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Sociality in a bark-dwelling huntsman spider from Australia, *Delena cancerides* Walckenaer (Araneae: Sparassidae)

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Summary

Social behavior is reported for the first time in a member of the family Sparassidae (Araneae), the Australian huntsman spider *Delena cancerides* Walckenaer. Unlike any previously known social spider, this is a bark dwelling species and, thus, its sociality cannot have its basis on an aerial web, the structure that has been considered central to the evolution of sociality in other spider species. Colonies of *D. cancerides* may comprise up to 300 individuals living in close physical contact under the exfoliating bark of dead *Acacia, Callitris* and *Casuarina* species. Specimens maintained in the laboratory feed communally and capture prey jointly. Although this intranest tolerance and communal feeding behavior is reminiscent of other highly social spiders, *D. cancerides* notably differs from these other species in the extreme aggression shown towards members of foreign colonies, its outbred population structure, and lack of sex ratio bias. We suggest that sociality in this species may have been facilitated by the presence of extended maternal care in the ancestral phylogenetic lineage, as suggested by the occurrence of such behavior in related nonsocial species, and that colonial living may have arisen as a consequence of the reduction and fragmentation of *Delena*'s habitat associated with the rise to dominance of the eucalypts. The apparent colony recognition observed may have evolved because *Delena*'s hunting habits may require mechanisms to locate one's own colony after foraging expeditions and to exclude wandering outsiders from entering one's nest, in contrast to web-bound species that do not need to leave their nest to forage. How the observed outbreeding is accomplished in the face of *Delena*'s extreme intolerance to members of other nests, as well as how new colonies are formed, are issues that have yet to be investigated.

Introduction

Social behavior has been reported in a few dozen of the over 34000 described spider species. Of the social species studied, all but three social Australian thomisids (Main, 1988; Evans, in press), rely on a web as an integral part of their social lifestyle. The web serves as a structural support for the colony and a platform for social

interaction and communication, as well as a snare for the capture of prey. In many species, prey capture itself is a cooperative activity, and prey items are shared among members of the colony.

Here we present preliminary observations on the social behavior of the Australian huntsman spider *Delena cancerides*. The presence of social behavior in *D. cancerides* is particularly remarkable because this is a hunting rather than a snare building species, and its social behavior has evolved in the absence of a heavy reliance on a web structure. *D. cancerides* is unusual in other aspects as well, including its chromosomal make up (Rowell, 1990), outbred population structure, lack of sex ratio bias, and extreme intolerance to members of other colonies. The discovery of social behavior in *D. cancerides* was incidental to a study on chromosomal variation in the Sparassidae, and has only been mentioned briefly in genetics publications dealing with its unusual chromosomal make up (Rowell, 1985, 1986, 1988, 1990, 1991a,b). In addition to both field and laboratory observations of this species, whenever possible, we present parallel observations on some of its non-social relaties, in particular members of the related genera *Pediana* and *Isopoda*.

The spider

D. cancerides is a large species, with adult female body lengths often in excess of 30 mm, and up to 45 mm. The flattened body and laterigrade legs are more marked than in other Australian sparassids (in Australia, Roewer 1954 recognizes 93 species in 10 genera, the commonest of which occur in *Olios, Isopoda*, *Heteropoda* and *Delena*). Adult coloration ranges from tan to orange, in contrast to the brown or gray of other large sparassids, and the anterior median eyes are much closer to each other than to the lateral eyes. The highly flattened body and eye distribution are sufficient to distinguish *D. cancerides* from all other sparassid species in Australia. The two species listed by Roewer in the genus *Delena* – *D. cancerides* Walckenaer and *D. crabioides* Walckenaer (1837) – are probably synonymous, since from its description (Walckenaer, 1837) the latter species is indistinguishable from the former and its type is lost (Simon, 1880).

