Kin recognition and cannibalism in a subsocial spider

T. BILDE & Y. LUBIN

Mitrani Department of Desert Ecology, Blaustein Institute for Desert Research, Ben Gurion University, Sede Boqer Campus, Israel

Abstract

Evolution of cooperation and group living in spiders from subsocial family groups may be constrained by their cannibalistic nature. A tendency to avoid cannibalizing kin may facilitate tolerance among spiders and implies the ability to identify relatives. We investigated whether the subsocial spider *Stegodyphus lineatus* discriminates kin by recording cannibalism among juveniles in experiments during which amount of food and size difference among spiders in groups were varied. We hypothesized that family groups should be less cannibalistic than groups of mixed-parental origin. Further, we tested whether food-stress would influence cannibalism rates differently in kin and nonkin groups and the effect of relatedness on cannibalism within groups of spiders of variable size compared with those of homogenous size. In groups of six spiders, more spiders were cannibalized in nonsib groups than in sib groups under low food conditions. A tendency for nonkin biased cannibalism in starved spider pairs supported that kin recognition in *S. lineatus* is expressed when food is limited. Size variance of individuals within well-fed groups of siblings and unrelated spiders had no influence on cannibalism rates. Apparently, both hunger and high density are important promoters of cannibalism. In addition to inclusive fitness benefits, we suggest that an ability to avoid cannibalizing kin will favour the evolution of cooperation and group living in phylogenetically pre-adapted solitary species.

Introduction

Social group living in spiders involving shared web and cooperative behaviour is found in fewer than 20 of more than 37 000 described species. Although sociality in spiders is rare, it has evolved independently 12 times in seven families (Avilés, 1997). Why then, are there so few social spiders? Cooperative group living appears to originate from family groups through extended maternal care and delayed dispersal of juveniles, referred to as the subsocial route, and is found exclusively in families where subsocial behaviour and maternal care is widespread (Avilés, 1997). Evolution of permanent sociality via the subsocial route requires prolonged association

Correspondence: Trine Bilde, Mitrani Department of Desert Ecology, Blaustein Institute for Desert Research, Ben Gurion University, Sede Boqer Campus, 84990 Israel.
Tel.: +972 8 6596776; fax: +972 8 6596772;
e-mail: tbilde@bgumail.bgu.ac.il

and continued tolerance among offspring, cooperative behaviour and philopatry. Based on Schneider (1995), we define tolerance as lack of aggression between individuals in competitive situations, for example when animals must share limited resources. Mutual tolerance may be the first requirement for the transition from solitary to social living to occur (Kullmann, 1972; Krafft, 1982; D'Andrea, 1987). Tolerance expressed within a taxon of animals that are otherwise asocial and commonly cannibalistic results in 'the paradox of predatory spiders living in communities' (Buskirk, 1981).

Spiders are well known for their cannibalistic tendencies in both sexual (Elgar, 1992) and nonsexual contexts (e.g. Wagner & Wise, 1996). Cannibalism may serve as a means of foraging when other prey is scarce (Fox, 1975; Polis, 1981; Evans, 1999). In social groups, cannibalism may reduce competition among individuals and play a significant role in the regulation of population densities (Elgar & Crespi, 1992; Wagner & Wise, 1996).

Food availability is potentially the single most important ecological factor influencing the occurrence of cannibalism (Dong & Polis, 1992). Food shortage affects the foraging behaviour and condition of animals and promotes cannibalism. On a short time scale, hunger increases foraging activity and lowers the attack threshold, whereas prolonged periods of food stress may weaken the animal and make it more vulnerable to cannibalism. The outcome of a contest between conspecifics depends on the attack propensity of the predator and the vulnerability of the potential prey individual (Dong & Polis, 1992). Size difference is a significant factor that will determine prey vulnerability, as victims of cannibalism are almost invariably smaller than the cannibal (Polis, 1981; Samu *et al.*, 1999). The risk of retaliation increases as the size difference between rivals decreases and thus the attack propensity of the predator may depend on its ability to assess an opponent's size (Samu *et al.*, 1999). The hunger state of the animal influences its assessment of risk and potential cannibals are likely to be more risk prone with increasing hunger (Samu *et al.*, 1999).

The apparent benefit of enhancing the fitness of the cannibal and reducing competition when prey is scarce should be balanced against possible costs. Loss of inclusive fitness as a result of killing and consuming a relative is one potential cost of cannibalism. Consequently, cannibalism of nonkin should be selected for when it is simply a means of food acquisition (Elgar & Crespi, 1992; Pfennig, 1997; Joseph *et al.*, 1999). Subsocial spiders are often found in clusters in close vicinity of the maternal nest (Avilés & Gelsey, 1998; Johannesen *et al.*, 1998; Lubin *et al.*, 1998). This makes frequent encounters with both related and unrelated conspecifics likely and should select for kin recognition to avoid cannibalism of relatives. In the transition from subsocial to permanent social group structure, competition for resources that leads to aggressive interactions among siblings may occur. Avoidance of cannibalism within family groups would lead to increased tolerance, which could facilitate prolonged association and cooperative behaviour.

