Offspring recognition by mother crab spiders with extreme maternal care

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Maternal care is provided by several spider species, but there are no reports of mother spiders recognizing their young, which suggests that maternal care can be exploited by unrelated individuals. *Diaea ergandros*, a crab spider with extreme, sacrificial maternal care, does accept unrelated spiderlings (ca. 43.9% of spiderlings) into its nest in areas of high nest density. However, a field and a laboratory experiment with mother spiders and natural and adoptive spiderlings demonstrated that mothers did recognize their own offspring. Recognition was not expressed in survival as adopted (unrelated) spiderlings had similar survival rate to that of natural offspring. Instead it was displayed in growth; mother *D. ergandros* caught large prey items for their own offspring, but not for adopted spiderlings, and so natural offspring grew more than adopted spiderlings. Also, mothers produced trophic oocytes, which are important for the sacrificial care that influences spiderling survival, only when they lived with their own offspring.

Keywords: Araneae, cannibalism, *Diaea ergandros*, maternal care, nepotism, recognition

1. INTRODUCTION

Kin recognition has been observed in a wide range of vertebrate and invertebrate taxa (Fletcher & Michener 1987; Hepper 1991). The benefits of kin recognition and discrimination systems include nepotism (Hamilton 1964*a,b*), optimal outbreeding (Bateson 1978) and avoiding disease transmitted via cannibalism (Pfennig *et al.* 1994), though these may not be mutually exclusive (Sherman *et al.* 1997). Although nepotism is common, especially parental nepotism (Eickwort 1981; Hamilton 1987; Clutton-Brock 1991), it has not been observed in some species where it may be expected (Keller 1997). Nepotistic recognition may not occur for several reasons. First, when the circumstances favouring its evolution are rare, such as when kin are grouped together and non-kin are unlikely to be found in the group. Second, when the costs of rejection errors and acceptance errors are greater than the benefits. Third, when the recipients of recognition benefit from a lack of discriminatory behaviour (Keller 1997; Sherman *et al.* 1997). This may be so when relatedness differences are small or difficult to detect (for examples, see Breed *et al.* 1994; Kempnaers & Sheldon 1996).

Spiders display a wide range of maternal care behaviours, from only a silken eggsac around the eggs, to extended care that provides shelter, food and protection (Kullman 1972; Foelix 1982; D'Andrea 1987; Schneider & Lubin 1997). Those spiders that provide extended maternal care should display nepotistic recognition to avoid exploitation by non-relatives, as found for other taxa. However, no such recognition has been reported in any spider, indeed, a lack of maternal discrimination has been noted

in several families, such as Agelenidae (Krafft 1969; Gundermann *et al.* 1988; Assi Bessekou *et al.* 1992), Araneidae (Simon 1891; Lubin 1974), Eresidae (Kullman *et al.* 1972; Jacson & Joseph 1973), Lycosidae (Engelhardt 1964; Miller 1989), Theridiidae (Kullman 1972; Christensen 1984) and Thomisidae (Morse 1989). The lack of maternal discrimination in spiders may be explained by a low probability of encountering another spider's offspring, or that spider maternal care may be relatively inexpensive to provide, or perhaps because spider reproductive output is high. Such factors vary between species and circumstances: distributions can be clumped, so oviposition can occur in shared retreats, care can be extensive and extreme, and fecundity varies by two orders of magnitude across the order (Kullmann 1972; Buskirk 1981; D'Andrea 1987; Simpson 1995; Avilés 1997). Those spider species that breed only once and then provide extensive maternal care to their offspring (Stearns 1992) would have greater pressure to evolve recognition systems, especially if the probability of encountering unrelated offspring is high.

The Australian social spider *Diaea ergandros* (Thomisidae) displays extended maternal care for a single clutch of eggs (mean 45) and because many spiders may nest on one tree, mothers have a high probability of encountering non-related spiderlings (Evans 1997). The maternal care that *D. ergandros* mothers provide is elaborated from typical thomisid care behaviour. Thomisids typically prepare a simple brood chamber from a single leaf, which they guard until the spiderlings emerge, then they lay again. Instead, *D. ergandros* add many *Eucalyptus* leaves onto their brood chamber to create a nest and they guard and provide their young with prey. *D. ergandros* also displays matrophagy (Seibt & Wickler 1987), where mothers store food in trophic oocytes, and are eventually eaten by their young (Evans *et al.* 1995). This extensive care occurs over several months during which spiderlings

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can and do migrate (Evans 1997). Here, I investigate the incidence of unrelated spiderlings in natural nests, and examine how *D. ergandros* mothers discriminate unrelated spiderlings from their own offspring.

