

# Cannibalism and kin recognition in *Delena cancerides* (Araneae: Sparassidae), a social huntsman spider

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## Keywords

kin recognition; *Delena cancerides*; social behaviour; spider sociality; tolerance.

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## Abstract

Social behaviour in spiders is rare: of the 39 000 species of spiders known, only 23 are considered to be cooperatively social. *Delena cancerides* is a social species of the huntsman spider that is endemic to Australia. This species is virtually unique among social spiders, having evolved social behaviour in the absence of a snare web. It is thought that this form of social behaviour in *D. cancerides* has evolved via the sub-social route, that is, the extension of an ancestrally occurring period of maternal care and the delayed dispersal of juveniles. Most social spiders show no aggression towards non-kin conspecifics, prompting suggestions that spiders cannot recognize kin; however, *D. cancerides* individuals are highly aggressive towards conspecifics introduced from outside their own colony. In order to determine whether selective aggression in *D. cancerides* has its basis in kin recognition, tolerance behaviour was assessed in the context of kinship and size. We observed that, in general, juveniles preferred to starve than engage in cannibalism of any conspecifics, related or not. However, where cannibalism did occur, non-kin were preferentially eaten, indicating that this species is clearly capable of kin recognition. Size thresholds were also established, below which juveniles are tolerated by adults and above which aggressive interactions leading to death occur. We conclude that kin recognition and juvenile dispersal explain the uncharacteristically high levels of genetic polymorphism in this species.

## Introduction

Social behaviour in spiders is a rare phenomenon. Of the 39 000 spider species identified worldwide, *c.* 60 have been defined as social and 23 are cooperatively social (Whitehouse & Lubin, 2005). Cooperative social (or 'non-territorial permanently social') spiders are those that spend their entire lives in communal webs or nests (Aviles, 1997). It is thought that this form of social behaviour in spiders has evolved via the sub-social route: the extension of an initial period of maternal care and the delayed dispersal of offspring (Shear, 1970; Wilson, 1971; Kullmann, 1972; Buskirk, 1981; Whitehouse & Lubin, 2005). The vast majority of spider species provides some degree of passive maternal care to post-emergent young (Assi Bessekon, 1997). This form of maternal 'care', otherwise referred to as 'tolerant' behaviour, comprises passive care behaviours. For example, a mother may protect her young from predators as a passive consequence of her presence, and food items in the form of discarded carcasses that she has previously fed upon may be available for her offspring to 'pick over' (Gundermann, Horel & Roland, 1991; Assi Bessekon & Horel, 1996). In contrast, female spiders will often actively defend egg sacs from potential predators (Assi Bessekon & Horel, 1996). Given the propensity of all spiders to be tolerant of post-

emergent young, the sub-social route to the evolution of social behaviour in spiders distinguishes social spiders from solitary species by the extent to which maternal care occurs rather than whether it occurs at all (Rowell & Aviles, 1995). In short, social spiders are those in which an initial phase of tolerance of post-emergence offspring is extended past the first instar of spiderling development (Shear, 1970; Wilson, 1971; Kullmann, 1972; Buskirk, 1981).

*Delena cancerides* Walckenaer (Sparassidae) is a group-living species of the huntsman spider endemic to Australia (Rowell, 1985, 1986; Rowell & Aviles, 1995). The spider inhabits the space beneath the exfoliating bark of dead *Acacia*, *Callitris*, *Casuarina* and (rarely) *Eucalyptus* trees, and occasionally under weathered granite exfoliations. Colonies may consist of up to 300 individuals. Adult females produce a strong, inelastic silk unique to *D. cancerides*, which is used to secure bark to the tree trunk. Colonies appear to be based upon the extension of maternal care, almost universally containing at least one adult female and occasionally more. This individual actively cares for the egg sacs she produces as well as caring for young and associating with other colony members (Rowell & Aviles, 1995).