Inclusive fitness theory predicts the ability of animals to identify relatives (Hamilton, 1964, 1987; Hepper, 1986), although the existence of kin recognition *per se* does not necessarily imply kin-selection (Grafen, 1990; Fellowes, 1998). Kin discrimination is found widely throughout the animal kingdom, mainly in social family-based groups (Fletcher & Michener, 1987; Pfennig, 1997; Fellowes, 1998; Evans, 1999). In this study, we investigated experimentally the ability of a subsocial species to recognize kin by measuring cannibalism rates in groups of kin and nonkin. We predicted that individuals in family groups would be less cannibalistic than those in groups of mixed-parental origin. We tested this hypothesis in the subsocial spider *Stegodyphus lineatus*, which belongs to a genus

(*Stegodyphus*) that includes three social and 14 subsocial species. We tested (1) whether cannibalism rates are lower in kin-groups compared with nonkin groups, (2) whether food-stress influenced cannibalism rates differently in kin and nonkin groups and (3) the effect of relatedness on cannibalism within groups of variable-size spiders compared with those of homogenous size individuals.

Materials and methods

Study species

Subsocial *Stegodyphus lineatus* Latreille (Eresidae) has a circum-Mediterranean distribution where they occupy arid and semiarid regions. The spiders are usually annual and semelparous with extensive maternal care and matriphagy. The female releases the young (40–140) from the egg sac and feeds them actively by regurgitation for approximately 2 weeks (Kullmann *et al.*, 1971). After two moults, prior to dispersal the spiderlings consume the mother. The spiderlings stay in the maternal nest for another 2–4 weeks before the first individuals initiate dispersal after the fifth moult (Millot & Bourgin, 1942 cited in D'Andrea, 1987), the entire dispersal period may be prolonged lasting 3–5 weeks (Aviram, 2000). During dispersal, spiderlings may subdivide into small groups that continue to hunt and feed together for some time (Millot & Bourgin, 1942 cited in D'Andrea, 1987). Dispersal distances are low, which explains the clustered distribution of *S. lineatus* within habitats (Lubin *et al.*, 1998).

Sub-adult *S. lineatus* were collected in Kfar Adumim, east of Jerusalem in Israel, in March 2000 and brought to the Sede Boqer Campus of Ben Gurion University. We kept spiders outdoors in plastic containers with mesh lids (height 10 cm, diameter 5 cm) under natural temperature and light conditions protected partially against direct sun by shade cloth, and reared them to adulthood on a diet of desert locusts (*Locusta migratoria*), crickets (*Acheta domestica*) and flour beetles (*Tenebrio molitor*). Females were mated after the final moult and produced offspring; juvenile spiders were assigned to the experiments when the majority of spiderlings had left the maternal nest, approximately 2 weeks after the first dispersing young.

Preliminary observations

In a preliminary experiment, we determined whether cannibalism occurs among siblings. Pairs of sib and nonsib young (*n* = 15 each) were kept together for 7–10 days with no food in Petri dishes (55 mm diameter) with a piece of filter paper in the bottom. The spiderlings were matched for size, with a mass difference of ≤10%. Observations were made daily to determine if one spider was feeding on another, and the frequency of cannibalism was determined in each group.

Cannibalism experiments

We compared cannibalism among full-sib and nonrelated groups of either two or six juvenile *S. lineatus* in four experiments (see below). The groups of six spiderlings allowed us to test the effect of increased density on the rate of cannibalism. Only one group of siblings from each family was used in each experiment. All spiderlings in nonsib groups originated from different families and were of similar age. We kept the spider pairs and groups in plastic containers with mesh lids (height 10 cm, diameter 5 cm) under natural conditions as described above. These containers were larger than the Petri dishes used in the preliminary observation, allowing space for nest construction and for individuals to retreat if attacked. Wild type fruit flies *Drosophila melanogaster* (hereafter 'Drosophila') were provided as prey every 5–6 days in amounts according to experimental design (see below). The *Drosophila* were given to the spider-group simultaneously, i.e. spiders within a group were not fed individually. Prior to feeding we recorded incidents of cannibalism. We checked all dead spiders under a dissecting microscope to determine whether they had been cannibalized or had died from other causes. A cannibalized spider was easily distinguished from one that died naturally (e.g. starvation) as its abdomen was partly digested and the spider was therefore deformed. Additionally, cannibalized spiders were usually incorporated into the nest.

