The influence of siblings on body condition in a social spider: is prey sharing cooperation or competition?

Eric C. Yip^{a,b,*}, Linda S. Rayor^{a,b}

^aDepartment of Entomology, Cornell University, Ithaca, NY, U.S.A.

^bResearch School of Biology, The Australian National University, Canberra, ACT, Australia

ARTICLE INFO

Article history:

Received 9 July 2012

Initial acceptance 3 October 2012

Final acceptance 27 February 2013

Available online 18 April 2013

MS. number: A12-00526R2

Keywords:

body condition
competition
cooperation
foraging
group living
prey sharing
producer–scrounger
sibling
sociality
spider

Siblings living together compete with each other for resources, yet they may also cooperate to maximize their inclusive fitness. In social spiders, siblings share prey and may both compete and cooperate to obtain this resource. In the laboratory, the social huntsman spider, *Delena cancerides*, readily shares prey captured by other colony members; however, these spiders only occasionally share prey in the field, making the importance of prey sharing to their social system difficult to assess directly. We examined the importance of prey sharing indirectly by measuring the body condition of spiders from 90 colonies at the time of collection. We compared body condition to colony demographics to determine whether the patterns were consistent with the hypothesis that younger spiders benefit from sharing prey captured by older siblings. We tested several alternative hypotheses that might also explain associations between condition and the presence of siblings. We further conducted a laboratory experiment to directly determine whether feeding on prey captured by older siblings improves the condition of younger spiders. Younger spiders collected from the field were heavier in the presence of older siblings, but there was no effect for older spiders or for any spider with younger siblings. Laboratory spiders gained access to additional prey captured by older siblings. We rejected the alternative hypotheses and concluded that younger spiders indeed benefit from the presence of older siblings. This system provides evidence that the exploitation of others' resources can provide a benefit of group living and act as a form of cooperation.

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The clustering of siblings in both time and space sets two forces in opposition to each other: competition for resources promotes sibling conflict, while relatedness promotes cooperation to maximize inclusive fitness (Mock & Parker 1998). This opposition produces a wide variety of sibling interactions, from siblicide (Mock & Parker 1998; Mackauer & Chau 2001; Heintze & Weber 2011) to alloparental care by siblings (Riedman 1982; Koenig et al. 1992; Hatchwell 2009).

In the subsocial and cooperative spiders ('nonterritorial periodic' and 'nonterritorial permanent' social, sensu Avilés 1997), offspring remain in the natal nest and compete and cooperate with their siblings. Improved foraging is a primary benefit of group living in spiders (Whitehouse & Lubin 2005), and siblings of some species will cooperate in prey capture, allowing spiders to subdue prey much larger than a single spider could capture (Buskirk 1981; Ward 1986; Jones & Parker 2002). However, competition for prey is also

intense (Ward 1986; Seibt & Wickler 1988), and some spiders in the colony fail to obtain enough resources to reproduce (Avilés & Tufiño 1998; Bilde et al. 2007). In addition, whether an individual is helped or hindered by a sibling may depend on size and age asymmetries. For example, in the cooperative spider, *Anelosimus eximius*, large females will often usurp smaller females' feeding positions rather than capture prey themselves (Ebert 1998). Interactions among siblings over prey are therefore crucial to the costs and benefits of spider sociality, both in determining whether spiders should tolerate siblings and whether mothers should allow older broods to stay with younger cohorts.

The Australian social huntsman spider, *Delena cancerides*, is unusual among social spiders in lacking a prey capture web. Instead, colonies, consisting of a single mother and multiple cohorts of offspring, live under the bark of trees (Rowell & Avilés 1995; L. S. Rayor, E. C. Yip & D. M. Rowell, unpublished data). Yip & Rayor (2011) investigated the foraging behaviour of these spiders, given that they lack a capture web to facilitate cooperative foraging. Spiders foraged nocturnally, predominantly away from the bark retreat, where they captured prey individually. Spiders occasionally shared prey captured within the retreat, and if spiders

* Correspondence and present address: E. C. Yip, Mitrani Department of Desert Ecology, The Jacob Blaustein Institute for Desert Research, Midreshet Ben-Gurion, 84990, Israel.