*Delena cancerides* is unlike all but one other social spider species (the thomisid *Diaea*; Evans, 1995), having evolved sociality in the absence of a snare web. It is thought that

*D. cancerides* has evolved sociality via the sub-social route, that is, through the permanent extension of maternal care (Rowell & Aviles, 1995). In contrast, for other social spider species the presence of a snare web (which facilitates gregariousness) is considered the major preadaptation to social behaviour (Shear, 1970; Kullmann, 1972; Buskirk, 1981; D'Andrea, 1987; Aviles, 1994; Whitehouse & Lubin, 2005). The lack of a snare web is not the only trait that distinguishes *D. cancerides* from other social spider species. Social spiders typically exhibit reduced aggression, to the extent that individuals are tolerant of non-kin conspecifics (Riechert & Roeloffs, 1993; Assi Bessekon & Horel, 1996; Assi Bessekon, 1997; Aviles, 1997). This fact has prompted suggestions throughout the literature that social spiders are unable to recognize kin (Evans, 1999; Bilde & Lubin, 2001). However, *D. cancerides* directs extreme aggression towards conspecifics belonging to other colonies. This behaviour is unique among social spiders (Rowell & Aviles, 1995) and suggests that kin recognition and discrimination may be present in *D. cancerides*.

A third characteristic that sets *D. cancerides* apart from other social spider species is that the species is peculiarly outbred, displaying high levels of genetic polymorphism and heterozygosity (Rowell, 1990; Rowell & Aviles, 1995). Social spider species that display a level of sociality comparable to that of *D. cancerides*, for example *Anelosimus eximius*, exhibit polymorphism levels of 5–8% (Vollrath, 1986). In contrast, levels of polymorphism in *D. cancerides* populations vary between 32 and 68% (Rowell, 1990). This intolerance of non-colony conspecifics, including potential mates, calls into question the way in which the high levels of outbreeding characteristic of the species are actually achieved (Rowell & Aviles, 1995). This paper investigates kin recognition and tolerance behaviours that have the potential to facilitate gene flow in *D. cancerides*. Specifically, we aim to establish whether kin recognition occurs and whether there is a size threshold over which adult females cannibalize juvenile spiders.

## Materials and methods

### Sample collection and standard treatment

*Delena cancerides* colonies were collected opportunistically from sites in the Australian Capital Territory and from the surrounding regions of New South Wales, Australia, between February and September 2002. We collected spiders from beneath the exfoliating bark of dead *Acacia* trees (*Acacia mearnsi* and *Acacia dealbata*). These spiders were kept in 750 mL capacity, clear, plastic containers at an average temperature of 23 °C and 60% humidity. Each spider was provided with water continuously via saturated wicking, and was fed 1–2 crickets twice weekly. Where colonies were large (consisting of multiple age-cohorts including juvenile, sub-adult and adult spiders), adult and sub-adult individuals were kept singly whereas juveniles were maintained as a group. Colonies consisting of an adult

female and one or two clutches of spiderlings were kept intact before the commencement of experiments.

### Kin recognition

*Delena cancerides* colonies frequently consist of several size cohorts of spiders (Rowell & Aviles, 1995). This characteristic, along with the aggressive nature of the species, led us to make the grounding assumption that spiders from within the same colony would generally be related, whereas spiders taken from separate colonies were non-kin. For this experiment, we defined separate colonies as those that were separated by a minimum of 1 km distance. We measured survival percentages for triplets of two colony members (kin) and one non-colony member (non-kin). The non-kin individual was size matched with one of the kin members according to carapace width, whereas the second kin member was selected to be one or two instars larger. Spiders were supplied with food in the week before the trial period. For identification purposes, we marked individuals with a painted dot on the carapace using one of four paint colours (chosen at random). The triplets were placed in 70 mL capacity plastic containers and supplied with water continually but deprived of food. There were 34 replicates.

In these experiments, the larger spider in each triplet was essentially presented with starvation pressure and a choice between kin and non-kin to cannibalize. Jars were examined several times daily for signs of cannibalism (i.e. a partially consumed carcass). Triplets were maintained until either cannibalism or starvation occurred. Triplets were scored for the date and the occurrence of cannibalism versus starvation. Data were analysed using a  $\chi^2$  test (JMP v. 3.0.1, SAS Institute Inc.).