Cannibalism in spider pairs with food

We tested whether spiderlings were more likely to cannibalize unrelated conspecifics than siblings by comparing pairs of full-sib ($n = 43$) and nonsib ($n = 46$) newly dispersed juveniles. Prior to the experiment the spiders were matched by weight so the maximal difference between individuals was 0.5 mg (spider mass was in the range of 2.5–6 mg). Each pair received two *Drosophila* per spider every 5–6 days. We compared the number of cannibalistic events in sib pairs vs. nonsib pairs after a period of 2 months with two-way contingency tables.

Cannibalism in spider pairs without food

We performed a starvation experiment to test whether cannibalism would occur more frequently among nonkin than kin under severe food stress. Pairs of sib ($n = 27$) and nonsib ($n = 29$) spiders of similar size (maximal within-pair weight difference 0.5 mg) were kept under complete starvation and incidents of cannibalism were compared after 3 weeks with two-way contingency tables.

Food-dependent cannibalism in groups of six spiders

We investigated whether food-dependent cannibalism is more likely to occur among nonkin than among kin, by varying the amount of food provided to groups of six sib or nonsib spiderlings of homogenous size (maximal weight difference between individuals in a group was 0.5 mg). In a low-food treatment, each group received one *Drosophila* per spider every 5–6 days (sib-groups $n = 28$, nonsib-groups $n = 25$), whereas a high-food treatment was provided two *Drosophila* per spider every 5–6 days (sib-groups $n = 28$, nonsib-groups $n = 25$). Both of these amounts of food were considerably less than consumption capacity (M. Salomon, personal communication) and were chosen to impose severe and mild food stress, respectively. We applied logistic regression (cannibalistic events at group level) and two-way ANOVA (number cannibalized) to analyse for effects of food regime and relatedness on cannibalism after an experimental period of 2 months.

Size-dependent cannibalism in groups of six spiders

We investigated whether size-dependent cannibalism occur and if it is higher among nonrelated than related spiders by comparing groups of six spiders of variable size with spider-groups of homogenous size. We composed groups so the largest spider had at least three times the mass of the smallest spider with the other individuals in the group distributed by weight within this range (spider weight ranged from 1 to 10 mg; sib-groups $n = 27$, nonsib groups $n = 25$). The groups were fed two *Drosophila* per spider every 5–6 days (i.e. mild food stress). Cannibalistic events were compared between the heterogeneous groups and the groups of homogenous-sized spiders in the high-food treatment of the food-dependent cannibalism experiment described above. We applied logistic regression (cannibalistic events at group level) and two-way ANOVA (number of spiders cannibalized) to analyse for effects of size variance and relatedness on cannibalism after an experimental period of 2 months.

Results

Preliminary observations

We observed biting and feeding of one individual on another. Cannibalism was observed in both sib pairs (26.7%) and nonsib pairs (60%) ($n = 15$ in each group; Pearson $\chi_1^2 = 3.394$, $P = 0.065$). Cannibalism occurred in sib pairs after 4–6 days (median = 5.5 days) and 1–10 days (median = 4) in nonsib pairs.

Cannibalism in fed and starved spider pairs

We found no significant effect of kinship on cannibalism in spider pairs with food. Cannibalism occurred in 22 of 46 sib pairs (48%) and in 19 of 43 nonsib pairs (44%) (Pearson $\chi_1^2 = 0.12$, $P = 0.73$). In starved pairs, we found nine incidents (39%, $n = 23$) of cannibalism in sib pairs

and 13 incidents (62%, $n = 21$) in nonsib pairs (Pearson $\chi^2_1 = 2.28$, $P = 0.13$). When we combined probabilities for the preliminary observations and the starved pair experiment, the tendency for starved spiders to cannibalize nonkin more frequently than kin was significant [Fisher's test for combined probabilities (Sokal & Rolf, 1995, p. 794); $\chi^2_4 = 9.54$, $P = 0.048$]. We analysed the effect of kinship and feeding regime on cannibalism with logistic regression combining the experiments with pairs and including experiment as a factor. The analysis showed a significant kinship × feeding interaction caused by differential treatment of kin as a result of more cannibalism of nonkin by starved spiders than by fed spiders (log-likelihood ratio = 3.90, d.f. = 1, $P = 0.048$; effect of experiment: log-likelihood ratio = 0.409, d.f. = 2, $P = 0.52$).

