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Preferential prey sharing among kin not found in the social huntsman spider, *Delena cancerides* (Araneae: Sparassidae)

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Abstract. Although the benefits of group foraging are important for evolution of sociality in spiders, the factors that influence group-level benefits of prey sharing in social spiders are still poorly understood. In the unusual transitional social spider *Delena cancerides* Walckenaer 1837 (Sparassidae), prey sharing almost certainly occurs occasionally among non-kin in the wild, and so we tested the effects of kin relationships and familiarity on the amount of prey consumed in this species. To determine whether the amount of prey sharing increased with relatedness or with familiarity, we fed treatment groups containing spiderlings of varying relatedness and familiarity a single prey item and measured the amount of weight gained by sharing groups. We found no effect of relatedness or familiarity on the amount of prey consumed by prey-sharing groups of *D. cancerides*. Increased duration of sharing, number and age of the spiders involved, and size of the prey item all increased the amount of prey consumed. The benefits of prey sharing in this species likely overwhelm any possible inclusive fitness benefits derived from kin discrimination in this highly outbred social spider. Hence, we reject the hypothesis that groups of kin consumed proportionately larger amounts of prey biomass than groups of non-kin, as proposed by Schneider and Bilde in 2008 with *Stegodyphus lineatus* Latreille 1817 (Eresidae).

Keywords: Cooperative foraging, kin recognition, social spiders, group-living, nutrition

Benefits of cooperative foraging have been proposed to be the driving force behind the evolution of social behavior in a diverse array of animals, from wild canids to predatory hemipterans (Travers 1993; Creel & Creel 1995; Krause & Ruxton 2002). Cooperative hunting allows the capture of prey too large for solitary individuals to handle, and prey sharing leads to increased foraging success and higher fitness for group-living individuals, although the average amount of food that an individual consumes during each predation event might be smaller (Clark & Mangel 1986; Caraco et al. 1995). Similar group foraging benefits are thought to be one of the major advantages of group living in social spiders (Araneae) (Buskirk 1981; Rypstra & Tirey 1991; Whitehouse & Lubin 2005; Lubin & Bilde 2007). However, many questions remain about the effects of group composition on the extent of prey sharing within groups.

Schneider and Bilde (2008) found that in the subsocial spider *Stegodyphus lineatus* Latreille 1817 (Eresidae), groups of close kin share more prey biomass with each other than groups of non-kin, regardless of the familiarity of individuals in the group. The authors hypothesized that individual spiders could preferentially decrease the amount of digestive enzymes they would inject into a prey item when sharing with non-relatives, which would explain the observed patterns. Previous work had shown that *S. lineatus* respond differentially to kin by increased cannibalism of non-kin under food stress (Bilde & Lubin 2001), but Schneider and Bilde (2008) were the first to indicate that the quantity of prey shared in groups was influenced by kin recognition.

However, unrelated *S. lineatus* spiderlings do not share prey naturally. This species is only known to share prey with siblings during the first 30 days following hatching, after which the spiders disperse during the fifth instar and apparently do not forage communally again (Schneider 1995; Schneider & Lubin 1997). When dispersing, *S. lineatus* display a high level of philopatry, and individuals from different natal groups tend to disperse in opposite directions in a given microhabitat (Lubin et al. 1998). Therefore, it is unlikely that *S. lineatus* juveniles would ever be in a situation where they would potentially share prey items with unrelated or unfamiliar conspecifics. Similarly, prey sharing among unrelated conspecifics is unlikely in highly social cooperative spiders exhibiting low rates of immigration and high levels of inbreeding (Avilés 1997; Lubin & Bilde 2007).

Like *S. lineatus*, the social spider *Delena cancerides* Walckenaer 1837 (Sparassidae) is known to be capable of kin recognition (Beavis et al. 2007; Yip et al. 2009). However, in contrast to *S. lineatus*, it is probable that immature *D. cancerides* occasionally share prey items with non-kin in the field. Thus, in the present study, we set out to determine whether different amounts of prey biomass are shared by groups of *D. cancerides* depending on the relatedness and familiarity of all of the individuals in the group.