E-mail address: ecy7@cornell.edu (E. C. Yip).

were feeding outside at dawn, they returned to the retreat with their prey. Prey remains found at the bottom of retreats further suggest that, over time, a considerable amount of prey is consumed inside the retreat where it might be shared (L. S. Rayor, E. C. Yip & D. M. Rowell, unpublished data). However, overall, shared prey made up a small percentage of the total prey captured by spiders (Yip & Rayor 2011). The rarity of an event, however, does not preclude its importance. For example, in *A. eximius*, very large prey account for only 8% of the number of captured prey, but 75% of the total captured biomass (Yip et al. 2008). Similarly, in orb-weaving spiders, large prey items are only 17% of the prey numbers but 85% of consumed biomass (Blackledge 2011). These relatively rare feeding events are critical for spider fitness. Despite the rarity of prey sharing in *D. cancerides*, these spiders remain in groups even in the absence of the mother, who is the primary benefactor of young spiders (Yip & Rayor 2011), suggesting that young spiders benefit from siblings in ways that are difficult to observe.

Here, we investigated the possibility that, though rare, prey sharing may provide substantial benefits to some spiders within the colony, yet the rarity of prey sharing in the field renders direct observations impractical. We therefore adopted an indirect approach, combining field data with a complementary laboratory experiment.

In the field, we recorded a snapshot of the 'body condition' of a large number of spiders at the time of collection and examined how condition changed with colony demographics. We hypothesized that younger spiders benefit from feeding on prey captured by older spiders for the following reason: one unusual characteristic of *D. cancerides* social structure is the retention of older cohorts alongside younger cohorts within the colony (see Fig. 1 for instar sizes), and this heterogeneity in individual size could lead to an asymmetry in prey sharing. Predator size positively correlates with prey size in spiders, generally (Buskirk 1981), and also in *D. cancerides* (E. C. Yip, unpublished data). Therefore, older and larger spiders have access to a greater range of prey and would be expected to capture prey of greater size and more frequently than

younger and smaller spiders. This would lead to younger spiders disproportionately benefiting from prey sharing and adopting prey sharing as a 'scrounger' tactic (Giraldeau & Beauchamp 1999; Beauchamp 2006). Small spiders, because of their size and relatively low metabolic rate, probably consume a relatively small portion of large spiders' prey (Auletta & Rayor 2011). This hypothesis yields two predictions: (1) younger spiders should be heavier (have a better condition) in the presence of older siblings, and (2) older spiders should fare slightly worse or about the same in the presence of younger siblings.

Other hypotheses may also yield one or both of the above two predictions. A prey-rich habitat may promote both the production of multiple eggsacs (i.e. multiple cohorts) and an increase in overall condition, thereby leading to an association between condition and the presence of older siblings. Female fecundity may decrease over time so that younger cohorts have fewer individuals, which may lead to decreased competition within cohorts and therefore improved condition. Older siblings may preferentially cannibalize younger siblings in poor condition so that only young spiders in good condition remain. All these alternative hypotheses predict either a reduction in the size of younger cohorts or the overall improved foraging success of the entire colony. Therefore, if younger spiders are truly benefiting from prey shared by older siblings, two additional predictions must be satisfied to falsify these alternative hypotheses: (1) colony size should not correlate positively with spider condition, as this would indicate a prey-rich environment that would promote both the production of multiple cohorts (and greater colony size) and improved condition, and (2) young cohorts should contain roughly the same number of individuals, regardless of the presence of older siblings.

In the laboratory, we further tested whether young spiders benefit from prey shared by older siblings by examining how the presence of older siblings affects the change in body mass following feeding. We distinguished among three competing outcomes: (1) older spiders monopolize all or most prey; (2) spiders eat what they capture, essentially independent of siblings; or (3) older siblings

Figure 1. The size of *D. cancerides* instars. Average carapace width was calculated from 984 spiders collected from Canberra, Australia. They were assigned instars based on size differences among individuals and on our experience with laboratory animals. Note that all instars are concurrently represented in some colonies.

share prey too large for small spiders to capture with younger siblings. Of these, only the third outcome supports our hypothesis that younger spiders can benefit from prey shared by older siblings.