### Size threshold for tolerance

Preliminary trials showed that adult females that possessed egg sacs, adult female singletons and adult males quickly cannibalized introduced spiderlings. Consequently, adult females that had been kept with their offspring before the experimental period were selected for this experiment. These females were separated from their offspring and placed singly in 750 mL capacity plastic containers. Females were provided with food as per standard treatment in the lead-up to this experiment series. To control for individual food requirements, spiders were supplied with one cricket 1 day before each tolerance trial, which was eaten in all trials. Spiderlings of varying sizes were then measured for carapace width and placed individually with each female for 24 h. Spiderlings and females that were placed together had been captured from geographic locations separated by a minimum 1 km to eliminate potential kin bias. The experiment was scored for survival of the spiderlings after 24 h. If the spiderling was alive at the end of this period, it was removed and the experiment was repeated with a different spiderling after a 24 h intermission. Results were grouped into carapace width size classes and assessed as percentage mortality according to size.

## Results

### Kin recognition

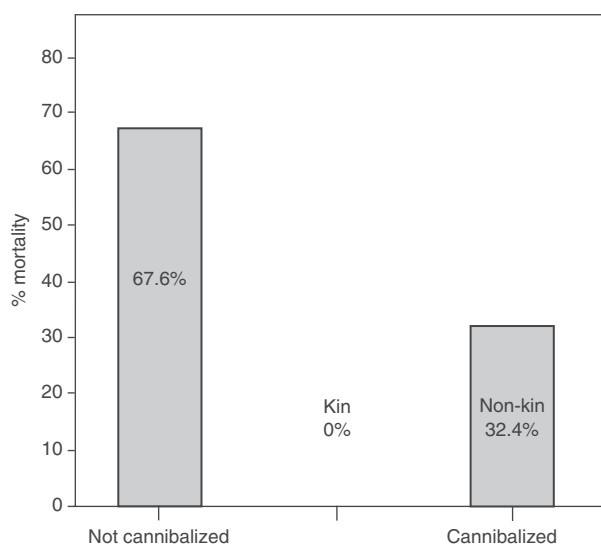
We performed 34 kin-recognition trials. All cannibalized individuals were non-kin ( $n = 11$ ,  $\chi^2 = 11.0$ , d.f. = 1,  $P < 0.001$ ; see Fig. 1). In the 23 trials where cannibalism did not occur, spiderlings died from starvation and the carcasses were left intact. All incidences of cannibalism occurred within 1 day, while starvation of individuals (without cannibalism taking place) occurred within 6 weeks.

### Size threshold for tolerance

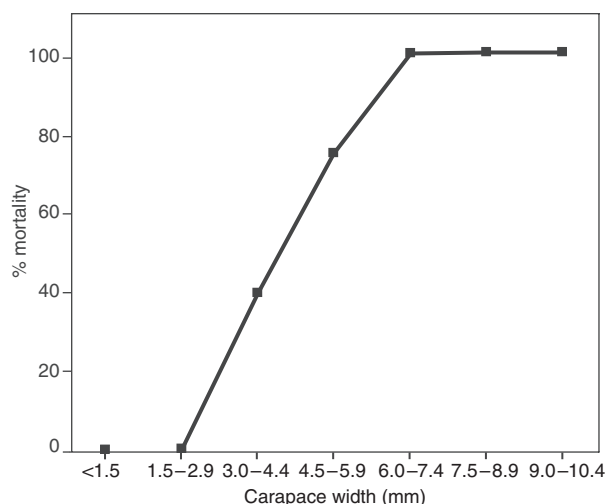
The percentage of mortality experienced by spiderlings of varying carapace widths ( $n = 50$ ) when placed with a non-kin adult female was 0% for the <1.5 mm (second instar) and 1.5–2.9 mm (third instar) carapace width size classes. The level of mortality subsequently increased to 40 and 75% for the 3.0–4.5 mm (fourth instar) and 4.5–5.9 mm (fifth instar) size classes, respectively. Spiderling mortality rates reached 100% for spiderlings with a carapace width of more than 6.0 mm (sixth instar; see Fig. 2).

## Discussion

This study found that *D. cancerides* spiderlings preferred not to engage in cannibalism even in the face of starvation; however, when cannibalism did occur, only non-kin were killed. Tolerance experiments showed that adult female spiders tolerated juvenile spiders with a carapace width under 3 mm. Spiderlings with a carapace width exceeding 6 mm were always eaten (Fig. 2).



