifth, 1 sixth, and 3 seventh instar spiders, with as many as 5 juveniles all attacking at once). The ant was eventually killed by the adult female.

Foraging observations

D. cancerides spiders are nocturnally active, and spiders depart from their retreats at dusk to forage. They would occasionally return to the retreat in the middle of the night, but the majority only returned at dawn the next day. Second instars (the first instar out of the egg sac which does not feed) were never seen leaving the colony. Third and fourth instars left the retreat, but tended to remain on the natal tree. Older instars usually headed directly to the ground upon leaving the retreat. They wandered erratically 3–10 m net distance from the retreat before climbing a tree. Short trees and shrubs (2–3 m in height) were explored but usually abandoned. When spiders climbed tall trees, they were visually lost after reaching ~4 m above the ground. We successfully followed only two spiders for the entire night. Only a small number of the spiders in each colony left the retreat each night (mean \pm SE=15 \pm 2%, range=0–43%). When not foraging, spiders remained in the retreat, with the exception of short periods to defecate, to molt, or to dispose of old molts.

Spiders captured a total of 64 prey items in the field, ranging from 1 to 11 mm in length. Two of these were instances of cannibalism (by an adult female eating a subadult female inside the retreat and by a seventh instar eating a fourth instar outside the retreat) and are not included in the total prey mass captured. Spiders fed on ants ($n=16$), flies ($n=7$), homopterans ($n=7$), beetles ($n=5$), roaches ($n=3$), moths ($n=3$), lepidopteran larvae ($n=3$), a nonformicid hymenopteran ($n=1$), and an oxyopid spider ($n=1$). Sixteen prey items were too small and/or too masticated to be identified. The estimated average weight of prey was 6.7 mg, median 1.2 mg, with the largest prey item being an 11-mm fly that weighed an estimated 137 mg based on Sage's (1982) biomass equations. Prey items averaged 6% (\pm 3% SE) of the estimated weight of the capturing spider. Only 5 of 62 prey items (cannibalism excluded) were captured inside the retreat, totaling an estimated 22 mg. The estimated consumption rate inside the retreat is 0.0034 mg/spider/h. Of these five prey items, only one was shared (by six fifth instar juveniles). The

remaining 57 prey items were all captured outside the retreat, totaling an estimated 393.4 mg. The estimated rate of consumption outside the retreat is 1.47 mg/spider/h. Spiders consumed the majority of prey captured outside the retreat at or near the site of capture. However, spiders feeding at dawn did return to the retreat with prey. Of the 57 items captured outside, 9 were brought into the retreat at dawn. Whether these prey items were subsequently shared is unknown. By the time the spiders returned at dawn, it was too bright to keep the retreat windows open, and if they were left open, spiders hid along the edge of the windows out of view.

The placement of the cricket either inside the retreat or at the retreat entrance had no effect on the probability of spiders contacting the cricket (GLM with spider age group as a covariable: F ratio=0.79, $p=0.38$, $n=63$), the probability of attacking the cricket once contacted (GLM with spider age group as a covariable: F ratio=0.13, $p=0.72$, $n=36$), or the probability of killing the cricket once attacked (GLM with spider age group as a covariable: F ratio=0.36, $p=0.55$, $n=32$). Therefore, data from the two types of cricket placements are pooled for further analyses. Of 28

crickets, 3 escaped after 1 h of observation. Of the remaining 25 crickets, most (21) were captured by adult females (Fig. 5). One was captured by an adult male and two were captured by subadults (one male and one female) in the 12 trials in which the cricket was captured and colonies contained subadults and adult males (Fig. 5). One was captured by a group of third instar spiders; however, this particular cricket was affixed at the entrance to the retreat by gum. While this shows that spiders as young as third instars attack prey wandering near the entrance of the retreat, it seems unlikely that the third instar spiderlings could have captured a cricket of this size had it been able to escape. For the purposes of analyses, these spiders are considered to have attacked but not killed the cricket. Adult females were more likely than subadults/males and juveniles to make contact with the cricket (Kruskal–Wallis rank sum test followed by Tukey–Kramer comparison: $\chi^2=26.16$, $df=2$, $p<0.0001$, $n=66$). Both subadults and juveniles were less aggressive toward crickets than adult females, in that they occasionally ignored or investigated crickets without attacking while all adult females attacked the cricket if they came into contact with it (Kruskal–Wallis