METHODS

Spider Collection and Measurement

We collected a total of 90 colonies, containing 2822 spiders, third instar and older, from 25 sites in and around Canberra, Australia and from one site near Oberon, New South Wales. An additional 10 adult females that had not yet reproduced were also collected. These females were only included in the analysis on the relationship between colony size and average colony condition (these data represented colony sizes of one). An additional 329 spiders escaped during collection; they were included only for purposes of calculating total colony size. *Delena cancerides* spiders emerge from the eggsac as second instars that do not feed. Non-feeding second-instar spiderlings were not included in our analyses. Entire colonies were collected from March 2006 to March 2010 in all months of the year except during the austral winter (May, June and July).

Spiders were measured immediately after collection, but due to large colony sizes the measurements occasionally took up to 3 days to complete. While measurements were taken, spiders were kept at room temperature without food or water. Spiders were kept in 45 or 120 ml plastic vials with at least four air holes poked in the top during the measuring process. We weighed spiders to the nearest 0.1 mg and used dial callipers to measure maximal carapace width to the nearest 0.1 mm. We noted whether spiders were missing legs, had recently regenerated smaller legs, were newly moulted, or were approaching a moult. As spiders become darker 1–3 days prior to moulting and remain pale for about 24 h afterward, we used the colour of the cuticle as an indicator of moult status. Eighteen spiders that died or may have cannibalized other spiders during collection were excluded from calculations involving condition; they were included in colony population size.

Comparing the Condition of Spiders with and without Siblings

The interval between clutches is typically such that siblings from subsequent clutches are two to three instars apart in development. We designated a given spider as having older or younger siblings if at least one other nonparental spider (i.e. excluding adult females) in the colony was at least two instars larger, in the case of an older sibling, or smaller, in the case of a younger sibling. A two-instar difference corresponded to a difference in carapace width of about 2 mm between juveniles (third to sixth instars), and about 4 mm between older juveniles and subadults (sixth to ninth instars) (see Fig. 1 for instar sizes).

We defined condition as the mass of a spider after controlling for carapace width, moult status, number of legs and regenerated legs, sex and the days until it was measured. We report condition as the ANCOVA adjusted mean mass, which is the predicted mass of a group at the average value of the covariates. We examined the correlation between condition and the presence of siblings using a mixed model ANCOVA with colony as a random effect to account for the nonindependence of spiders from the same colony. The response was the natural log of spider mass. The presence of younger siblings and the presence of older siblings were the fixed effects of primary interest, with log-transformed carapace width, moult status, number of legs and regenerated legs, sex and the days until measurement included as covariates to control for these effects on mass. Interactions among these variables were included if they explained a significant portion of the variance. We also

included the presence of the adult female and season (defined as the ordinal progression of months starting in August, the Austral spring) as covariates. The relationship between carapace width and mass was similar among all instars except for third instars, for which the slope was more shallow (multiple linear regression: instar (third) $\times$ carapace width: $t = -7.8$, $P < 0.0001$; Fig. 2). Therefore, instars were analysed separately. We excluded adult males from our analyses because we did not know whether adult males were adult sons (and therefore long-term residents of the colony) or immigrants (Yip et al. 2012). Altogether, we include 2597 spiders, from the third to the ninth instar, in this analysis. This analysis and all other analyses were conducted in JMP.

Here, we assume that mass is a correlate of fitness. Increased body mass is correlated with increased mating success in male spiders and with increased fecundity in female spiders (Vollrath 1987). The second deposition of yolk in the eggs is contingent on the adult female having adequate food supplies (Foelix 1996). In the present study, we were primarily concerned with immature spiders for which mass is critical to development and moulting time and adult size (Vollrath 1987; Jakob & Dingle 1990; Foelix 1996).