2. METHODS

(a) *Incidence of non-offspring spiderlings in natural nests*

I collected 37 nests with mothers and young spiderlings (1st–3rd instars) from *Eucalyptus* forest in south-eastern Australia and recorded the number of other nests in the same or adjacent trees for each nest. I determined relatedness between the presumptive mothers and seven spiderlings from each nest using 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. I compared alleles from mothers and spiderlings and considered spiderlings that did not have at least one copy of the mother's alleles to be unrelated. I then compared the number of adjacent nests for those nests that contained unrelated spiderlings, with those that did not.

(b) *Mother type in the field*

I investigated the influence of genetic relatedness between adult females and spiderlings on their survival, growth and on nest construction in a field experiment. I collected mothers and spiderlings (1st and 2nd instar) from trees that contained only single nests in the Yan Yean Water Catchment near Melbourne in April 1994. A total of 20 replicate groups of ten spiderlings were randomly assigned to either their natural mother or an adoptive mother: all mothers were separated from their spiderlings, and returned to either their own natural or adoptive spiderlings.

All spiders were weighed into plastic vials (4 cm × 1.2 cm diameter), which were capped and 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 through the bag, which prevented dispersal from the site. The *L. cuprina* were subsequently eclosed providing prey inside the plastic bags. Unable to disperse, the spiders began constructing nests and the bags were removed *ca.* 1 week later. Nests were observed daily and nightly for 1 week after bag removal, then *ca.* fortnightly, for weaving and dispersal behaviours. The experiment ran through autumn and winter and ended after 6 months (October) 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. All surviving mothers were dissected under a binocular microscope, their ovaries examined and the number and size of oocytes in the ovaries were recorded.

(c) *Mother type and prey size in the laboratory*

This experiment investigated the influence of genetic relatedness between adult females and spiderlings on the prey capture of the adult females, and how this behaviour affected the survival and growth of the spiderlings. Spiders were collected coincidentally with those used in (a). A total of five replicate groups of ten

sibling spiderlings were randomly assigned into two experimental treatments: mother type and prey type. Mother type had three categories; natural (the adult female found in the nest with the spiderlings), adoptive (an adult female from a different nest which contained spiderlings), and none (no adult female). Prey type had two categories: *Drosophila melanogaster*, which can be caught by spiderlings, or *Lucilia cuprina*, which cannot be caught by spiderlings (Evans 1997).

Spiders were assigned into experimental treatments, weighed and placed in plastic containers (20 cm × 10 cm diameter) with two pieces of cut and folded paper (7 cm × 4.5 cm each). Spiders were fed twice a week with 52 *D. melanogaster* or two *L. cuprina*. This was considered to be equivalent available biomass (Rypstra 1993; Evans 1997). Prey capture was recorded and all dead and living flies removed before new flies were added. The experiment ran through autumn and ended after 2 months when the surviving spiders were counted and weighed. Surviving mothers were dissected and their ovaries examined for oocyte development as previously mentioned.

3. RESULTS

(a) *Incidence of non-offspring spiderlings in natural nests*

A total of 20 nests contained mothers that shared at least one allele with all the spiderlings screened, whereas 17 nests had between one and four of the seven spiderlings assayed that did not share alleles at one or more loci with the mother. One nest was exceptional; all seven spiderlings were genetically different from the presumed mother found in the nest. The presence of non-related spiderlings was related to nest density: there were significantly more *D. ergandros* nests in either the same or adjacent trees for those nests with unrelated spiderlings (3.71 ± 0.31 nests) than those nests without unrelated spiderlings (0.90 ± 0.26 nests) (unpaired *t*-test $t=4.72$, 38 d.f., $p<0.001$). Therefore, a mother *D. ergandros*'s brood is entirely her own offspring in areas of low *D. ergandros* densities, but contains only *ca.* $57.1 \pm 6.54\%$ offspring in areas of high nest density (overall brood average: $80.3 \pm 4.6\%$ offspring and $19.7 \pm 4.6\%$ unrelated, presumably immigrant spiderlings).

(b) *Mother type in the field*

Nest construction began in the first week in all groups and few spiderlings were seen walking from the attachment sites during the first days after bag removal. There was no significant difference in group survival rate: ten out of ten groups with natural mothers survived compared with eight out of ten groups with adoptive mothers (Fisher's exact $p>0.4$). Spiderling survival within groups was not affected by mother type (natural mother groups 6.20 ± 0.77 spiderlings, adoptive mother groups 5.80 ± 1.22 spiderlings, one-way ANOVA, $F=0.08$, 18 d.f., $p>0.7$). Survival did not depend on spiderling weight (multiple regression, $F=0.60$, 17 d.f., $p>0.3$), nor mother weight ($p>0.5$).