D. cancerides is a very widespread species, which has been found wherever major collections have been made in Australia and its associated islands (Hogg, 1902). We have collected specimens from subtropical woodlands in Queensland, through to areas in the southern highlands and Tasmania which are subject to freezing temperatures and snowfalls in winter. This species was also recently accidentally introduced to New Zealand, and established itself in the Avondale region, where it is commonly referred to as the "Avondale spider". Six distinct chromosomal races of *D. cancerides* have been identified (Rowell, 1990), as well as a hybrid population between two of these races (Hancock and Rowell, in press). Despite major chromosomal differences, the chromosomal races show little genetic divergence at the electrophoretic level (Rowell, 1990).

Materials and methods

Field observations

Spiders were collected from eastern and southern Australia. Colonies were sought by lifting segments of exfoliating bark from tree trunks in search of the golden webbing peculiar to *D. cancerides*. When a colony was found, the bark was removed from the tree while one or two additional people tried to capture the rapidly dispersing spiders with a large net and vials. Because the collections were aimed at obtaining males and a single colony member for chromosome and population-level allozyme analyses, the methods did not ensure the collection of representative samples of entire colonies. Nevertheless, it was possible to make a number of qualitative observations on the size and age structure of these colonies. Additionally, more thorough samples (but still not complete) were obtained from 6 colonies used to measure the sizes of different instars and to do a preliminary survey of within-colony, allozyme polymorphism.

Laboratory observations: intraspecific tolerance and feeding

A number of individuals and a colony that was dispensable to other aspects of the wider study were tested for intraspecific tolerance by placing them together in glass jars in various combinations. In tests involving small numbers of individuals, $3'' \times 8''$ glass jars were used, which ensured that individuals were able to avoid physical contact. The whole colony was housed in a larger jar ($\sim 10'' \times 14''$). Data on intraspecific tolerance were also collected while performing breeding trials. Male and female spiders collected from separate trees from Kioloa, NSW, were placed in pairs into each of six wood and screen-wire cages ($15'' \times 15'' \times 24''$) with several large pieces of *Acacia* bark, a petri dish of damp cotton wool, and a number of *Galleria* larvae for food (these were previously found to be readily accepted by *D. cancerides*).

In addition to feeding for specimen maintenance purposes, *Galleria* larvae and wingless butterflies were introduced into 2 colonies in order to observe feeding behavior.

Sex ratio estimates

Primary sex ratios were estimated by karyotyping embryos (Avilés and Maddison, 1991; Rowell and Main, 1992) from one egg sac collected from the Australian Capital Territory in November 1993 (other egg sacs could not be collected undamaged). This egg sac belonged to the CIX race, which has a male karyotype of $2n = 22$, consisting of 21 metacentrics and one telocentric chromosome, and a female karyotype of $2n = 24$, of which 22 are metacentric and two telocentric (Rowell, 1985). In addition, preadult individuals were sampled from one colony collected near Newcastle on 21/5/86 and hatchlings from single colonies at 3 sites were dissected to determine their sex. Homogeneity among populations was tested using the G-test for homo-

geneity of Sokal and Rohlf (1981). Ninety five percent confidence intervals were calculated on the basis of binomial probabilities.

Genetic structure

Allozyme electrophoresis was used to assess the genetic structure of populations and colonies. Twenty presumptive loci were assayed with methods as described in Rowell (1990). These were GPD, LDH, MDH1 & 2, IDH1 & 2, 6PGD, G6PD, GAPDH, AAT1 & 2, HK, AK, PGM, ALD, FUM, PGI and three general protein loci. Results for only nineteen of these loci are presented since the ALD locus was found to be sex-linked in one of the races (Rowell, 1990). Four individuals each of three nonsocial species (*Isopoda vaster, Isopoda* sp. and *Olios diana*) were also examined electrophoretically. Two loci (IDH1 & 2) could not be scored for these species.