**Figure 1** Percentage mortality of *Delena cancerides* spiderlings under starvation conditions. In 67.6% of kin-recognition trials, spiderlings died without engaging in cannibalism of conspecifics. In 32.4% of trials, non-kin conspecifics were cannibalized. Spiderlings never cannibalized kin.



**Figure 2** Percentage mortality of *Delena cancerides* spiderlings ( $n = 50$ ) of various carapace width classes when placed with a non-kin mother.

The majority of spider species displays cannibalistic behaviour (Reeve, 1989; Bilde & Lubin, 2001). To the individual, the potential benefits of cannibalism include reductions in competition for food items and retreat sites (Burgess & Uetz, 1982; Dong & Polis, 1992; Bilde & Lubin, 2001). However, in systems where an individual spider is likely to encounter kin, the costs of cannibalism (via a loss of inclusive fitness) may outweigh the benefits (Hamilton, 1964). Consequently, kin-recognition and discrimination systems are expected to evolve in social spider species (Evans, 1998, 1999; Agrawal, 2001; Baras & d'Almeida, 2001; Michimae & Wakahara, 2001). There are also well-documented benefits associated with kin recognition in the absence of cannibalistic behaviour, especially in social spider species. Kin recognition may, for example, act to reduce competition among kin for resources, particularly in social spiders that display delayed dispersal (Aviles & Gelsey, 1998). Similarly, kin recognition may provide a means of achieving outbreeding (Johannessen & Lubin, 2001). *Delena cancerides* is an outbred social spider species with delayed dispersal and, as such, kin recognition would be particularly beneficial to the inclusive fitness of individuals of this species.

Given the extreme aggression displayed by *D. cancerides* towards extra-colony conspecifics (Rowell & Aviles, 1995), it was predicted that *D. cancerides* would recognize kin and that the kin-recognition starvation trials would produce results rapidly. In a similar experiment, *Diaea* – the only other social spider taxon that does not depend on an aerial web as a platform for sociality – exhibited cannibalistic behaviour within 16–26 days (Evans, 1999). In contrast, while kin discrimination was found to occur, *D. cancerides* spiderlings cannibalized non-kin within hours of the triplet trial or not at all, the experiment sometimes lasting as long as 6 weeks before one or more spiderlings died of starvation. This was an unexpected result because, although it has been

found previously that social spiders may 'resist' engaging in cannibalism for significant periods of time (D'Andrea, 1987; Bilde & Lubin, 2001), individuals 'preferring' to die rather than to cannibalize have not been found elsewhere in the literature; *D. cancerides* appears to be unique in this behaviour. The fact that this tolerance mechanism occurs in juvenile *D. cancerides* individuals suggests that although individuals will discriminate between kin and non-kin conspecifics under extreme deprivation, they may be reasonably tolerant of non-kin individuals when conditions are good. This finding is significant as this species has previously been characterized by its extreme aggression towards non-colony individuals; our results suggest that juvenile dispersal could be the means by which outbreeding is possible in this outbred species.

The second major finding of this study concerned maternal tolerance of juvenile spiders, adult females being found to unequivocally tolerate non-kin spiderlings of under 3.0 mm carapace width. A key parameter of the experimental design was the use of nursing and incubating adult females. Preliminary tests showed that, in contrast to the aforementioned adult females, pre-laying and incubating females always cannibalized introduced juveniles. Previous studies have also shown similar results; for example, a study by Assi Bessekon & Horel (1996) on *Coelotes terrestris* (Wilder) (Araneae, Agelenidae) found that pre-laying and incubating females cannibalized introduced conspecific young, whereas brooding and post-dispersal females were tolerant towards introduced spiderlings. This finding is particularly important given that this species is generally aggressive towards conspecifics from other colonies (Rowell & Aviles, 1995). Although the sample size was insufficient to identify a precise size threshold, these results clearly indicate that smaller spiderlings are tolerated. The results show that tolerance of non-kin juveniles by adults is possible, despite the aggression characteristic of the species.

Together, our findings provide a means by which dispersal and gene flow may occur in this species, that is, through the dispersal of juvenile spiders. In a species that is distinguished by the degree of outbreeding it displays and the high levels of aggression towards non-colony individuals, this study suggests a means by which *D. cancerides* colonies recruit new members.

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