Kin recognition in a social spider

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Social spiders accept immigrant spiders into their kin-based groups, suggesting that spiders cannot recognize kin and may lose inclusive fitness benefits. A field and two laboratory experiments on *Diaea ergandros*, a social crab spider, demonstrated that younger and older instar *D. ergandros* do discriminate siblings, but potential benefits were variable and not equally distributed. First, proportional survival was greater in large groups regardless of the within-group relatedness, so accepting immigrants increases probability of group survival (although relatedness was more important among smaller groups). Second, juvenile *D. ergandros* ate unrelated spiders instead of siblings when starved, so immigrants might represent a food reserve in times of food shortage. Third, subadult resident, sibling females cannibalized unrelated, immigrant females and their brothers instead of immigrant males when starved, suggesting that subadult female spiders may maximize outbreeding opportunities. These benefits provide selective pressure for groups to accept immigrants, but as benefits are realized differentially, conflict and cooperation will exist within spider groups similar to that shown in other group-living taxa.

Keywords: Araneae; cannibalism; nepotism; outbreeding

1. INTRODUCTION

Spider sociality appears to be based on family groups, originating from extended maternal care (D'Andrea 1987; Avilés 1997). But unlike most vertebrate and invertebrate family-based groups that have some form of kin recognition (Fletcher & Michener 1987; Hepper 1991), social spiders have been shown to accept artificially introduced, unrelated individuals into their family-based groups without any form of discrimination, prompting suggestions that spiders are unable to distinguish kin (Darchen & Delage-Darchen 1986; D'Andrea 1987; Pasquet *et al.* 1997). This indiscriminating acceptance of 'immigrants' into social spider groups poses a theoretical dilemma because it appears to decrease the potential benefits of kin recognition and discrimination systems. The benefits include nepotism (inclusive fitness benefits) (Hamilton 1964*a,b*, 1987; Eickwort 1981; Clutton-Brock 1991), optimal outbreeding (Bateson 1978) and avoiding disease transmitted via cannibalism (Pfennig *et al.* 1994).

Perhaps social spiders do not need to have nepotistic recognition (Keller 1997; Sherman *et al.* 1997) because social spiders have low levels of genetic diversity and groups are usually highly inbred, suggesting that non-kin are unlikely to be found in the group (Avilés 1997). Alternatively, the costs of recognition errors may be high, especially if the chances of error types are asymmetric (Reeve 1987), which is likely among inbred social spider groups. Another possibility mitigating against recognition arises when the recipients of recognition benefit from a lack of discriminatory behaviour and so they scramble

recognition systems (Keller 1997; Sherman *et al.* 1997). All possible explanations are more likely when relatedness differences are small or difficult to detect (e.g. Breed *et al.* 1994; Kempenaers & Sheldon 1996).

Another alternative explanation for the lack of discriminatory treatment might be that there are several potential benefits of accepting unrelated immigrants into a family group. They might improve the probability of survival, as larger groups of social spiders generally have a higher chance of survival, which has been related to the size of the nest or web constructed (D'Andrea 1987; Evans 1998*a*, and references therein). This benefit does not require kin recognition, but other possibilities do. Diet supplementation via cannibalism may occur when regular prey are in short supply. If so, kin recognition is necessary to avoid inclusive fitness costs. Any outbreeding opportunity might be important for the typically highly inbred social spiders, and so immigrants might represent a chance to outbreed, with the added benefit of avoiding any potential dispersal risk.

I investigated this dilemma in *Diaea ergandros* Evans (Thomisidae), a social crab spider that lives in Australian *Eucalyptus* (Myrtaceae) forests (Evans 1995). Groups originate as the offspring of a single female, and live in globular nests built from *Eucalyptus* leaves. This nest is critical for survival as it protects against predation, provides the foraging area for their ambush predation (Evans 1998*a*), and mating appears to occur inside it (Main 1988; Evans 1995). *D. ergandros* appeared to be an ideal model species to use as many nests may occur on one tree, so there is a high probability of encountering non-related spiders (Evans 1998*a,b*). *D. ergandros* mothers are able to discriminate unrelated spiderlings (Evans 1998*b*), which may indicate that *D. ergandros* offspring might be able to detect and respond to non-siblings. In this study I aimed to investigate the incidence of

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unrelated spiders in natural nests of *D. ergandros*, and to test if kin recognition occurred in *D. ergandros*, and if so, to describe what kinds of nepotistic or outbreeding benefits were gained as a result.