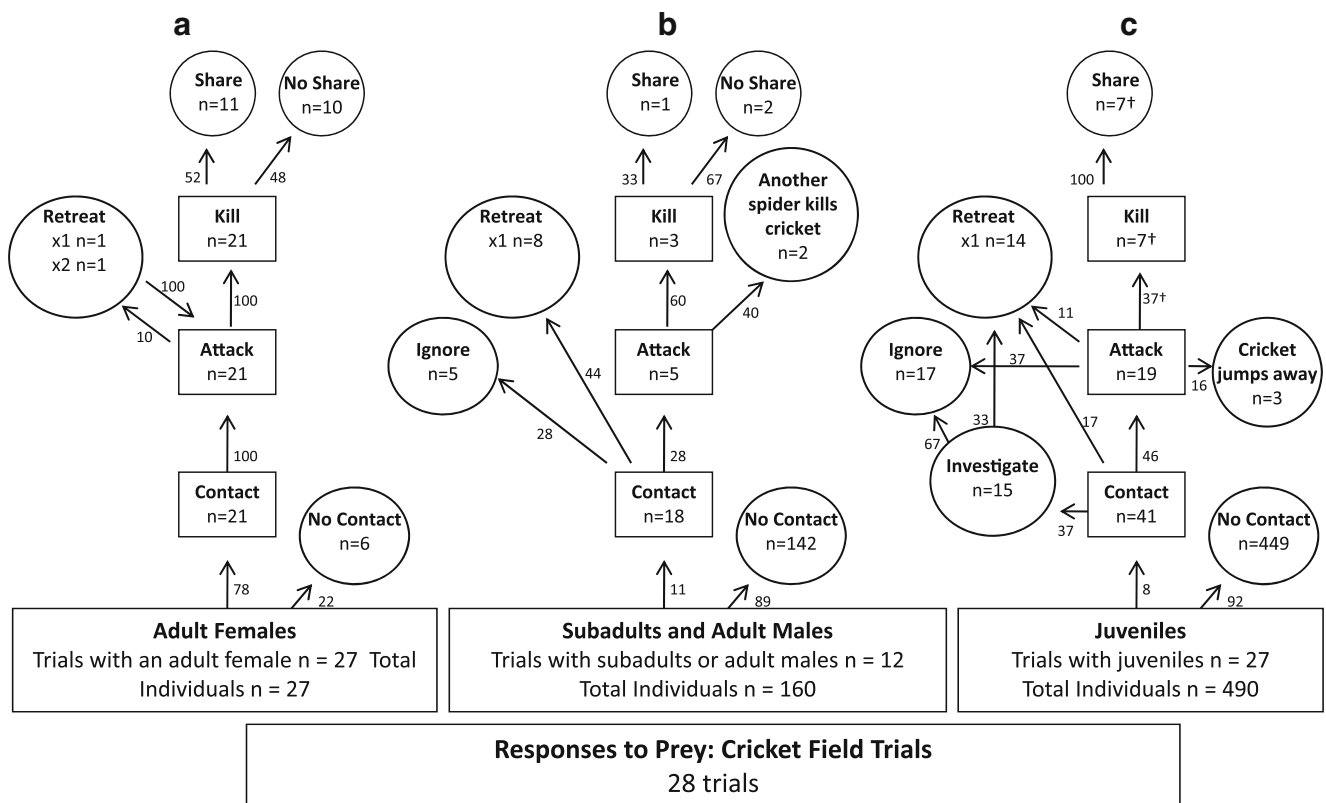


Fig. 5 A flowchart of **a** adult female, **b** subadult and adult male, and **c** juvenile behavior in response to the introduction of house crickets into field colonies. n indicates the total number of spiders of that age group engaging in the behavior summed over all trials. Numbers adjacent to arrows indicate the percentage of spiders in the previous box moving down that behavioral path. The multiplier under “Retreat” indicates

the number of times a particular individual retreated from a single cricket. Of the 160 subadult and adult males, 4 were adult males. One adult male contacted the cricket, killed it, and ate it without sharing. The dagger indicates that all seven of the juveniles moving down this behavioral path were from a single trial where a cricket was held at the entrance of the retreat (see the “Results” section)

rank sum test followed by Tukey–Kramer comparison: $\chi^2=11.84$, $df=2$, $p=0.0027$, $n=36$). Even when they did attack, single juveniles were unable to capture prey as large as the crickets. Subadults and adult males captured the crickets nearly as often as they attacked them (Fig. 5b).