Delena cancerides is an unusual transitional social spider from Australia that shares subsocial and cooperative spider traits (L.S. Rayor unpubl. data). Individuals of this species live in kin-based groups of up to 300 individuals under the exfoliating bark of dead trees, and these groups typically consist of one adult female and one to four cohorts of immature offspring (Rowell & Avilés 1995; L.S. Rayor unpubl. data).

Delena cancerides populations are patchily distributed and in habitats where there are multiple suitable trees for retreats, such that *D. cancerides* colonies are frequently found on

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neighboring trees (L.S. Rayor unpubl. data). As the spiders forage for prey outside their retreat, sometimes traveling as much as 5–10 m before returning to the retreat in the morning (Yip & Rayor 2011), young spiders occasionally return to the incorrect retreat (Yip and Rayor 2011). Although initial studies on the species indicated that *D. cancerides* were highly aggressive towards conspecifics from other colonies (Rowell & Avilés 1995), more recent studies (Beavis et al. 2007; Yip et al. 2009) demonstrated that younger individuals below a certain size threshold ($<$ seventh instar) were readily accepted into alien colonies without overt aggression. These findings suggest that individuals in any one colony have a reasonable probability of encountering juveniles from other, unrelated colonies and potentially sharing prey with them.

Among juvenile spiders, prey sharing occurs in approximately 30% of all feeding events in the laboratory (L.S. Rayor unpubl. data), although it is less frequent in the field when individuals forage away from the retreat (Yip & Rayor 2011). Young spiders, especially, benefit (in the form of increased growth) from prey sharing at the retreat due to the presence of older siblings, which can capture larger prey items (E.C. Yip unpubl. data).

In this study, we tested whether Schneider and Bilde's (2008) finding that both groups of familiar and unfamiliar kin consume more biomass while sharing prey than groups of non-kin could be extended to a spider species in which this behavior actually occurs. To test this hypothesis, we examined the total ingested biomass of prey items in groups of related and unrelated individuals. To examine the effects of familiarity independent of relatedness, we repeated the experiments with groups of unfamiliar-related and familiar-unrelated spiders. We predicted that if Schneider and Bilde's (2008) results would also apply to *D. cancerides*, the spiders would share more prey biomass in groups of related individuals than they would in groups of unrelated individuals.

METHODS

Study organisms.—We reared the specimens of *Delena cancerides* used in this experiment in the laboratory from July–December 2009. They were descendants of wild individuals originally collected in 2006 and 2008 from sites in southeastern Australia. Because this species is highly outbred (Rowell & Avilés 1995; Gruetzner et al. 2006), we kept detailed long-term records of the origins and all cross-breeding events for each colony in order to maintain outbreeding. The spiders live for $\sim$ 2.5 yr and do not reach sexual maturity until $\sim$ 1 yr, so the spiderlings used from 2008 wild-caught spiders were only the F_1 generation in the laboratory, while spiderlings from parents collected in 2006 were $\sim$ F_3 generation. We housed laboratory colonies of spiders in 9.5 and 19-l terraria with sheets of clear plexiglass "bark" affixed $\sim$ 2 cm from the glass to emulate their natural retreat structure. Prey items included adult flesh flies (*Neobellieria bullata* Diptera: Sarcophagidae), common house crickets (*Acheta domesticus* Orthoptera: Gryllidae) and large house flies (*Musca domestica* Diptera: Muscidae).

Group benefits of prey sharing relative to relatedness and familiarity.—Our methodology closely follows that used by Schneider and Bilde (2008) in examining the effects of relatedness and familiarity on sharing in *Stegodyphus lineatus*. Spiders digest their food externally by secreting digestive enzymes into the body of the prey item and then imbibing the liquefied remains (Foelix 2011). Since the spiders leave behind the indigestible parts of prey items, the amount of biomass that spiders ingest from their prey can be measured by recording the weight of the prey item before and after it is fed on by a group of spiders (Tso & Severinghaus 1998).