For each of the six chromosomal races and a hybrid population (Rowell, 1990) polymorphism, heterozygosity, and inbreeding coefficients were calculated separately. A total of 231 individuals (representing 231 colonies or potential colonies) from 39 sites were assayed. The spiders were collected either as solitary individuals or as single representatives of colonies occurring in separate trees. The latter were presumed to belong to distinct colonies, even though, owing to the absence of data on dispersal patterns in this species, it is possible that individuals collected from nearby trees were related and/or recently derived from the same colony. All but eight of the individuals assayed were sufficiently mature to establish their sex on the basis of morphology (i.e. they were adults or subadults). In order to prevent any bias in calculations, only collections consisting of ten or more individuals (i.e. colonies) from any one chromosomal race were included. Data are also included from a collection in the vicinity of the hybrid zone between the Southern tII race and the CIX race (Hancock and Rowell, in press).

Polymorphism levels and observed and predicted heterozygosity levels were calculated for the *D. cancerides* data using the BIOSYS-2 Package of Swofford and Selander (1981). Inbreeding index (F_{IS}) was calculated as $(H_e-H_o)/H_e$, where H_o is the observed average heterozygosity per individual per locus, and H_e is the expected value assuming Hardy-Weinberg equilibrium.

A preliminary analysis of the genetic structure within colonies was also conducted by assaying the polymorphic loci in one cohort of juveniles and the single adult female contained in each of three separate colonies. An adult male associated with one colony was also included. Cohorts were identified as groups of individuals of similar size, with a distinct discontinuity between these and the next highest and lowest size classes. The loci which showed variation within any given colony were analyzed to determine patterns of relationship within groups.

Results

Distribution and habitat of D. cancerides

Colonies of *D. cancerides* are most commonly found under sheets of exfoliating bark on dead *Callitris, Acacia, Banksia* and *Casuarina* species. When these trees die, the trunk contracts, leaving a narrow, uniform gap between the bark and the trunk, often around the full circumference of the tree. *D. cancerides* populations may become very dense in large stands of their preferred tree species, especially on *Casuarina* which occurs densely along rivers and floodplains. Occasionally, *D. cancerides* may be collected on *Eucalyptus* species, particularly in areas where individuals of the related sparassid genus *Isopoda* are uncommon or absent, however the different patterns of bark exfoliation in eucalypts result in fewer appropriate nesting sites for *D. cancerides*. Solitary individuals are also encountered, and these tend to be primarily adult females, although solitary males and juveniles are also found.

Nonsocial relatives

Although the common solitary huntsman spiders in Australia may be very numerous at any given locality, only one or very few individuals are found on a single tree. Occasionally an adult male and female may be found under the same piece of exfoliating bark.

Prior to egglaying, individual females of the solitary genera *Isopoda, Pediana* and *Olios* (usually) construct a sealed, web-lined cavity under bark, slightly wider than the female's leg span (Fig. 1). Here they lay a parchment-like, lens-shaped or spherical egg sac, which is suspended by tough silk threads attached to the bark and tree trunk. They remain in the cavity during incubation and for 2 to 3 weeks after hatching. In *Pediana regina*, the hatchlings congregate on the mother's body.

Females of *Isopoda vaster*, a large sparassid common in south eastern Australia, are often found in nests with a currently incubating egg sac and two or three empty sacs that have previously hatched, indicating that the female remains in the general vicinity for long periods of time, repeatedly using the same site for incubation of successive egg sacs. Alternatively, it may reflect consecutive use of the same site by several different females. Only gravid females or females with eggs or young appear to construct nests.

Nest and colony structure in D. cancerides

D. cancerides colonies generally consist of a single female and a number of size classes of juveniles, with some colonies containing up to twelve adults of both sexes and 300 juveniles. In very large colonies all instars may be present. Colonies that contain multiple size classes appear to have a pyramidal size structure, with small spiders the most numerous, and decreasing numbers of successively larger individuals (Fig. 2).