2. METHODS

(a) *Within-group relatedness from natural nests*

I collected 119 nests from south-eastern Australian forests in 1993, and dissected them in the laboratory. I categorized groups into age classes based on the most numerous age class of spiders in the nest (spiderlings, instars 1 and 2; juveniles, instars 3 and 4; subadults, instar 5; adults, instar 6). This was a measure of group age, as groups tend to grow as a cohort due to their origin from a single clutch. The exceptions that did not have a numerically dominant age class were categorized as 'mixed' groups. I determined the within-group relatedness by sampling eight spiders from each nest (762 spiders from 119 nests) and used allozyme analysis (Richardson *et al.* 1986); extracts from whole ground spiders were run on potato starch gels (Starch Art) and stained for four polymorphic enzymatic loci: isocitrate dehydrogenase, lactate dehydrogenase, 6-phosphogluconate dehydrogenase and phosphoglucose isomerase with 22 alleles in total (Evans 1995). Relatedness was calculated using the computer program Relatedness 4.2 (Goodnight & Queller 1994), and compared between groups of different age classes.

(b) *Group size and composition*

I investigated the influence of group size and composition on survival, spider growth and nest construction in a field experiment. I collected nests that contained third and fourth instar spiders from trees that contained only single nests in the Yan Yean Water Catchment near Melbourne in April 1993. Nests were collected from trees bearing single nests to maximize the chances of excluding immigrants (Evans 1998a). Groups of five sizes (1, 5, 10, 20 and 40 individuals) were made from the occupants of these nests. Group composition was either siblings (spiders from one nest only) or unrelated spiders (only one spider from any one nest). Note that all spiders from both treatments were separated and recombined to control for handling. There were 40 singleton spiders, 11 groups of siblings and 12 groups of unrelated spiders for group sizes 5, 10 and 20, and six groups each of siblings and unrelated spiders for groups of 40, a total of 1325 spiders.

All spiders were weighed into plastic vials, which were placed into separate perforated plastic bags with ten *Lucilia cuprina* pupae (Diptera, Calliphoridae). Bags with vials and spiders were returned to the collection site and each plastic bag was placed over the growing end of a branchlet (one bag per tree that did not contain other *D. ergandros* nests) so that several leaves were enclosed, and the open end of the bag was tied around the stem with string. The vial was carefully opened within the bag, which prevented dispersal from the site. The *L. cuprina* subsequently eclosed providing prey inside the plastic bags. Unable to disperse, the spiders began nest construction; the bags were removed about one week later (after Evans 1998b). Nests were observed daily and nightly for one week after bag removal, then approximately fortnightly, for weaving and dispersal behaviours. The experiment ran for five months during winter and spring 1993, until November, when the nests were collected and dissected in the laboratory. All occupants in the nest were collected and weighed in the

laboratory and all leaves used in construction were counted and dry weighed.

(c) *Cannibalism in juveniles*

Spiders that use sit-and-wait ambush predation tactics, such as crab spiders, are usually inactive in order to be successful ambushers. Therefore, using active behaviours to discern or measure kin-bias in such spiders is problematic, especially over short time-periods. Instead of behaviour, I measured survival in a laboratory experiment that tested for kin-biased cannibalism during starvation in July 1994. Triplets of two siblings and one unrelated spider were assembled in plastic jars. One sibling was an instar larger (fourth or fifth) than the other (third or fourth instar), with the unrelated spider matched in size (i.e. equivalent instar and similar weight) to the smaller sibling. In order to identify spiders, either the rear-most left or right leg was removed from the two smaller spiders two weeks prior to the experiment, with no apparent alteration to behaviour. There were 40 replicate triplets.