Spiderlings did not differ in weight between mother types initially (one-way ANOVA, $F=0.01$, 18 d.f., $p>0.9$), but by the end of the experiment spiderlings with natural mothers were significantly heavier than those with adoptive mothers (one-way ANOVA, $F=8.84$, 18 d.f., $p<0.01$, see figure 1a). A total of eight natural mothers and five

Figure 1. Spider weights (mean $\pm$ s.e.) from the field experiment. (a) Spiderling weight. (b) Mother weight. Open columns, initial weight; filled columns, final weight. Significance levels: ns, not significant; * $p < 0.05$; ** $p < 0.01$.

adoptive mothers survived the experiment. Mother types did not differ in their initial weight (one-way ANOVA, $F=1.22$, 18 d.f., $p > 0.2$), however, natural mothers were significantly heavier than adoptive mothers at the end of the experiment (one-way ANOVA, $F=7.11$, 11 d.f., $p < 0.05$, see figure 1b). The dry weight of leaves in the nest was not significantly different between natural (0.902 ± 0.129 g) and adoptive (0.699 ± 0.124 g) treatments (ANCOVA, $F=0.05$, 15 d.f., $p > 0.8$), but was related to the final spiderling weight ($F=7.90$, 15 d.f., $p < 0.05$), suggesting that spiderlings did contribute to nest construction.

(c) Mother type and prey size in the laboratory

All spiders could capture *D. melanogaster* and did so as soon as they were released into the containers. Spiderlings almost always fed individually on *D. melanogaster*. However, each type of mother behaved differently when fed *L. cuprina*. Natural mothers typically killed both flies in

rapid succession after release into the containers and then sat by the carcasses as spiderlings fed, often feeding after spiderlings, whereas adoptive mother types would kill and feed on only one fly, ignoring the other. Spiderling survival was not affected by either mother type (two-way ANOVA, $F=0.25$, 18 d.f., $p > 0.7$) or prey type ($F=0.23$, 18 d.f., $p > 0.6$), because although spiderlings could not subdue *L. cuprina* easily, they did scavenge the carcasses of dead flies. The final weight of spiderlings was compared between different treatments and a significant interaction between mother type and prey type was found (two-way ANOVA interaction, $F=3.42$, 24 d.f., $p < 0.05$). Consequently, the two treatments were considered separately.

Comparisons of spiderling growth between prey types for each mother type showed that spiderlings with adoptive mothers fed *D. melanogaster* were significantly heavier than those fed *L. cuprina* (one-way ANOVA, $F=14.74$, 8 d.f., $p < 0.01$), which was also true for spiderlings without mothers (one-way ANOVA, $F=8.73$, 8 d.f., $p < 0.02$), whereas spiderlings with natural mothers were not significantly different (one-way ANOVA, $F=0.15$, 8 d.f., $p > 0.7$, see figure 2a). Comparing spiderling growth between mother types for each prey type, showed that spiderling growth was similar when they were fed *D. melanogaster*, regardless of mother type (one-way ANOVA, $F=0.44$, 11 d.f., $p > 0.9$), but spiderlings fed *L. cuprina* grew more when they were with natural mothers (one-way ANOVA, $F=3.49$, 11 d.f., $p < 0.05$, see figure 2a). Therefore, only natural mothers caught and fed large prey to spiderlings at a rate equivalent to spiderlings catching small prey for themselves.

Mother types appeared to have different survival: more natural mothers survived (eight) than adoptive (three), also more mothers survived fed *L. cuprina* (seven) than *D. melanogaster* (four). Only natural mothers gained weight during the experiment, as initial mother weight was not different between mother type (one-way ANOVA, $F=0.76$, 18 d.f., $p > 0.3$) or prey type (one-way ANOVA, $F=0.67$, 18 d.f., $p > 0.4$) treatments, but final natural mother weight was significantly heavier than that of adoptive mothers (one-way ANOVA, $F=5.72$, 12 d.f., $p < 0.05$, see figure 2b).

The surviving mothers that gained weight appeared to do so in their ovaries. The combined results for field and laboratory experiments showed that the total number of regenerated oocytes in both ovaries was significantly higher for natural mothers (one-way ANOVA, $F=8.80$, 21 d.f., $p < 0.01$, see figure 3a). The diameter of regenerated oocytes was significantly larger for natural mothers (two-way ANOVA, $F=9.00$, 19 d.f., $p < 0.01$), but it was also dependent on prey type, with mothers fed *L. cuprina* in the laboratory regenerating the largest oocytes ($F=9.70$, 19 d.f., $p < 0.001$, see figure 3b,c).