To assess the possible differential benefits for prey-sharing groups of different relationships and levels of familiarity, we randomly assigned individuals from 19 laboratory source colonies to four experimental treatments:

- Related Familiar (RF) = spiders that were full siblings from a single clutch and that had been reared together in the same cage since birth.
- Related Unfamiliar (RU) = spiders that were also full siblings from a single clutch but that had been separated from the natal colony immediately after they had emerged from the egg sac (at the second instar) and raised in isolation until they were reintroduced to each other directly before the experiments began as fourth instar spiderlings.
- Unrelated Familiar (UF) = spiders that were 100% unrelated to all other spiders in the same group, but which had been separated from their natal colonies immediately after they had emerged from the egg sac and reared together.
- Unrelated Unfamiliar (UU) = spiders that were also 100% unrelated to all other spiders in the group and that were only introduced to each other directly before the experiments began.

Each group consisted of six individual spiders, which were housed in $10 \times 10 \times 13$ cm plastic cages. Due to instances of individual mortality, some groups were reduced to five individuals. Prior to group formation we weighed each spider and minimized initial size differences between the spiders in each group by purposefully forming groups of spiders with similar body weights. We performed the prey-sharing experiments when the spiders reached the fourth instar and continued until the spiders reached the seventh instar, at which point we determined them to be too large for the experiment.

Several minutes prior to each experimental trial, we anesthetized the spiders in each group with CO_2, and measured the total mass of the entire group of pre-feeding spiders to the nearest 0.0001 g using a Mettler Toledo AG285 electronic scale. After several minutes, when the spiders began to recover from anesthesia, we weighed a single prey item (either a fly or cricket) and placed it into each group. Prey type was determined by spider size, as smaller spiders (fourth and fifth instars) captured house flies most readily. Larger instars (fifth-seventh instars) were given sarcophagid flies or crickets, depending on availability.

Once the spiders had successfully captured the prey item, we recorded the number of spiders sharing it every 10 min for 2 h. During each observation, we also noted the behavior of the spiders and recorded any solicitations for prey sharing or attempts to pull away from a sharing group. We recorded groups as not having eaten during a trial if the spiders did not successfully capture the prey item within two hours, and we discarded these trials. After the 2-h observation period following successful prey capture, we separated any spiders that were still feeding from the prey, and recorded both the combined post-feeding weight of the entire group and the remains of the prey item.

We repeated these trials every several days over 20 wk, for a total of 138 replicates from 18 groups in the RF treatment, 11 replicates from three groups in the RU treatment, 44 replicates from seven groups in the UF treatment and 37 replicates from nine different groups in the UU treatment. To increase our sample sizes, we used individual groups within each treatment for multiple trials: RF groups were used a mean of 2.88 times, RU groups a mean of 3.67 times, UF groups a mean of 8.80 times and UU groups a mean of 4.27 times. After the end of the experiment, we calculated the percentage of trials in each treatment during which prey sharing occurred. In between feeding trials, we fed the groups with small house flies once per week in order to keep all spiders properly nourished.

To determine whether kinship or familiarity affected the amount of prey consumed in prey sharing events, we used a series of mixed linear models to analyze the effect of treatment (RF, RU, UF, or UU) and other parameters, including initial prey weight and mean spider instar of all spiders involved in feeding on the change in mass of each group of spiders. In these models, group ID was coded as a random effect variable in order to account for repeated measurements of the same groups, and treatment type, initial prey weight, and mean spider instar were coded as fixed effects. To quantify the amount of sharing that occurred in each trial we calculated a "sharing metric" for each successful trial that reflected both the number of spiders that shared the prey item and the duration of prey sharing that occurred by totaling the number of spiders sharing during each ten-minute interval. For example, if three spiders shared prey for 50 min and then a fourth joined to share for 20 min, the sharing metric would be $(3 \times 5) + (4 \times 2) = 23$. This sharing metric we encoded as a fixed effect in the model for groups in which there was prey sharing. The response in all models was the change in weight of the spider group, to which we applied a square-root transformation in order to homogenize variances. We also incorporated prey type (flies or crickets) into the original model in order to confirm that it had no significant effect on the weight change of the spiders. We examined the correlation between the change in weight of the spider group and the change in weight of the prey item using a linear regression. All statistical analyses were performed in JMP 8.0.