Food-dependent cannibalism in groups of six spiders

We found fewer cannibalistic incidents in groups of sibs than in groups of nonsibs (logistic regression: log-likelihood ratio = 17.71, d.f. = 2, $P < 0.001$; effect of kinship: t-ratio$_1$ = 3.06, $P = 0.002$, Fig. 1) and a significant effect of food treatment with more incidents of cannibalism in the low-food groups (t-ratio$_1$ = −2.81, $P = 0.005$). Kinship and food regime significantly influenced the number of spiders cannibalized within each group (Fig. 1B). More spiders were cannibalized in nonsib groups compared with sib groups (two-way ANOVA: $F_{3,105} = 8.04$, $P < 0.001$; effect of kinship: $F_{1,102} = 8.83$, $P = 0.003$) and in the low-food treatment relative to the high-food treatment ($F_{1,102} = 13.31$, $P < 0.001$). The kinship × food-level interaction was not significant ($F_{1,102} = 1.81$, $P = 0.18$).

Size-dependent cannibalism in groups of six spiders

We found no significant effects of relatedness (logistic regression: log-likelihood ratio = 3.21, d.f. = 2, $P = 0.20$; effect of kinship: t-ratio$_1$ = 1.26, $P = 0.21$) or size variance (t-ratio$_1$ = −1.26, $P = 0.21$) on the proportion of groups in which cannibalism occurred (Fig. 2A). Likewise, neither kinship (two-way ANOVA: $F_{3,104} = 0.69$, $P = 0.56$; effect of kinship: $F_{1,101} = 1.35$, $P = 0.25$) nor size variance within groups ($F_{1,101} = 0.008$, $P = 0.93$) affected the number of spiderlings cannibalized (Fig. 2B). The kinship × size–variance interaction was not significant ($F_{1,101} = 0.73$, $P = 0.39$).

Discussion

Our experiments with starved pairs showed a trend of more cannibalistic events among nonsib pairs of spiderlings than among sib pairs, suggesting that kin recognition occurs in these spiders. Furthermore, a strong bias towards cannibalism of nonkin occurred in groups of six spiders that were food limited. This is the first time
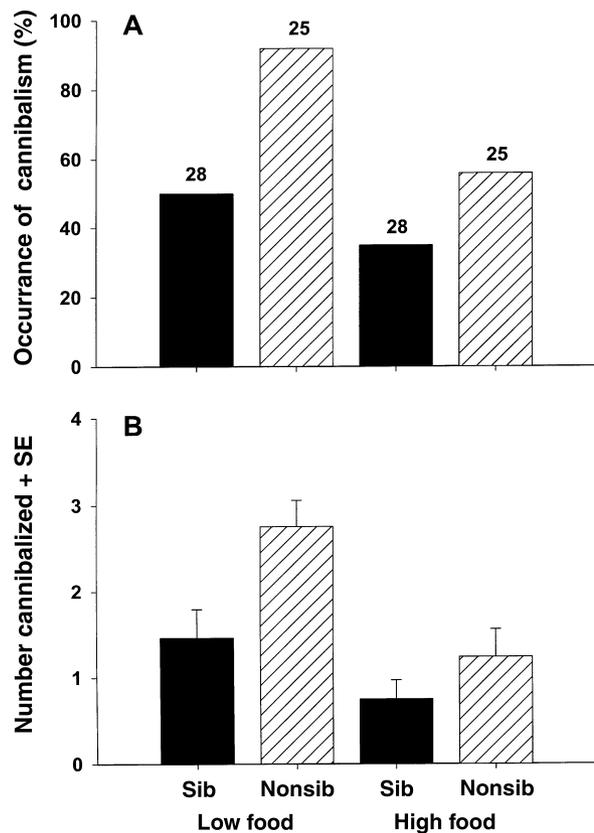

Fig. 1 (A) Proportion of groups consisting of six sib (solid bars) or nonsib (hatched bars) *Stegodyphus lineatus* spiderlings, in which cannibalism occurred in a low-food treatment and a high-food treatment. More cannibalistic events occurred in nonsib-groups than in sib-groups and when spiders were food limited (logistic regression, see text for details). Numbers above bars indicate sample sizes. (B) Number of spiderlings cannibalized (mean + SE) in groups consisting of six sib (solid bars) or nonsib (hatched bars) *Stegodyphus lineatus* spiderlings in a low-food treatment and a high-food treatment. More spiders were cannibalized in nonsib-groups than in sib-groups and when spiders were food limited (two-way ANOVA).