4. DISCUSSION

At first inspection, this study would suggest that *D. ergandros* mothers did not recognize their own, natural offspring from unrelated, adoptive spiderlings. The genetic data showed that mothers accepted unrelated spiderlings into their nests, built nests in the field experiment regardless of their relatedness to the cohabiting spiderlings, and spiderlings survived equally well in both

Figure 2. Spider weights (mean $\pm$ s.e.) from the laboratory experiment. (a) Spiderling weight. (b) Mother weight. Open columns, initial weight; hatched columns, final weight in the *L. cuprina* treatment; filled columns, final weight in the *D. melanogaster* treatment. Significance levels as for figure 1, *** $p < 0.001$.

experiments regardless of their relatedness to the resident adult female spider. However, closer examination showed that mothers behaved differently when they were with their own offspring. The field experiment demonstrated that mothers and spiderlings in natural families grew more than those in adoptive groups, perhaps, as the results from the laboratory experiment suggest, because mothers caught more large prey. Furthermore, mothers in both experiments regenerated their ovaries as food storage devices only when they were with their own natural offspring. This weight increase represents maternal investment and care as mothers are eventually eaten by their offspring, and heavier mothers can provide more food over longer periods of time, which reduces potential sibling cannibalism (Evans *et al.* 1995).

This is the first time that maternal recognition of offspring has been demonstrated in a spider species. Perhaps the extreme maternal care provided in this species, combined with the high probability of encountering non-related spiderlings, has provided the selective

Figure 3. Number and size of oocytes (mean $\pm$ s.e.) from mothers in the field and laboratory experiments. (a) Number of oocytes in both ovaries. (b) Oocytes diameter from different mother types. Open columns, mothers from field experiment; filled columns, mothers from laboratory experiment. (c) Oocytes diameter from different prey types. Field, from field experiment; *D. m.*, *D. melanogaster* treatment; *L. c.*, *L. cuprina* treatment. Significance levels as for figures 1 and 2.

pressure necessary for the evolution of maternal recognition. However, this discrimination was subtle, i.e. it was displayed in growth, not survival. Unrelated spiderlings benefited from a lack of discriminatory behaviour, perhaps because the cost of a rejection error to the mother is large (as she will not reproduce again) and so she hedges her bets by allowing unrecognized-unrelated spiderlings to live, but without expending extra effort in prey capture (Keller 1997; Sherman *et al.* 1997). Perhaps discrimination is difficult when relatedness differences are small or difficult to detect (for examples, see Breed *et al.* 1994; Kempenaers & Sheldon 1996), which may occur when populations are clumped.

An investigation of species with similarly costly maternal care and limited reproduction (reviewed by Schneider & Lubin 1997) to that of *D. ergandros* may show further examples of maternal discrimination in spiders. For example, two social conspecifics, *D. socialis* (Main 1988) and *D. megagyna* (Evans 1995), have similar life history strategies. The Eresidae (cob-web weavers) and Theridiidae (scaffold-web weavers) contain several solitary and social species with extended maternal care which includes feeding with prey and/or regurgitation and matrophagy (Seibt & Wickler 1987) and these species may have clumped distributions, often with webs and/or retreats touching (reviewed in Kullman 1972; Jacson & Joseph 1973; Buskirk 1981; D'Andrea 1987). The eresid genus *Stegodyphus* provides a similar range of maternal care behaviours to *Diaea*, and therefore may also display nepotistic maternal discrimination. For example, *S. lineatus* provides extreme care, similar to *D. ergandros*, except that mothers can produce a second eggsac should the first be destroyed (Schneider & Lubin 1996, 1997).

Extensive care provides selective pressure for nepotistic kin recognition in other taxa (Hamilton 1987; Fletcher & Michener 1987; Hepper 1991; Sherman *et al.* 1997). Such care, especially when combined with limited fecundity or opportunities for reproduction, may also select for recognition in spiders. Only one, *Delena cancerides* (Sparassidae), has been reported to display aggression against non-nest-mates (Rowell & Avilés 1995), although care and fecundity are not well understood in this species. However, the more subtle influence of kin recognition in growth has been detected in sibling and non-sibling groups of juvenile *S. lineatus* (Schneider 1996). Further careful testing of discriminatory care in other care-providing species, such as those in the Eresidae and Theridiidae, may show that spiders conform to the patterns of selection that have produced recognition in other taxa.

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