RESULTS

Group benefits of prey sharing relative to relatedness and familiarity.—The levels of relatedness and familiarity among spiders in a prey-sharing group did not significantly influence the amount of prey biomass ingested by members of the group. Although the linear mixed model applied to the data for groups in which prey sharing occurred was a good fit for these data ($R^2 = 0.7314$, $P < 0.001$), this model showed no significant effect of treatment on the weight gained by sharing groups (treatment effect, Table 1). Groups of older spiders consumed more prey than groups of younger individuals (mean spider instar effect, Table 1), groups consumed more prey when the prey item was larger (initial prey weight effect, Table 1) and older spiders could handle larger prey items. Greater prey biomass was also consumed when more spiders shared prey or when sharing events lasted longer, the two factors included in the "sharing metric" (sharing metric effect, Table 1).

Table 1.—Results of the linear mixed model that incorporates all trials in which prey sharing occurred. The measured change in spider weight was used as the response variable, and treatment type, mean spider instar, initial prey item weight, and the calculated "sharing metric" were used as fixed effects. All factors, with the exception of treatment type, were found to have significant effects on the amount of weight gained by spider groups. Asterisks (***) indicate significant *P*-values.

Factor	*df*	*F*	*P*	*N*
Treatment	12	2.55	0.1053	136
Mean spider instar	123	26.86	< 0.001***	136
Initial prey weight	122	97.50	< 0.0001***	136
Sharing metric	122	17.64	< 0.0001***	136

There was no significant difference between weight gained by groups of six spiders and groups of five spiders ($F_{1,45} = 0.18$, $n = 136$, $P = 0.6736$). Nor was there a difference between weight gained by groups feeding on crickets or flies of comparable size ($F_{1,24} = 1.3371$, $n = 34$, $P = 0.2590$). The weight lost by the prey was directly correlated with weight gained by the spiders ($F_{1,136} = 1563$, $n = 136$, $P < 0.0001$, $R^2 = 0.92$), with prey losing more weight (mean $= -0.0569$ g, $n = 136$) than was gained by the spiders (mean $= 0.0339$ g, $n = 136$).

Prey sharing only occurred in 50.2% of all trials, and in the trials for which prey sharing occurred, in 26.8% the sharing was for relatively brief periods (≤ 20 min). To minimize the effect of trials in which minimal prey sharing occurred, we reanalyzed the data including only those trials in which the prey item was shared for ≥ 20 min. The new model ($R^2 = 0.75$) shows that spiders still did not share more with kin or familiar individuals (treatment effect, Table 2); rather, spiders consumed more prey when the prey item was larger (initial prey weight effect, Table 2), and older spiders consumed more prey (mean spider instar effect, Table 2). However, there was no difference in the prey biomass consumed associated with duration or the number of spiders sharing (sharing metric effect, Table 2) in this analysis.

Given that spider instar had an effect on the amount of prey consumed by sharing groups, we also examined whether the amount of sharing (measured by mean sharing metric) differed relative to treatment group by instar. When the mean age of individuals in a group was fifth instar, we found that RF groups shared prey for longer and in larger groups than UF groups, while there were no significant differences between any other treatments (Tukey Kramer HSD test, $n = 34$, all $P > 0.07$). By the time the mean age of the spiders in a group was sixth instar, related spiders did not share more than unrelated spiders, nor did familiar spiders share more than unfamiliar spiders (Tukey-Kramer HSD test, $n = 100$, all $P > 0.22$; Figure 1A).

Although there was no significant effect of treatment type on the amount of biomass consumed in any of the analyses, we calculated the frequency of sharing separately to determine whether kin groups shared more often and found no consistent effect: prey sharing occurred nearly 20% more frequently in RU and UF groups than in RF and UU groups (Figure 1B).

Table 2.—Results of the linear mixed model that excludes all instances of low-duration prey sharing (defined as < 20 min). The measured change in spider weight was used as the response variable, and treatment type, mean spider instar, initial prey item weight, and the calculated "sharing metric" were used as fixed effects. Only the mean instar of spiders within the group and the initial weight of the prey item were found to have significant effects on the amount of weight gained by spider groups. Asterisks (***) indicate significant *P*-values.