differential treatment of relatives, i.e. kin recognition, has been found in a nonsocial spider. We did not find a significant effect of kinship on cannibalism in the experimental groups that were not food stressed, which suggests that hunger increases the propensity to attack and cannibalize. Our results suggest that the likelihood of cannibalism increases with group size, perhaps because of a higher encounter rate in larger groups. Cannibalism rates in *S. lineatus* were generally low, and only when spiders were starved was the bias towards nonkin significant. The reluctance to cannibalize is even more pronounced in some social spiders, where spiders in groups may be kept without food for extended periods without any occurrence of cannibalism (Jackson, 1980; D'Andrea, 1987).
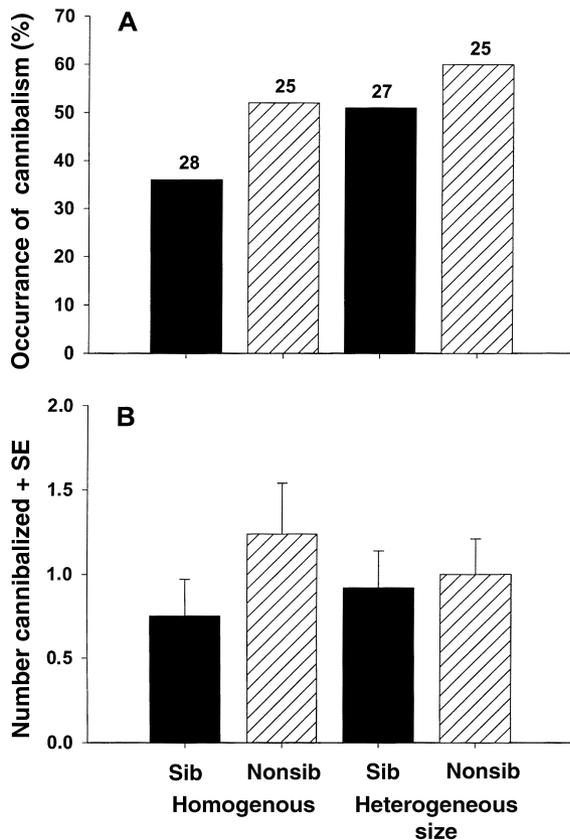
Fig. 2 (A) Proportion of groups consisting of six sib (solid bars) or nonsib (hatched bars) *Stegodyphus lineatus* spiderlings, in which cannibalism occurred. Groups were composed of spiders of homogenous size and of heterogeneous size. Numbers above bars indicate sample sizes. Size variance did not result in more cannibalism within nonsib-groups compared with sib-groups. (B) Number of spiderlings cannibalized (mean + SE) in groups consisting of six sib (solid bars) or nonsib (hatched bars) *Stegodyphus lineatus* spiderlings, groups were composed of spiders of homogenous size and of heterogeneous size.

The ability to recognize siblings and reduce kin cannibalism may facilitate a prolongation of the social period in the transition from subsocial to social living (Kullmann, 1972; Michod, 1993; Pfennig, 1997). During the initial dispersal period, *S. lineatus* young may live together, hunt in groups and feed communally, indicating a predisposed tendency for cooperation that might be reinforced by reciprocal tolerance (Kullmann, 1972). Avoidance of kin cannibalism may be particularly beneficial en route to sociality under low food conditions as this is a situation often experienced by spiders (Anderson, 1974; Wise, 1993; Avilés, 1997). When prey is scarce, consumption of nonkin may enhance the fitness of the cannibal and lower resource competition for members of the family group. Evans (1999) provided evidence for this hypothesis when he found that juveniles of the social crab spider *Diaea ergandros* consume

unrelated immigrant spiderlings instead of siblings when starved. Subadult females, however, consumed their own brothers and unrelated immigrant females rather than unrelated males, suggesting a strategy that maximizes outbreeding opportunities (Evans, 1999).

In social spiders, little or no cannibalism would suggest kin recognition. Some social spiders, however, were shown to accept unrelated individuals into their groups without apparent discrimination (Kullmann, 1968; Darchen & Delage-Darchen, 1986; D'Andrea, 1987; Seibt & Wickler, 1988; Pasquet *et al.*, 1997). Such open societies differ from the closed groups found in social insects, which are characterized by antagonistic behaviour towards conspecific newcomers (group closure) that implies some form of kin (or nest mate) recognition (Wilson, 1971; Darchen & Delage-Darchen, 1986). Nevertheless, the acceptance of foreign individuals into colonies cannot be taken as evidence that kin recognition does not exist in these groups (Sherman *et al.*, 1997). Rather, the lack of discriminatory behaviour could reflect the benefits of accepting unrelated immigrant spiders into the society, such as enhanced group survival, decreased individual cost of web construction and outbreeding possibilities (Lubin & Robinson, 1982; Avilés, 1986, 1997; Riechert *et al.*, 1986; Leborgne *et al.*, 1994; Uetz & Hieber, 1997; Evans, 1999).