Testing Alternative Hypotheses

To determine whether condition correlates with total colony size, we examined the regression of mean condition within colonies to colony population size. To calculate the colonies' average conditions, we performed a multiple linear regression, with log-transformed spider mass as the response variable and log-transformed carapace width, moult status, number of legs and regenerated legs, sex, the days until measurement and season as explanatory variables. Because the relationship between mass and carapace width differs between third-instar spiderlings and other instars, we analysed instars separately. For each spider, we then summed the residual off its predicted mass with the average mass of all collected spiders to calculate each spider's 'adjusted mass'. We then averaged the 'adjusted mass' for all spiders within in each colony. This method is similar to averaging the 'residual index' of condition (Jakob et al. 1996), except instead of the global average

Figure 2. Relationship between the log transformations of spider mass and carapace width. The slope of the dotted line gives the regression line for third instars; the solid lines give the regression lines for all other instars.

value being zero, the global average is the mass of the average collected spider. This is also similar to using the ANCOVA adjusted mean mass of each colony, which gives the predicted response of a group at the mean values of the covariates, but this method accounts for possibly different allometry among instars.

To determine whether second cohorts are smaller than first cohorts, we compared the number of third and fourth instars in colonies with one cohort to colonies with multiple cohorts (third and fourth instars are too young to have younger siblings that feed). We compared the number of fifth instars in colonies with one cohort to colonies with multiple cohorts. Colonies in which fifth instars had younger siblings were removed from this analysis because we were only concerned with the presence of older cohorts and wished to remove the presence of younger cohorts as a possible confounding factor. Because transformations did not normalize the residuals, we used Wilcoxon (two-sample) tests to compare cohort sizes.

The Effects of Older Siblings on Condition in the Laboratory

We selected 20 laboratory colonies that had multiple cohorts of young. All colonies were descendants of spiders originally collected near Canberra, Australia and kept under laboratory conditions described in Yip et al. (2009). From each colony, we randomly selected three young juveniles (third–fifth instar), although spiders near a moult or that had recently moulted were excluded because these spiders typically do not feed. We randomly assigned each spider to one of three treatments: (1) solitary feeding; (2) feeding with a sibling of the same instar; (3) feeding with an older sibling (at least two instars larger). Each spider and its sibling (if appropriate) were placed in $7.5 \times 5.5 \times 5.5$ cm plastic containers. These containers were small because, in natural retreats, spiders typically rest in contact with each other (L. S. Rayor, E. C. Yip & D. M. Rowell, unpublished data). We weighed all spiders to the nearest 0.1 mg and measured their carapace to the nearest 0.1 mm. We supplied one prey item that could be captured by the young spider (*Drosophila melanogaster*, house flies, or house cricket nymphs depending on spider size) to each treatment. We attempted to standardize this small prey mass among treatments. In all but six trials, all individual prey masses were within 20% of the mean mass. In the remaining six trials, individual prey masses were within 40% of the mean mass. A post hoc analysis found no difference in prey mass among treatments (mean prey mass for single spiders = 9.8 mg; for spiders with same-instar siblings = 9.3 mg; for spiders with older siblings = 9.8 mg; ANOVA: $F_{2,59} = 0.015$, $P = 0.99$). In addition to these small prey items, one cricket, too large to be captured by the young spider (at least three times the younger spider's mass), was supplied to the treatment with an older sibling that could capture the prey item. No water was provided in any trial, so any mass gain could only be due to ingesting prey. All spiders were reweighed 24 h after the introduction of prey.

We tested for differences among treatments using a matched-pairs design comparing treatments within each colony. Within each colony we calculated the difference in mass change among the three treatments. To control for small differences in spider size, we also calculated the difference in carapace width among spiders in the three treatments. We then performed a simple linear regression of the difference in mass change by the difference in carapace width and tested whether the intercept was zero (i.e. when there was no difference in carapace width, was the difference between treatments significantly different from zero).

This design allowed us to generate predictions distinguishing among our three prey-sharing outcomes. (1) If older spiders are monopolizing the prey, we predicted that spiders kept with older siblings would have the poorest change in condition. (2) If spiders

eat what they capture independent of siblings, we expected the spiders with the older siblings to perform about as well as spiders with siblings of the same size, as spiders in both treatments would have about a 50% chance of capturing the only prey item small enough to capture. Under this hypothesis, we expected the solitary spider to perform the best because it had sole access to the prey item. (3) If spiders take prey captured by their older siblings, spiders with older siblings gain access to two prey items instead of one and therefore should outperform spiders with siblings of the same size. They may also outperform solitary spiders if sharing the large prey item more than compensates for any of the small prey item lost to the older sibling.