Factor	*df*	*F*	*P*	*n*
Treatment	10	1.57	0.2567	87
Mean spider instar	78	18.27	< 0.0001***	87
Initial prey weight	77	87.70	< 0.0001***	87
Sharing metric	78	1.31	0.2560	87

When we excluded spiders in the RU treatment from the data analysis (on the basis that the relatively small sample size collected for this treatment was too small to draw reliable conclusions) and ran the model again, treatment type also had a significant effect ($F_{2,16} = 4.78$, $n = 127$, $P = 0.0247$, overall model $R^2 = 0.72$), with UF groups consuming more prey than RF or UU groups ($t = 3.03$, $df = 13$, $P = 0.0103$).

DISCUSSION

Spiders that share prey with unrelated individuals would be expected to experience the same direct benefits of prey sharing as those individuals that share prey with genetic relatives in the form of direct consumption of food. However, individuals that share prey with kin might additionally gain inclusive fitness benefits such as the increased production of digestive enzymes in kin groups suggested by Schneider and Bilde (2008). Given that the biology of *D. cancerides* is such that there is some level of interaction between non-kin young in the wild, we hypothesized that there would be more prey consumed in kin-only groups due to greater indirect fitness benefits. However, our results do not support this hypothesis. Rather, our data indicate that the overall benefits of prey sharing to young *D. cancerides* are so substantial that the benefits derived from discriminating preferentially against non-kin in a prey sharing event to increase potential inclusive fitness benefits is not productive.

The general benefits of prey sharing include an increased frequency of feeding and access to larger prey items (Buskirk 1981; Rypstra & Tirey 1991; Whitehouse & Lubin 2005; Yip et al. 2008). Recent field studies have shown that younger *D. cancerides* are in better condition when they have older siblings that capture and share larger prey items (E.C. Yip, unpubl. data). Additionally, *D. cancerides* has an exceptionally low metabolic rate, resulting in low foraging requirements (Gilbert et al. unpubl. data): prey sharing with any partners may provide a substantial contribution to their overall nutrition.

A major difference between the two species that might influence prey-sharing patterns is the extent of their social behavior: *Delena cancerides* is a significantly more social species than *S. lineatus*. *Delena cancerides* colonies have multiple cohorts of siblings living together for approximately 10–12 mo until individuals reach sexually maturity, after which individual females establish their own colonies (L.S. Rayor et al., unpubl. data). In contrast, *S. lineatus* siblings only live together for ~30 days before dispersing, after which they live solitarily, and individual females have single clutches prior to matriphagy (Schneider 1995; Schneider and Lubin 1997). Furthermore, although the majority of prey-sharing behaviors observed in *D. cancerides* are between younger individuals (fourth-sixth instars), individuals continue to share prey throughout their lifetimes (L.S. Rayor unpubl. data), whereas *S. lineatus* feed communally only as juveniles prior to dispersal (Schneider 1995). There may be greater inclusive fitness pay-offs for subsocial species to discriminate kin than