In contrast to the tolerance exhibited by highly inbred cooperative spiders (Riechert & Roeloffs, 1993; Avilés, 1997), post-dispersal individuals of *S. lineatus* are aggressive and show territorial behaviour towards other individuals (personal observations). *Stegodyphus lineatus* young are philopatric and often found in close proximity to the maternal nest (Johannesen & Lubin, 1999), which makes frequent encounters with kin most likely, at least during the initial stages of dispersal. Although reproducing females within a patch are likely to be sisters, mating with wandering males results in a basically outbred population structure (Johannesen & Lubin, 1999, 2001). In such circumstances, where encounters are likely to occur between kin as well as nonrelatives, kin selection could favour recognition and biased cannibalism. A similarly outbred population structure is found in the social crab spiders *Diaea ergandros* and *Delena cancerides* (Rowell & Avilés, 1995; Evans, 1995). *D. cancerides* spiders are extremely aggressive towards members of foreign colonies, which implies recognition of both kin and colony members (Rowell & Avilés, 1995). These spiders appear to be at the transition between solitary and social living, where the potential benefits of kin-biased behaviour (i.e. nepotism and outbreeding) should favour selection for kin recognition (Fellowes, 1998). Whether kin recognition is lost in the inbred social species or simply not expressed in most interactions remains to be determined.

Sherman *et al.* (1997) define kin recognition as differential treatment of conspecifics differing in relatedness, and not by the functional significance or proximate

mechanisms of recognition. The ability to discriminate kin from nonkin implies the presence of a reliable cue, which may be any aspect of the phenotype that signifies kinship. Kin recognition cues can be of genetic or environmental origin and should optimize the balance of acceptance and rejection errors (Sherman *et al.*, 1997; Joseph *et al.*, 1999). The mechanism underlying recognition in *S. lineatus* and whether the recognition cue is of environmental or genetic origin is the subject of further investigation.

Prey availability is without doubt the most significant factor in determining mutual tolerance in spiders (e.g. Burgess & Uetz, 1982; Rypstra, 1986). In our high-food treatments, cannibalism rates were relatively low and spiders coexisted in shared webs; in fact *S. lineatus* can be reared communally to adulthood under favourable food conditions (Schneider, 1996). Several studies on subsocial spiders show that experimental supplementation of food prolongs the tolerant phase and delays dispersal of juveniles [*Stegodyphus lineatus* (Schneider, 1995; Aviram, 2000), *Coelotes terrestris* (Krafft *et al.*, 1986; Gundermann *et al.*, 1993); *Theridion pictum* (Ruttan, 1990) and *Amaurobius ferox* (Kim, 2000)]. Although *S. lineatus* young are mutually tolerant when food is not limited, Schneider (1996) found that communal feeding with siblings as compared with unrelated spiders translated into higher consumption and growth rates; this experiment suggested that there is a benefit to feeding with kin and thus, kin discrimination. Single spiders, however, always gained more mass than spiders in groups suggesting costs of competition (Schneider, 1996). In addition to generally lower growth rates when feeding communally, variance in body size of individuals of *S. lineatus* resulted in differential growth rates and increased mortality (Schneider, 1995). In contrast, in our experiments we found no effect on cannibalism rates of groups of different size individuals. Schneider (1995) suggested that small individuals might have starved following monopolization of prey (*Calliphora* flies) by larger individuals. In our experiment, spiders received smaller *Drosophila* as prey, but in higher numbers (one to two *Drosophila* per spider in a group), which may have enabled all spiders to gain access to prey. The quantity and size of the fruit flies provided in our experiment thus may have been sufficient to keep the attack propensity at a low level, perhaps by reducing differences in competitive abilities between spiders (Samu *et al.*, 1999).

The potential adaptive benefits of kin-biased behaviour are less apparent in solitary than in social species. Benefits of kin recognition could be reduced competition for resources among kin, particularly when coupled with delayed dispersal and philopatry, as in *S. lineatus* and other subsocial spiders (Avilés & Gelsey, 1998). Kin recognition could also serve to maintain an outbred population structure (Johannesen & Lubin, 1999), which

could be obtained by discrimination against kin as mates. Thus, the study of kin recognition in subsocial species is particularly interesting in the context of evolution of sociality. We suggest, that kin-biased behaviour in the form of kin cannibalism avoidance, in addition to inclusive fitness benefits, will favour the evolution of cooperation and group living in phylogenetically pre-adapted solitary species.

Acknowledgments

References

Anderson, J.F. 1974. Responses to starvation in the spiders *Lycosa lenta* Hentz and *Filistata hibernalis* Hentz. *Ecology* **55**: 576–585.

Avilés, L. 1986. Sex-ratio and possible group selection in the social spider *Anelosimus eximius*. *Am. Nat.* **128**: 1–12.

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

Avilés, L. & Gelsey, G. 1998. Natal dispersal and demography of a subsocial *Anelosimus* species and its implications for the evolution of sociality in spiders. *Can. J. Zool.* **76**: 2137–2147.