Bark sheltering the colonies is firmly secured to the tree surface with lines of extremely tough, shiny, golden-brown webbing peculiar to this species. Similar

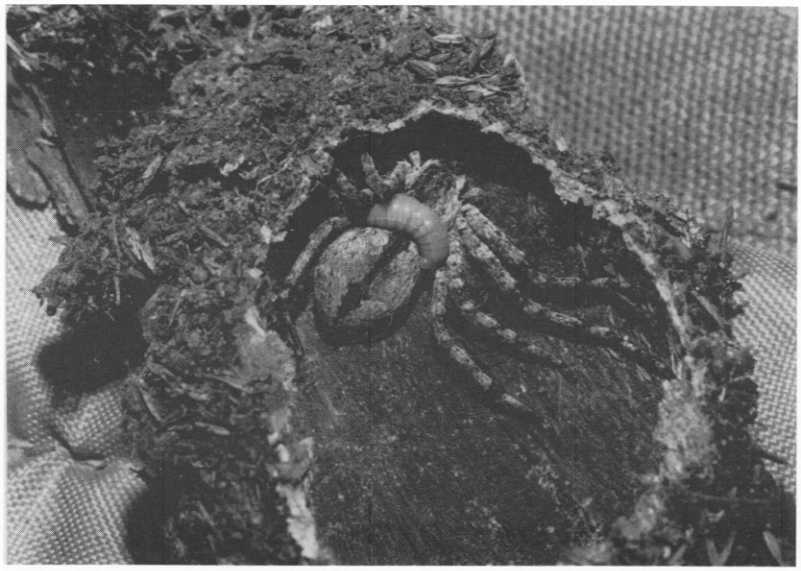

Figure 1. Gravid *Pediana regina* showing structure of web-lined nursery cell. This individual is being parasitized by a hymenopteran larva

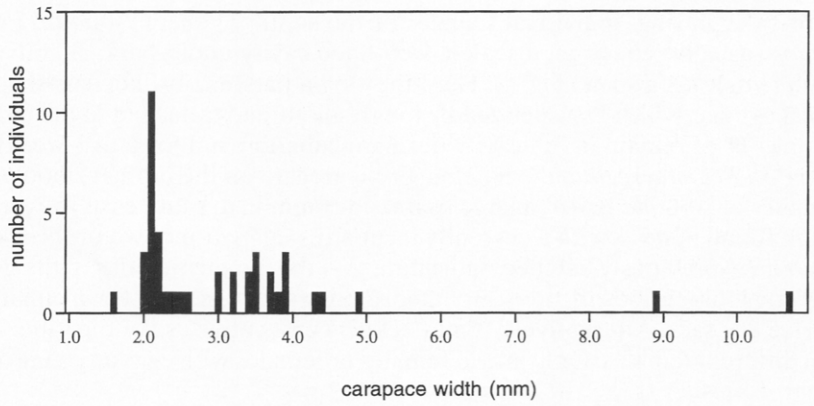

Figure 2. Size distribution histogram for a *D. cancerides* colony collected from Greenways, S. A.

sheets of webbing seal cracks and gaps in the bark (Fig. 3). These sheets are water repellant but permit airflow. This distinctive web was also found associated with solitary females of *D. cancerides*, but not solitary males or juveniles.

In contrast to the tough, parchment-like egg sacs of *Isopoda, Olios* and *Pediana*, the eggs of *D. cancerides* are contained in a fine, more loosely woven silk envelope which is securely anchored flat to the trunk, or occasionally the inner surface of the bark. In colonies with multiple adult females, more than one egg sac may be present, and evidence of numerous, hatched egg sacs is common.