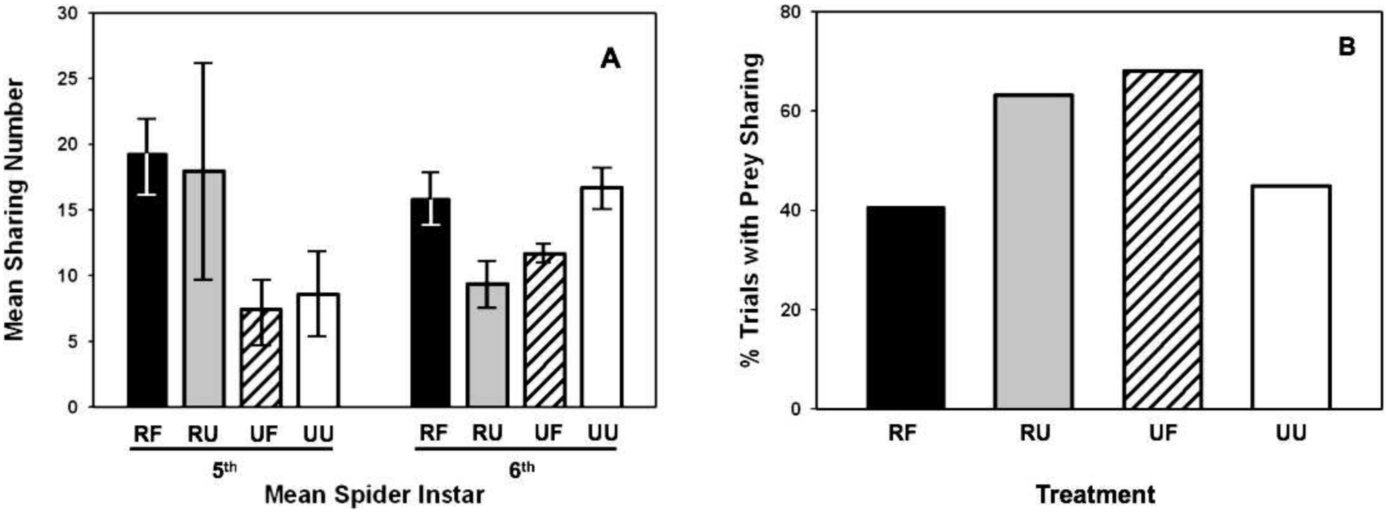

Figure 1.—A. The variation among treatment groups in the mean sharing metric (= composite measure of number of individuals sharing and duration of sharing) observed in trials where prey was shared, as a function of the mean instar of all spiders in the group. When the spiders were younger (fifth instar), the RF and RU treatment groups shared more prey than the other groups. By the sixth instar, when individuals were more familiar with each other in all treatments, sharing did not differ. B. The percentage of trials in which prey sharing occurred in each of the four treatments. Sharing patterns are unrelated to kin or familiarity. In 50.2% of all trials, the prey item was consumed entirely by a single individual without any sharing.

for more social species that likely experience more long-term payoffs from tolerant behaviors, including the willingness to share prey.

Differences in outbreeding may also influence the ability of the two species to identify non-kin during prey sharing events. *Stegodyphus lineatus* displays a significant degree of inbreeding tolerance in the laboratory, as females did not discriminate against related males in breeding experiments and offspring produced from such pairings did not differ from outbred offspring in fecundity and survivorship (Bilde et al. 2005). Some degree of inbreeding likely occurs in the field, as $\sim 50\%$ of adult males recovered in field observations mated within their natal patches (Bilde et al. 2005). Because related individuals in these populations may share a relatively large amount of genetic material, *S. lineatus* may be better able to detect kin through self-phenotype matching.

The high levels of outbreeding in *D. cancerides* might make this type of kin-recognition harder, as there are often high levels of genetic (and therefore phenotypic) polymorphism within populations (Rowell 1990; Gruetzner et al. 2006). Although it has been shown that *D. cancerides* can differentiate between nestmates and non-nestmates (Beavis et al. 2007; Yip et al. 2009), possibly based on chemical signals from the nest itself, this process might require a relatively large number of complex cues. At the age of the spiders used in the study, *D. cancerides* may not have produced sufficient markers for recognition cues. Our only indication of kin preference is that there was a non-significant trend toward a higher sharing metric among kin during the fifth instar, which disappeared by the sixth instar when the spiders were more familiar with one another. Future research that incorporates these possible mechanisms for nestmate recognition may help explain the patterns observed in the present study.

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LITERATURE CITED

Avilés, L. 1997. Causes and consequences of cooperation and permanent-sociality in spiders. Pp. 476–498. *In* The Evolution of Social Behavior in Insects and Arachnids. (J.C. Choe & B.J. Crespi, eds.). Cambridge University Press, Cambridge, UK.

Beavis, A.S., D.M. Rowell & T. Evans. 2007. Cannibalism and kin recognition in *Delena cancerides* (Araneae: Sparassidae), a social huntsman spider. Journal of Zoology 271:233–237.