Aviram, A. 2000. Maternal effects on dispersal decisions and fitness of juveniles in a desert spider *Stegodyphus lineatus* (Eresidae). MSc Thesis, Ben Gurion University, Israel.

Burgess, J.W. & Uetz, G.W. 1982. Social spacing strategies in spiders. In: *Spider Communication: Mechanisms and Ecological Significance* (P. N. Witt & J. S. Rovner, eds), pp. 317–351. Princeton University Press, Princeton, NJ.

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

D'Andrea, M. 1987. Social behaviour in spiders (Arachnidae, Araneae). *Ital. J. Zool., N.S. Monogr.* **3**: 1–156.

Darchen, R. & Delage-Darchen, B. 1986. Societies of spiders compared to the societies of insects. *J. Arachnol.* **14**: 227–238.

Dong, Q. & Polis, G.A. 1992. The dynamics of cannibalistic populations: a foraging perspective. In: *Cannibalism: Ecology and Evolution Among Diverse Taxa* (M. A. Elgar & B. J. Crespi, eds), pp. 13–37. Oxford University Press, Oxford.

Elgar, M.A. 1992. Sexual cannibalism in spiders and other invertebrates. In: *Cannibalism: Ecology and Evolution Among Diverse Taxa* (M. A. Elgar & B. J. Crespi, eds), pp. 128–155. Oxford University Press, Oxford.

Elgar, M.A. & Crespi, B.J. 1992. Ecology and evolution of cannibalism. In: *Cannibalism: Ecology and Evolution Among*

Diverse Taxa (M. A. Elgar & B. J. Crespi, eds), pp. 1–12. Oxford University Press, Oxford.

Evans, T.A. 1995. Two new species of social crab spiders of the genus *Diaea* from eastern Australia, their natural history and distribution. *Rec. West Austral. Mus. Suppl.* **52**: 151–158.

Evans, T.A. 1999. Kin recognition in a social spider. *Proc. R. Soc. Lond. B* **266**: 287–292.

Fellowes, M.D.E. 1998. Do non-social insects get the (kin) recognition they deserve? *Ecol. Entomol.* **23**: 223–227.

Fletcher, D.J.C. & Michener, C.D. 1987. *Kin Recognition in Animals*. Wiley, New York.

Fox, L.R. 1975. Cannibalism in natural populations. *Annu. Rev. Ecol. Sys.* **6**: 87–106.

Grafen, A. 1990. Do animals really recognize kin? *Anim. Behav.* **39**: 42–54.

Gundermann, J.L., Horel, A. & Krafft, B. 1993. Experimental manipulations of social tendencies in the subsocial spider, *Coelotes terrestris*. *Insect. Soc.* **40**: 219–229.

Hamilton, W.D. 1964. The genetical evolution of social behaviour. I & II. *J. Theor. Biol.* **7**: 1–52.

Hamilton, W.D. 1987. Discriminating nepotism: expectable, common, overlooked. In: *Kin Recognition in Animals* (D. J. C. Fletcher & C. D. Michener, eds), pp. 417–437. Wiley, New York.

Hepper, P.G. 1986. Kin recognition: functions and mechanisms, a review. *Biol. Rev.* **61**: 63–93.

Jackson, R.R. 1980. Comparative studies of *Dictyna* and *Mallos*. V. Tolerance and resistance to starvation. *Psyche* **87**: 211–220.

Johannesen, J. & Lubin, Y. 1999. Group founding and breeding structure in the subsocial spider *Stegodyphus lineatus* (Eresidae). *Heredity* **82**: 677–686.

Johannesen, J. & Lubin, Y. 2001. Evidence for kin-structured group founding and limited juvenile dispersal in the subsocial spider *Stegodyphus lineatus* (Eresidae). *J. Arachnol.* (in press)

Johannesen, J., Baumann, T., Seitz, A. & Veith, M. 1998. The significance of relatedness and gene flow on population genetic structure in the subsocial spider *Eresus cinnaberinus* (Araneae: Eresidae). *Biol. J. Linn. Soc.* **63**: 81–98.

Joseph, S.B., Snyder, W.E. & Moore, A.J. 1999. Cannibalizing *Harmonia axyridis* (Coleoptera: Coccinellidae) larvae use endogenous cues to avoid eating relatives. *J. Evol. Biol.* **12**: 792–797.

Kim, K.W. 2000. Dispersal behaviour in a subsocial spider: group conflict and the effect of food availability. *Behav. Ecol. Sociobiol.* **48**: 182–187.

Krafft, B. 1982. The significance and complexity of communication in spiders. In: *Spider Communication: Mechanisms and Ecological Significance* (P. N. Witt & J. S. Rovner, eds), pp. 15–66. Princeton University Press, Princeton, NJ.