This combination was designed to give the larger sibling a choice of two easy to subdue and cannibalize spiders, identical except for their relationship to the larger spider. The spiders were provided with water only, and were inspected daily until cannibalism had occurred in all jars.

(d) *Cannibalism in subadults*

I examined unrelated 'immigrant' spiders as potential outbreeding opportunities in a laboratory experiment on subadults (i.e. penultimate instars) in August 1997. I assembled groups of 1:1 sex ratio from nests in the field (collected as above): ten groups of four spiders, nine groups of ten spiders and five groups of 20 spiders. These 'resident' sibling spiders were housed in glass jars containing *Eucalyptus* leaves from their nests.

Two unrelated subadult spiders, one male and one female, removed from a nest at least 5 km away were used as 'immigrants'. These 'immigrant' spiders were double marked, externally with pink fluorescent paint and internally with the histological fat stain Nile Blue A. Spiders were marked by eating *Coptotermes lacteus* (Isoptera) stained with Nile Blue A and by spray-painting a week before the experiment began, with no apparent alteration to behaviour (Evans & Gleeson 1998). The blue colour is clearly visible through the translucent opisthosomal walls. Cannibalism can be inferred using the blue stain and paint, as the former is transferred via feeding but the latter is not. Immigrant spiders were placed into the jars with the resident spiders and then fed once with *L. cuprina* (one fly per four spiders). The flies' remains were removed and only water was provided thereafter. Jars were inspected every few days for seven weeks and all cannibalisms were recorded.

3. RESULTS

(a) *Within-group relatedness from natural nests*

The relatedness of natural groups decreased significantly with the age class of the group (one-way ANOVA, $F=11.46$, 4, 108 d.f., $p<0.001$). Spiderling groups (first and second instars) were significantly more closely related ($p<0.01$) than were juveniles (third and fourth instars), subadults (fifth instars) and adults (sixth instars). Mixed groups (without a dominant age class) were significantly less related ($p<0.01$), suggestive that these groups were likely to have several immigrants (figure 1).

Figure 1. The mean ($\pm$ s.e.) within-group relatedness of natural *D. ergandros* groups of differing age classes. Number of groups tested appears above columns. Significance levels: n.s., not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

(b) Group size and composition

Singletons did not attempt to build nests within their plastic bags, and no singletons were found two days after the plastic bags were removed. No analyses were performed on singletons. Survival differed among groups of different size and relatedness (two-way ANOVA interaction, $F = 4.23$, 3, 73 d.f., $p < 0.01$). The groups of five spiders had very low survival, which did not differ significantly between sibling and unrelated spiders ($t = 0.09$, 10 d.f., $p > 0.8$). The groups of 40 had very high survival, which also did not differ between sibling and unrelated spiders ($t = 0.30$, 10 d.f., $p > 0.7$). The survival of the intermediate-sized groups was somewhat between these extremes, but sibling groups had significantly higher survival than their equivalent sized groups of unrelated spiders (groups of 20, $t = 2.10$, 21 d.f., $p < 0.05$ and 10, $t = 5.78$, 21 d.f., $p < 0.01$) (figure 2a).

The difference in survival did not appear to be related to spider growth. All spiders that survived the experiment grew by similar amounts. Growth did not differ between group size (two-way ANOVA, $F = 0.39$, 2, 26 d.f., $p > 0.6$) or group composition ($F = 0.09$, 2, 26 d.f., $p > 0.9$) (with no interaction effect) (figure 2b). Survival appeared to depend on nest construction instead. Larger groups built heavier nests (two-way ANOVA, $F = 37.4$, 3, 67 d.f., $p < 0.001$), and so did sibling groups ($F = 5.96$, 1, 67 d.f., $p < 0.02$) (with no interaction effect) (figure 2c).

(c) Cannibalism in juveniles

Cannibalisms occurred between 16 and 26 days after food deprivation commenced. In the 40 replicate groups of three spiders, the large sibling ate the small unrelated spider in 36 groups and their small sib in two groups; in the two remaining groups the small unrelated spider ate the small sib. This pattern of cannibalism differed significantly from random ($\chi^2 = 25.6$, 38 d.f., $p < 0.001$), suggesting that the larger spiders were able to detect their relationship to the smaller spiders.