RESULTS

Colony Demographics

Demographics of the 90 colonies varied from 2 to 113 spiders. Colony age structure ranged from single females with third-instar spiderlings to subadults without an adult. Eight colonies lacked an adult female, and all eight of these colonies contained at least one subadult. Sixteen colonies had nearly every instar represented (six to seven instars out of seven feeding instars present). Forty-two colonies consisted of a single cohort of young; 48 colonies had two or more cohorts.

Comparing the Condition of Spiders with and without Siblings

Young spiders (fourth and fifth instars) were heavier in the presence of older siblings (Table 1). The ANCOVA adjusted mean mass of fourth instars with older siblings was 6.4 mg (17% of the average body mass of fourth instars) heavier than that of fourth

Table 1

Summary statistics for the mixed ANCOVA testing for correlations between mass and the presence of siblings, the presence of the mother and season applied to each instar and subadults

Instar	Fixed effect	Test statistic	Effect on mass	N	P
3rd	Older siblings	$F_{1,132.1}=1.9$	+0.029	711	0.17
	Younger siblings	NA	NA		NA
	Season	$F_{1,32.6}=22.8$	−0.054		<0.0001**
	Adult female	$F_{1,40}=5.8$	+0.13		0.021*
4th	Older siblings	$F_{1,90}=7.1$	+0.064	437	0.009**
	Younger siblings	NA	NA		NA
	Season	$F_{1,44.4}=11.8$	−0.040		0.0013**
	Adult female	$F_{1,56.1}=2.1$	−0.079		0.16
5th	Older siblings	$F_{1,336.4}=5.2$	+0.031	546	0.024*
	Younger siblings	$F_{1,292.8}=1.1$	−0.023		0.30
	Season	$F_{1,52.3}=12.8$	−0.038		0.0008**
	Adult female	$F_{1,59.4}=3.0$	−0.072		0.091
6th	Older siblings	$F_{1,70.3}=2.0$	+0.034	460	0.16
	Younger siblings	$F_{1,318.6}=0.77$	+0.013		0.38
	Season	$F_{1,48.8}=7.9$	−0.033		0.007**
	Adult female	$F_{1,60}=0.48$	−0.027		0.49
Subadult	Older siblings	$F_{1,424.3}=0.003$	+0.002	443	0.96
	Younger siblings	$F_{1,206}=0.14$	−0.007		0.70
	Season	$F_{1,38.3}=3.7$	−0.025		0.062
	Adult female	$F_{1,50.8}=0.02$	+0.005		0.88

Third and fourth instars were too young to have younger siblings, so this effect was not applicable (NA) for these instars. In addition to the fixed effects presented here, physiological covariates (ln carapace width, sex, number of legs and regenerated smaller legs, and moult status) were included in the model. Colony was included as a random effect to account for the nonindependence of spiders from the same colony.

* $P < 0.5$; ** $P < 0.01$.

instars without older siblings (Fig. 3). The ANCOVA adjusted mean mass of fifth instars with older siblings was 5.7 mg (7% of the average body mass of fifth instars) heavier than that of fifth instars without older siblings. Third instars with older siblings had an ANCOVA adjusted mean mass that was 1.0 mg (6% of the average body mass of a third instar) greater than those without, but the difference was not significant (Table 1). There was no correlation between condition and the presence of older siblings for older spiders or the presence of younger siblings for spiders of any age. As the season progressed from spring to winter, spider condition consistently declined, although the difference was not significant in subadults. The presence of the adult female was correlated with increased condition in third instars but not in any other instar (Table 1).

Tests for Alternative Hypotheses

There was no correlation between average condition of a colony and the number of spiders in the colony (linear regression: $R^2 = 0.004$, $t = 0.64$, $N = 100$, $P = 0.52$; Fig. 4). Younger cohorts contained about the same number of spiders, regardless of the presence of older cohorts. The numbers of third and fourth instars (instars that would only have older and not younger siblings) were similar between colonies with only one cohort and colonies with multiple cohorts (mean $\pm$ SE number of third instars: single cohort = 17.3 ± 3.8 ; multiple cohorts = 16.3 ± 2.8 ; mean $\pm$ SE number of fourth instars: single cohort = 10.7 ± 1.9 ; multiple cohorts = 6.4 ± 1.6 ; Wilcoxon two-sample test: third instars: $Z = 0.25$, $N = 45$, $P = 0.79$; fourth instars: $Z = 0.98$, $N = 57$, $P = 0.32$). The number of fifth instars was also similar between colonies with and without older cohorts (mean $\pm$ SE number of fifth instars: single cohort = 9.2 ± 2.0 ; with older cohorts = 10.0 ± 1.8 ; Wilcoxon two-sample test: $Z = -0.22$, $N = 54$, $P = 0.82$).