Krafft, B., Horel, A. & Julita, J.-M. 1986. Influence of food supply on the duration of the gregarious phase of a maternal-social spider, *Coelotes terrestris* (Araneae, Agelenidae). *J. Arachnol.* **14**: 219–226.

Kullmann, E.J. 1968. Soziale Phaenomene bei Spinnen. *Insect. Soc.* **15**: 289–298.

Kullmann, E.J. 1972. Evolution of social behavior in spiders (Araneae; Eresidae and Theridiidae). *Am. Zool.* **12**: 419–426.

Kullmann, E.J., Sitterz, H. & Zimmermann, W. 1971. Erster Nachweis von Regurgitationsfütterungen bei einer cribellaten Spinne (*Stegodyphus lineatus* Latreille, 1817, Eresidae). *Bonn. Zool. Beitr.* **22**: 175–188.

Leborgne, R.B., Krafft, B. & Pasquet, A. 1994. Experimental study of foundation and development of *Anelosimus eximius* colonies in the tropical forest of French Guiana. *Insect. Soc.* **41**: 179–189.

Lubin, Y.D. & Robinson, M.H. 1982. Dispersal by swarming in a social spider. *Science* **216**: 319–321.

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

Michod, R.E. 1993. Inbreeding and the evolution of social behavior. In: *The Natural History of Inbreeding and Outbreeding* (N. W. Thornhill, ed.), pp. 74–96. University of Chicago Press, Chicago.

Millot, J. & Bourgin, P. 1942. Sur la biologie des *Stegodyphus* solitaires. *Bull. Biol. Fr. Belg.* **76**: 299–314.

Pasquet, A., Trabalon, M., Bagnères, A.G. & Leborgne, R. 1997. Does group closure exist in the social spider *Anelosimus eximius*? Behavioural and chemical approach. *Insect. Soc.* **44**: 159–169.

Pfennig, D.W. 1997. Kinship and cannibalism. *Bioscience* **47**: 667–675.

Polis, G.A. 1981. The evolution and dynamics of intraspecific predation. *Annu. Rev. Ecol. Syst.* **12**: 225–251.

Riechert, S.E. & Roeloffs, R.M. 1993. Evidence for and the consequences of inbreeding in the cooperative spiders. In: *The Natural History of Inbreeding and Outbreeding* (N. W. Thornhill, ed.), pp. 283–303. University of Chicago Press, Chicago.

Riechert, S.E., Roeloffs, R. & Echternacht, A.C. 1986. The ecology of the cooperative spider *Agelena consociata* in Equatorial Africa (Araneae, Agelenidae). *J. Arachnol.* **14**: 175–191.

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

Ruttan, L.M. 1990. Experimental manipulations of dispersal in the subsocial spider, *Theridion pictum*. *Behav. Ecol. Sociobiol.* **27**: 169–173.

Rypstra, A.L. 1986. High prey abundance and a reduction in cannibalism: the first step to sociality in spiders (Arachnida). *J. Arachnol.* **14**: 193–200.

Samu, F., Toft, S. & Kiss, B. 1999. Factors influencing cannibalism in the wolf spider *Pardosa agrestis* (Araneae, Lycosidae). *Behav. Ecol. Sociobiol.* **45**: 349–354.

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

Schneider, J.M. 1996. Food intake, growth and relatedness in the subsocial spider, *Stegodyphus lineatus* (Eresidae). *Ethology* **102**: 386–396.

Seibt, U. & Wickler, W. 1988. Bionomics and social structure of 'family spiders' of the genus *Stegodyphus*, with special reference to the African species *S. dumicola* and *S. mimosarum* (Araneida, Eresidae). *Verh. Naturwiss. Ver. Hamburg,* **30**: 255–303.

Sherman, P.W., Reeves, H.K. & Pfennig, D.W. 1997. Recognition systems. In: *Behavioral Ecology: An Evolutionary Approach*, 4th edn. (J. R. Krebs & N. B. Davis, eds), pp. 69–96. Blackwell Science, Oxford.

Sokal, R.R. & Rolf, F.J. 1995. Biometry, 3rd edn. Freeman, New York.

Uetz, G.W. & Hieber, C.S. 1997. Colonial web-building spiders: balancing the costs and benefits of group-living. In: *The*

Evolution of Social Behavior in Insects and Arachnids (J. C. Choe & B. J. Crespi, eds), pp. 458–475. Cambridge University Press, Cambridge.

Wagner, J.D. & Wise, D.H. 1996. Cannibalism regulates densities of young wolf spiders: evidence from field and laboratory experiments. *Ecology* **77**: 639–652.

Wilson, E.O. 1971. *The Insect Societies*. Harvard University Press, Cambridge, MA.

Wise, D.H. 1993. *Spiders in Ecological Webs*. Cambridge University Press, Cambridge.