Figure 2. Spider survival, growth and nest construction data (mean $\pm$ s.e.) from the field experiment on group size and relatedness. (a) Proportion survival of spiders; (b) growth of spiders; (c) nest weight (dry weight of leaves). Open columns, unrelated spiders; filled columns, sibling spiders. Significance levels as for figure 1. For (a) the interaction is significant, so significance levels indicated for pairwise comparisons; for (b) and (c) the interaction is not significant, so significance levels indicated for treatment effect. See text for details.

Table 1. *Survival of subadult D. ergandros during the cannibalism in subadults laboratory experiment*

(Survival expressed as total number alive (all replicates added). Resident, sibling resident spiders; immigrant, unrelated immigrant spider.)

group size	spider type	sex	number alive (days)		
			0	22	44
4	resident	female	20	15	9
		male	20	4	0
	immigrant	female	10	6	0
		male	10	4	4
10	resident	female	45	28	12
		male	45	22	0
	immigrant	female	9	5	0
		male	9	9	4
20	resident	female	50	31	13
		male	50	29	2
	immigrant	female	5	2	0
		male	5	5	4

(d) *Cannibalism in subadults*

The first cannibalisms occurred between 15 and 22 days; I observed seven independent (i.e. in separate jars) cannibalistic events during this time; three resident females ate immigrant females, and four immigrant males ate resident males. The observed cannibalisms produced blue females without pink paint (cannibalistic resident females), dead females with pink paint (cannibalized immigrant females), blue males with pink paint (cannibalistic immigrant males), dead males without pink paint (cannibalized resident males). I used these changes in colour patterns to infer cannibalistic events that were not observed (table 1).

Other cannibalism events were more scattered over the following weeks (from 30–44 days). Larger resident females ate their brothers (five observed cases) and smaller sisters (three observed cases) and ignored the immigrant male. The immigrant male managed to moult to imago stage in five cases, but only one resident female did so. After 44 days, immigrant females and resident males were completely absent and immigrant males had begun to eat the smaller resident females. These results were consistent across all group sizes (table 1).

4. DISCUSSION

This study showed that *D. ergandros* groups can contain unrelated, immigrant spiders, and that *D. ergandros* had some form of differential treatment of relatives, i.e. kin recognition, in all three experiments performed. However, the behavioural response elicited by this kin recognition was not consistent. Instead, the way relatives were treated appeared to change over the life of the spider.

Kin recognition was nepotistic when the spiders were young. Juveniles spiders (third and fourth instars) contributed greater effort in nest construction when they lived in groups of siblings. As nests were the major determinant of the spiders' survival (i.e. the success of the group, see Evans 1998b), this higher contribution can be interpreted as nepotistic kin recognition. This effect

produced survival differences between sibling and unrelated groups only in intermediate-sized groups (see figure 2), as small groups could not build adequate nests and so had low survival regardless of within-group relatedness, whereas the opposite was true for large groups. The intermediate groups had differential survival, due to larger, adequate nests built by siblings compared with the smaller, inadequate nests built by unrelated spider groups.

These young spiders also displayed a very different behaviour when they were alone: they did not attempt any nest building, instead singletons always dispersed. Perhaps they may choose dispersal over nest building in order to search for a larger group with higher probability of survival. It is possible that spiders from smaller groups acted similarly, and abandoned their inadequate nests to find larger, more adequate ones, and thus increase their chance of survival.

Why should the larger groups accept these immigrants? Immigrants increase group size and so increase nest construction (perhaps also decreasing individual costs thereof), and thereby increase chances of group survival. This should occur without affecting growth rates negatively, since growth was similar in groups of siblings and unrelated spiders, and in all size groups. These benefits do not require any kin recognition, but kin recognition is required for other potential benefits. A second benefit of accepting immigrants identified in this study was gaining a potential food source, should normal food (pollinating and folivorous insects) diminish. Like other social spiders, *D. ergandros* did not cannibalize quickly (Buskirk 1981; D'Andrea 1987). However, once starved to a critical level, juvenile spiders chose to eat non-relatives instead of siblings in 95% of cases, further demonstration of nepotism.