Figure 4. Average condition of spider colonies (including single adult females) in relation to the number of individuals in the colony. The solid line represents the regression line between average condition and colony size.

The Effects of Older Spiders on Condition in the Laboratory

Our laboratory experiment examined how prey sharing with and without older siblings impacted the change in spider mass after feeding, and the results supported the hypothesis that young spiders can benefit from prey shared by older siblings (Fig. 5). Young spiders commonly fed on prey captured by their older siblings, and in 6 of 20 trials, where young spiders were paired with an older sibling, the young spider gained more mass than the mass of the

Figure 3. Relationship between spider mass and presence of siblings by instar. Diamonds give the ANCOVA adjusted mean (the predicted mass of the group at the mean values of the covariates). Straight lines connect the means to indicate the differences between them. Box plots give the median and quartiles, calculated by applying the residuals to the ANCOVA adjusted mean. (a) Spiders without older siblings are shown in white box plots, and spiders with older siblings are shown in grey. (b) Spiders without younger siblings are shown in white box plots, and spiders with younger siblings are shown in grey. Significant differences between spiders with and without siblings were determined using a mixed model ANCOVA with colony as a random effect and season, presence of the mother and physiological variables (ln carapace width, sex, number of legs and regenerated smaller legs, and moult status) as covariates. The statistics are provided in Table 1. * $P < 0.05$; ** $P < 0.01$.

Figure 5. The change in mass of spiders after feeding in three laboratory treatments: (1) solitary feeding; (2) feeding with a similarly sized sibling; and (3) feeding with an older sibling. White box plots provide mass prior to feeding, and grey box plots provide mass after feeding. Diamonds give the ANCOVA adjusted mean (the predicted mass of the group at the mean value of the covariate). Straight lines connect the means to indicate the differences between them. Box plots give the median and quartiles, calculated by applying the residuals to the ANCOVA adjusted mean. The effects of treatments on mass gain were compared within colonies using matched-pairs analyses that controlled for differences in carapace width. * $P < 0.05$; ** $P < 0.01$.

small prey item provided, indicating that it fed extensively on the large prey item captured by the older sibling. The ANCOVA adjusted mean mass of spiders with older siblings improved by 6 mg after feeding. This was more than spiders feeding alone, which averaged an increase of 1.7 mg (linear regression between difference in mass change by difference in carapace width: intercept = 0.16, $t = 3.55$, $N = 20$, $P = 0.002$) and spiders feeding with siblings of the same age, which averaged an increase of 0.25 mg (linear regression between difference in mass change by difference in carapace width: intercept = 0.23, $t = 5.4$, $N = 20$, $P < 0.0001$). The condition of spiders feeding alone improved more than that of spiders feeding with siblings of the same age, but the difference was not significant (linear regression between difference in mass change by difference in carapace width: intercept = 0.04, $t = 1.4$, $N = 20$, $P = 0.17$).

DISCUSSION

We tested the importance of prey sharing indirectly by examining how the condition of spiders varied with the presence of siblings of different ages both in the field and under laboratory conditions. In the field, we found that young spiders (fourth to fifth instar) were heavier in the presence of older siblings. Older spiders gained no similar benefit from the presence of older siblings, nor did any spider benefit or suffer from the presence of younger siblings. These results satisfy both predictions of the hypothesis that young spiders benefit from older siblings sharing their prey, suggesting that even though prey sharing is rare, it provides a significant benefit for individuals that are less capable hunters and require only a relatively small amount of prey for sustenance. Our laboratory data further show that sharing prey in a confined space, similar to that of a bark retreat, can benefit small spiders because they gain access to large prey caught by older siblings.