Eleven of 21 crickets (52%) captured by adult females were shared with juveniles (third to fifth instars) at some point during the first hour after capture (Fig. 5). The adult female initially appeared reluctant to share prey, often batting juveniles away with her legs and securing prey for herself if she could. Adult females and the three subadults/males that captured crickets were forced to share more often in trials with more juveniles present (logistic regression: $\chi^2=4.28$, $df=1$, $p=0.039$, $n=24$), as the number of actively soliciting juveniles overwhelmed their defenses. Young *D. cancerides* juveniles have a distinctive solicitation behavior and will often attempt to share prey held by other individuals (Rayor, unpublished data). We never observed subadults sharing or attempting to share with adult females. There was a single instance when subadults shared with another subadult and one juvenile (Fig. 5), but no other subadults were ever seen sharing prey.

Discussion

Our study examined two potential benefits of group living, cooperative defense and cooperative foraging, to determine whether these are major payoffs supporting sociality in *D. cancerides*, given the constraint that they lack a web. We had predicted that, even without a capture web, older siblings would help defend the colony and that spiders would capture prey individually but share with nestmates. Instead, our data show that, other than the adult female, spiders generally acted individually when defending themselves from predators or obtaining food. Maternal defense and prey sharing provided some benefits from remaining in the natal retreat. Overall, *D. cancerides* spiders do not derive the same defense and foraging benefits as most of the web-based social species, yet they have evolved to live in groups despite lacking a parallel mechanism to mediate cooperative prey capture or defense.

One clear benefit of staying in the natal retreat demonstrated by our data is maternal defense. The adult female was far more aggressive and effective in eliminating potential predators than any other spider in the colony. While all offspring benefited from maternal defense, the relative benefits were almost certainly greatest to smaller spiders that are less able to defend themselves. Contrary to our prediction, spiders derived no similar benefit from older siblings. The subadults were ineffective in eliminating predators, even though subadults (seventh through ninth instars) are in the same size range as the smaller

species of solitary huntsman in the area (*P. regina* and *I. pessleri*) and larger than other potential predators such as *M. pyriformis* ants.

We observed one remarkable instance in which multiple spiders mobbed a single predator (*M. pyriformis* ant), which suggests the possibility that spiders may together drive away predators too large for a single spider; however, such mobbing behavior appears to be very rare. In other organisms, such mobbing behavior is sometimes accomplished through the active recruitment of other group members to the threat (Macedonia and Evans 1993; Breed et al. 2004; Yorzinski and Vehrencamp 2009). In this case, however, spiders persistently (though ineffectively) attacked the ant only when it contacted each particular spider, so that the ant accumulated attackers as it moved through the retreat. Thus, this one instance of mobbing was not an example of active recruitment, but rather the result of spiders displaying persistent aggression not seen in other predator trials.

In web-building social spiders, vibrations sent through the web can act to recruit spiders to defend against a large predator (Vollrath and Windsor 1983) or as an advanced warning system (Hodge and Uetz 1992). Even without a web, spiders are known to communicate both chemically (Gaskett 2007) and acoustically (Hebets and Uetz 1999; Elias et al. 2005). However, despite the ability to communicate, we found no obvious evidence that *D. cancerides* spiders recruited other individuals to aid in an attack on a predator or to emit signals with information about the nature or direction of the threat. Our study did not explicitly examine passive defense benefits, such as the selfish herd (Hamilton 1971), nor was our study designed to detect information spiders might convey that results in very subtle changes in spiders' behavior. Thus, while our data show that active cooperation in predator defense is very rare, we cannot rule out other defensive benefits they might derive from living in groups.

In other social spider species, silk acts as a barrier to predation, and this barrier improves as colony size increases (Rayor and Uetz 1990; Uetz and Hieber 1997; Evans 1998). *D. cancerides* spiders, however, probably do not derive a similar benefit of group living. The bark retreat of a *D. cancerides* colony is sealed around the edges with silk, with only one or two entrances that are usually just large enough to accommodate the adult female spider that frequently stands at the entrance (personal observation). This severely restricts access to the retreat by predators. We witnessed no natural predation within the retreat besides one instance of cannibalism, suggesting that the retreat acts as an effective barrier to most predators. Most predation probably occurs outside the retreat while spiders forage individually and is, therefore, unassociated with either group size or retreat size. Unlike a web, which increases proportionally as colony size

increases in other social spiders, the bark does not increase in size or improve as a barrier to predation as the number of spiders in the colony increases. Indeed, the opposite may be true, in that the area under a given piece of bark may fail to accommodate all spiders, especially as the young mature and increase in size.