Bilde, T. & Y. Lubin. 2001. Kin recognition and cannibalism in a subsocial spider. Journal of Evolutionary Biology 14:959–966.

Bilde, T., Y. Lubin, D. Smith, J.M. Schneider & A.A. Maklakov. 2005. The transition to social inbred mating systems in spiders: role of inbreeding tolerance in a subsocial predecessor. Evolution 59:160–174.

Buskirk, R.E. 1981. Sociality in the Arachnida. Pp. 281–367. *In* Social Insects, Volume II. (H.R. Hermann, ed.). Academic Press, London.

Caraco, T., G.W. Uetz, R.G. Gillespie & L.A. Giraldeau. 1995. Resource consumption variance within and among individuals: on coloniality in spiders. Ecology 76:196–205.

Clark, C.W. & M. Mangel. 1986. The evolutionary advantages of group foraging. Theoretical Population Biology 30:45–75.

Creel, S. & N.M. Creel. 1995. Communal hunting and pack size in African wild dogs, *Lycaon pictus.* Animal Behaviour 50:1325–1339.

Foelix, R.F. 2011. Biology of Spiders. Oxford University Press, New York.

Gruetzner, F., T. Ashley, D. Rowell & J. Graves. 2006. How did the platypus get its sex chromosome chain? A comparison of meiotic multiples and sex chromosomes in plants and animals. Chromosoma 115:75–88.

Krause, J. & G.D. Ruxton. 2002. Living in Groups. Oxford University Press, Oxford, UK.

Lubin, Y. & T. Bilde. 2007. The evolution of sociality in spiders. Advances in the Study of Behavior 37:83–144.

Lubin, Y., J. Hennicke & J. Schneider. 1998. Settling decisions of dispersing *Stegodyphus lineatus* (Eresidae) young. Israel Journal of Zoology 44:217–225.

Rowell, D.M. 1990. Fixed fusion heterozygosity in *Delena cancerides* Walck. (Araneae: Sparassidae): an alternative to speciation by monobrachial fusion. Genetica 80:139–157.

Rowell, D.M. & L. Avilés. 1995. Sociality in a bark-dwelling huntsman spider from Australia, *Delena cancerides* Walckenaer (Araneae: Sparassidae). Insectes Sociaux 42:287–302.

Rypstra, A.L. & R.S. Tirey. 1991. Prey size, prey perishability and group foraging in a social spider. Oecologia 86:25–30.

Schneider, J.M. 1995. Survival and growth in groups of a subsocial spider (*Stegodyphus lineatus*). Insectes Sociaux 42:237–248.

Schneider, J.M. & T. Bilde. 2008. Benefits of cooperation with genetic kin in a subsocial spider. Proceedings of the National Academy of Sciences USA 105:10843–10846.

Schneider, J.M. & Y. Lubin. 1997. Does high adult mortality explain semelparity in the spider *Stegodyphus lineatus* (Eresidae)? Oikos 79:92–100.

Travers, S.E. 1993. Group foraging facilitates food finding in a semi-aquatic hemipteran, *Microvelia austrina* Bueno (Hemiptera: Veliidae). Pan-Pacific Entomologist 69:117–121.

Tso, I.M. & L.L. Severinghaus. 1998. Ingested biomass of prey as a more accurate estimator of foraging intake by spider predators. Journal of Arachnology 26:405–407.

Whitehouse, M.E.A. & Y. Lubin. 2005. The functions of societies and the evolution of group living: spider societies as a test case. Biological Reviews 80:347–361.

Yip, E.C., S. Clarke & L.S. Rayor. 2009. Aliens among us: nestmate recognition in the social huntsman spider, *Delena cancerides*. Insectes Sociaux 56:223–231.

Yip, E.C., K.S. Powers & L. Avilés. 2008. Cooperative capture of large prey solves scaling challenge faced by spider societies. Proceedings of the National Academy of Sciences USA 105: 11818–11822.

Yip, E.C. & L.S. Rayor. 2011. Do social spiders cooperate in predator defense and foraging without a web? Behavioral Ecology and Sociobiology in press.

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