We were unable to detect a significant effect of older siblings on third instars. This is a curious result, given that third instars are the youngest spiders that feed and would be expected to be the poorest

hunters because of their small size. This instar was also the only age for which the presence of the adult female was significantly correlated with greater mass (Table 1), and field observations have shown that the mother shares her prey with young offspring about 50% of the time (Yip & Rayor 2011). One hypothesis is that any benefit third instars might derive from older siblings is small compared to the benefit from the adult female and thereby undetectable with our methods. In support of this hypothesis, the effect size of the presence of the mother on the mass of third instars was quite large, over twice the size of the effects of older siblings or season for any instar (Table 1). One prediction of this hypothesis is that the presence of older siblings should have a strong effect on third instars in the absence of the adult female. However, we could not test this prediction with our data because orphaned third instars always had older siblings with them in the colony.

We further tested alternative hypotheses that might explain the association between good condition in young spiders and the presence of older siblings. None of these hypotheses was supported by the data. If environments exceptionally rich in prey are responsible for the association between heavier spiders and multiple cohorts, then all spiders in these environments should be heavier and colonies should be larger, as the adult female produces more eggsacs and fewer spiders die of starvation. Instead, improved condition was only found in the younger instars, and there was no association between colony size and condition. If either decreasing female fecundity or the preferential cannibalism of younger siblings in poor condition is responsible for the association between heavier spiders and the presence of older siblings, then we would expect subsequent cohorts to be smaller than first cohorts. Instead, subsequent cohorts were the same size as first cohorts.

Our results strongly support the conclusion that young spiders benefit from the presence of older siblings. The results of our laboratory experiment support prey sharing as the likely mechanism behind this benefit, as prey sharing in a confined space is common and large spiders do not monopolize prey. However, mechanisms other than directly sharing prey are also possible. Young spiders readily scavenge for bits of masticated prey and dropped limbs at the bottom of the retreat (E. C. Yip & L. S. Rayor, personal observation). The direct sharing of prey may therefore not be necessary for younger spiders to gain resources from older siblings.

Prey sharing is common to many social spiders and serves a variety of functions. Prey sharing allows for more efficient feeding, as each spider expends less digestive enzymes, and the combined enzymes break down the prey more quickly (Amir et al. 2000; Schneider & Bilde 2008; but see Ward & Enders 1985 for a decrease in feeding efficiency). Prey sharing is also a means by which the parental generation cares for the offspring (e.g. Evans 1998; Marques et al. 1998). While there are reports of larger (although not necessarily older) spiders sharing food with their smaller siblings (i.e. Marques et al. 1998), we provide the first evidence in spiders that, on average, older siblings improve the fitness of younger siblings. Whether *D. cancerides* is exceptional in this regard awaits further study on other species, but we note that many other social spiders produce a single clutch per female under field conditions, so that siblings sharing prey are roughly equal in size (Jacson & Joseph 1973; Schneider & Lubin 1997; Marques et al. 1998; Kim et al. 2005; Viera et al. 2007). *Delena cancerides* is unusual in that there is tremendous size variation within a single generation (Fig. 1), and this heterogeneity allows small spiders to benefit by scrounging off of their older siblings to a degree that would be impossible in the single-brood social spiders.

The benefits young spiders derive from their older siblings helps explain why spiders remain in groups even without an adult female. Yip & Rayor (2011) found that parental care provides the most important benefits for young spiders in the natal nest, and

Yip et al. (2012) found that young spiders (third–sixth instar) move into adjacent colonies rather than stay in their natal retreat after it has been abandoned by their mother. When young spiders do remain in their natal retreat without their mother, usually older siblings are present. All eight of the orphaned colonies collected in this study had at least one spider that was seventh-instar or older along with younger siblings. From the older spiders' perspective, allozyme analyses have shown that most offspring in the colony are full or half siblings (Yip et al. 2012), so older spiders gain some amount of inclusive fitness from the presence of younger siblings while suffering relatively little cost. Thus, even though prey sharing may be infrequent and difficult to observe in the field, it may help maintain group cohesion, particularly in the absence of the adult female.