The importance of prey, as a resource both gained cooperatively and contested competitively, has garnered considerable attention in the social spider literature. Several studies have suggested that competition for prey intensifies as colonies grow larger, and prey intake fails to keep pace (Ward 1986; Seibt and Wickler 1988; Rypstra 1993), while other studies show group living increases individual prey capture success (Uetz 1988; Uetz 1989) or the size of the insects captured (Ward 1986; Jones and Parker 2002; Yip et al. 2008), providing a net benefit for spiders, within a certain range of colony sizes (Yip et al. 2008). Yip et al. (2008) further suggest that the cooperative capture of large prey and the presence of large prey in the environment are key to the distribution of sociality in the genus *Anelosimus*. Whether social foraging provides a net benefit or cost and what role social foraging plays in the evolution of group formation and size have generated debate in the social vertebrates as well (e.g., Packer et al. 1990; Creel and Creel 1995; Creel 1997; Packer and Caro 1997). The balance between cooperation and competition in securing prey appears to be of far less importance in *D. cancerides*, as spiders gain the vast majority of their food resources away from the retreat, where spiders have no opportunity to interact with any frequency.

Contrary to our predictions, prey sharing appears to be relatively rare. Only juveniles regularly shared the prey that was captured inside the retreat, only about half of prey captured inside the retreat was shared, and spiders captured over 431 times as much prey mass outside as inside the retreat. Using these data, only an estimated 0.1% of prey mass is shared with other spiders. Furthermore, the spiders exhibited behaviors that limited prey sharing. Adult females usually attempted to brush juveniles away from the prey item. After capturing crickets within the retreat, two spiders left the safety of the retreat to feed outside alone. Whether prey brought back to the retreat at dawn is subsequently shared is unknown, but spiders returning with prey appeared reluctant to enter the retreat, instead preferring to continue to feed near the retreat entrance or only half inside, with the prey item outside and shielded from other spiders by the body of the feeding spider. However, we cannot rule out the possibility that sharing even small amounts of prey may be an important benefit to younger spiders that have a more limited capacity to capture prey on their own, particularly larger prey items. Subadults appear to gain virtually no benefits from group foraging.

Compared to the more advanced web-building social spiders (see reviews by Avilés 1997; Lubin and Bilde 2007), active cooperation in *D. cancerides* is limited in terms of foraging and defense, and spiderlings benefited most through the presence of the mother rather than from siblings. This supports the hypothesis that the absence of the web acts as a constraint, not necessarily for group living, but certainly for certain cooperative behaviors in the spiders. However, group living in *D. cancerides* cannot be attributed to maternal care alone, as orphaned colonies (lacking an adult female) are known to persist for months. We argue two reasons for the persistence of these groups. (1) Spiders delay dispersal because the relative costs of group living are low. Although older spiders may not benefit from cooperative prey capture or share to any great extent in the field, neither do they suffer from intense food competition within the colony. Thus, the absence of a capture web in *D. cancerides* may act as a double-edged sword in social evolution: while it limits the extent of cooperative behaviors that in turn mitigate the costs of group living, it also frees spiders to forage outside the limits of a web and away from close relatives. (2) Under the ecological constraints hypothesis (Emlen 1982), habitat saturation is known to promote group living in a variety of species, including birds (Komdeur 1992; Kappes 2008), fish (Wong 2009), mammals (Blumstein and Armitage 1999; Schradin et al. 2010), and ladybeetles (Honěk et al. 2007), but has never been documented for a social spider. The bark retreats these spiders require to successfully breed appear to be quite rare, with colonies occupying nearly 100% of suitable retreats at many collection sites (Rayor et al., in preparation). Furthermore, laboratory data show that larger *D. cancerides* adult females almost always push smaller adult females out of artificial retreats (Yip, unpublished data). Dependence on a rare retreat may then have allowed evolution to circumvent the web in selecting for group living, as spiders remain in their natal retreat until adulthood because dispersing at a smaller size would put them at a competitive disadvantage for securing an unoccupied retreat. We are currently conducting a field experiment examining the relationship between retreat abundance and occupancy of artificial retreats to test this hypothesis.

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