Nepotistic cannibalism might not necessarily persist into later life, because female subadult instars cannibalized their siblings instead of the immigrant male. This implies a third potential benefit, i.e. outbreeding. Starved resident females ate immigrant females, reducing potential competition, but they also ate their brothers and (eventually) their sisters, rather than unrelated males.

This pattern suggests that female resident subadult spiders might be protecting an outbreeding opportunity (Bateson 1978; reviewed by Birkhead & Parker 1997; Sherman *et al.* 1997). Immigrant males reduced potential competition by cannibalizing resident males. Since more immigrant males matured than resident females, this might suggest that females have greater maturation costs due to their larger size (Evans 1995, 1998b), or greater restraint in eating their siblings.

This is the first time that kin recognition by siblings has been demonstrated in a spider. The observed acceptance of immigrants into *D. ergandros* groups does not pose a theoretical dilemma because behaviours can be discriminating. Other studies have not found kin discrimination in social spider species, perhaps because discrimination has not been tested under these circumstances (see Buskirk 1981; D'Andrea 1987; Avilés 1997, for reviews). For example, Pasquet *et al.* (1997) did not observe any obvious discrimination when they tested one immigrant adult female with ten resident adult female *Anelosimus eximius*, but their protocol provided prey and ran for only 24 h. It is possible that kin recognition does not exist in other social spiders, because non-kin are unlikely to be found in the group (Breed *et al.* 1994). This might be true for some social species with poor dispersal, including *Anelosimus eximius* and *Agelena consociata* (Riechert & Roeloffs 1993; Avilés 1997), but remains to be investigated in others, such as *Tapinillus* and *Theridion* and other related *Anelosimus* species. Other explanations might include the high costs of recognition errors, or because the recipients of recognition benefit from a lack of discriminatory behaviour (Reeve 1987; Breed *et al.* 1994; Kempenaers & Sheldon 1996; Keller 1997; Sherman *et al.* 1997).

These possibilities remain to be tested conclusively. Some work suggests subtle effects that might be the result of kin discrimination. For example, sibling groups of *Stegodyphus lineatus* had higher growth from more efficient prey consumption than equivalent groups of unrelated spiders (Schneider 1996). More extreme experimental procedures, such as starvation, may be necessary to detect kin discrimination in other social spider species, since immigrants provide benefits such as improved survival and decreased individual costs of nest (or web) construction, e.g. *Agelena consociata* (Riechert *et al.* 1986; Riechert & Roeloffs 1993), *Achaearanea wau* (Lubin & Robertson 1982), *Anelosimus eximius* (Vollrath 1986; Avilés 1986; Venticinque *et al.* 1993; Leborgne *et al.* 1994), *Stegodyphus* spp. (Seibt & Wickler 1988), *Mallos gregalis* (Tietjen 1986) and *Metepeira spinipes* spp. (Uetz 1988; Uetz & Hieber 1994, 1997).

The benefits of kin recognition found for *D. ergandros* will not be distributed equally among individuals within the nest—smaller juveniles and brothers are vulnerable when food is short and perhaps during mating (although agonistic behaviours between courting males is not unusual). Unequal distribution of benefits from intense competition have been reported for *A. eximius* and *S. lineatus*; large individuals monopolize food resources and have higher fecundity (Rypstra 1993; Schneider 1995). Similar competitive behaviours have been reported in the field in other species (Jackson 1979; Burgess & Uetz 1982; D'Andrea 1987). These behaviours suggest that unequal distribution of benefits might be common in all

social spider groups. If so, kin-recognition systems might be necessary and common to all social spiders. The unequal distribution benefits within a group is common to other social taxa that have open groups, especially vertebrates (Trivers 1985; Emlen 1997), social insects (Seeger 1991), and colonial orb-weaving spiders (Uetz & Hieber 1997). More extreme experimental methods on social spiders may find other similar cases of kin discrimination in otherwise apparently peaceful groups.

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