Our results suggest that older spiders and their younger siblings conform to an asymmetrical producer–scrounger model (Giraldeau & Beauchamp 1999), where the payoff for each tactic varies with age. Similar age-dependent tactics have been found in some birds, where younger group members that are inefficient foragers adopt the scrounger role (Verbeek 1977; Steele & Hockey 1995; Goss-Custard et al. 1998). Goss-Custard et al. (1998) found that, as the season progressed, juvenile oyster catchers became better at foraging for mussels and their rate of scrounging declined. In this study, we did not track individuals over time. Interestingly, the age at which *D. cancerides* spiders no longer benefit from older siblings, demonstrated by our data here, coincides with the age at which spiders stop attempting to take prey captured by the mother (sixth instar and older; Yip & Rayor 2011). Presumably, if spiders could continue to benefit from taking prey captured by older spiders, then they would, suggesting that at this age a spider's resources are better spent as a producer.

It is not a general rule, however, that younger and less efficient feeders adopt the scrounger tactic. In some birds, older individuals scrounge from younger individuals (Burger & Gochfeld 1981), and generally, dominant individuals are expected to maximize their fitness by exploiting the food produced by subordinates (Barta & Giraldeau 1998). Large *D. cancerides* spiders probably do steal food from younger spiders occasionally, and we have observed such behaviour in the laboratory. However, two factors allow young spiders to be the predominant scroungers. One is, again, the dramatic size variation among siblings. It may simply be unprofitable for a 716 mg spider (the average mass of an eighth instar) to steal the small prey of a 37 mg spider (the average mass of a fourth instar), while the reverse is not true. The second factor may be that spiders, regardless of size or dominance, are poorly equipped to defend their kill. The chelicerae, and their associated venom glands, are a spider's primary weapons, and when they are engaged in feeding, a spider is largely helpless and must run from an aggressor or drop the prey. In a confined space, such as a bark retreat, spiders may be forced to share with siblings, and there is some evidence to suggest this is true. In field colonies, older spiders (primarily the adult female) share more often when more juveniles are present, and juveniles appear to overwhelm the capturing spiders' efforts to secure the prey (Yip & Rayor 2011).

We have thus far interpreted the relationship between young spiders and their older siblings as a producer–scrounger game. Because younger siblings obtain prey through their older siblings, this could be considered an example of incipient alloparental care, although we lack evidence that older siblings are actively feeding younger individuals, as in the cooperative breeding birds (Koenig et al. 1992; Hatchwell 2009). Prey sharing in *D. cancerides* is similar to 'tolerated theft' described in primate literature, in which one individual allows another to take a share of food (Blurton Jones 1984). It has been noted that there is little functional difference between tolerated theft and cooperation (Blurton Jones 1984),

demonstrating that the line between exploitation and cooperation can be fine. In other social spiders, it is often the case that more spiders feed on a prey item than attempt to capture it (e.g. Ward 1986; Kim et al. 2005), so some spiders benefit from the cooperation of others while avoiding its costs. In this case, the difference between cooperation and exploitation may change depending on when spiders arrive at the site of prey capture: early arrivals aid the attack and late arrivals feed on the spoils (Kim et al. 2005). 'Cheating' such as this is thought to threaten the stability of cooperative societies; however, the destabilizing effects of cheating are mitigated if the participants are related (Sachs et al. 2004). In *D. cancerides*, relatives may compete over individual prey items, but, on average, interactions over prey act as cooperation for young spiders that benefit from older siblings. In addition, we did not detect a cost of competition for older siblings, suggesting that if there is a cost to sharing prey with younger siblings, it is relatively small. Therefore, the producer–scrounger system, which might be exploitative in one context, can be cooperative and a benefit to group living in a context where the benefits of feeding a relative outweigh the costs.

Acknowledgments

Funding was provided by the Australian–American Fulbright Commission and the National Science Foundation's Graduate Research Fellowship to ECY, and by the President's Council on Cornell Women (PCCW) to LSR. We thank Dr David Rowell for graciously sharing his knowledge and laboratory facilities at the Australian National University. We thank Drs Andrea Leigh and Adrienne Nicotra, Australian National University, for lending their laboratory facilities for weighing spiders, and we thank the thoughtful comments of three anonymous referees.

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