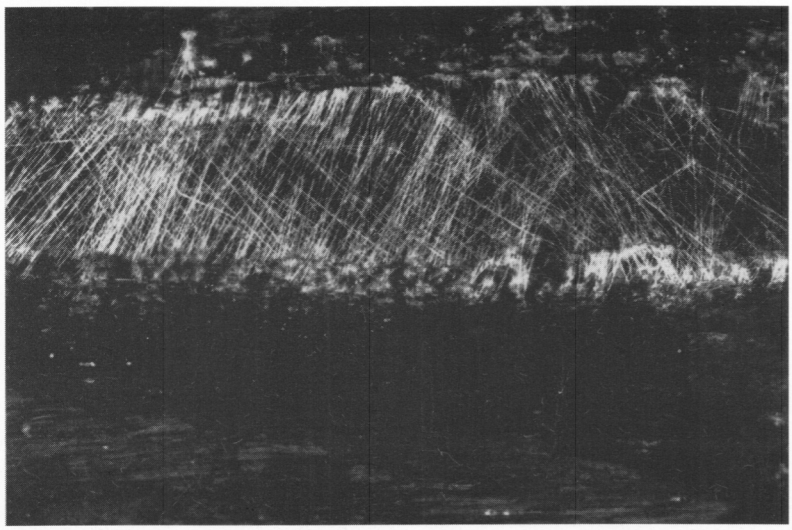

Figure 3. Golden webbing sealing a crack in a piece of *Casuarina* bark. This type of web is peculiar to *D. cancerides*

Prey capture and feeding

Foraging and feeding has not been observed in the field. In the laboratory, *D. cancerides* spiders readily feed on moth larvae (*Galleria* sp.) and mealworms (*Tenebrio mollitor* larvae). When the colony from Greenways, SA (vi, next section) was fed wingless butterflies or *Galleria* larvae, the prey items were often subdued by more than one individual, although this appeared to take the form of independent, uncoordinated attacks rather than a concerted effort. Spiders would pull the prey in different directions before finally settling down to feed from it (Fig. 4). Often more than one individual would feed on any particular prey item, and small juveniles frequently crowded the surface of the prey being fed on.

Intraspecific tolerance and nest defense

The density of spiders in the nests can be very high (see above) and individual spiders are generally in physical contact with one another. Spiders from the same nest often lie on top of each other when maintained in the laboratory. In contrast to this extreme intra-nest tolerance, spiders belonging to foreign colonies were readily attacked.

The following observations relating to intraspecific tolerance were made in the laboratory:

(i) In all six breeding trials involving a male and female from separate trees, the female killed and partially devoured the male within 24 hours.

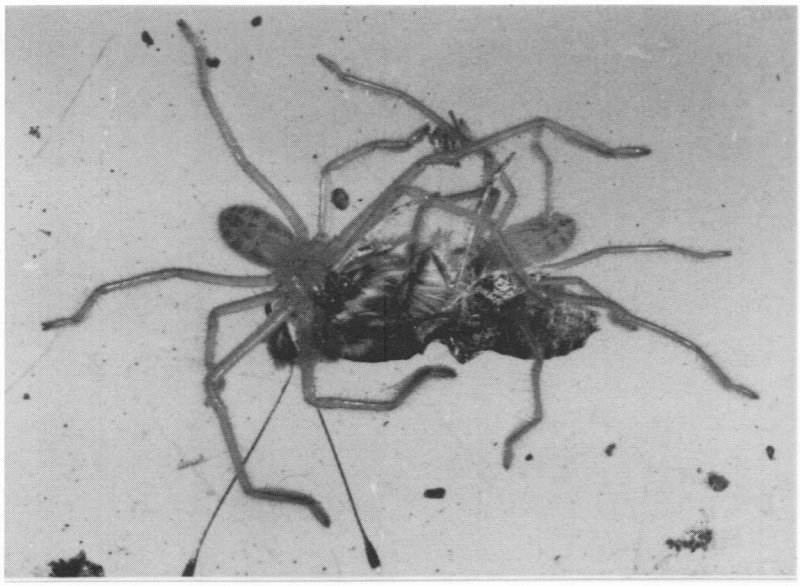

Figure 4. Two juvenile *D. cancerides* feeding on the same prey item

(ii) Two specimens – a subadult male from Bugaboi, Vic (CIX race) and a small juvenile from Bega, NSW (CIX) – were placed in a jar together. The following morning the small juvenile had been killed and eaten.
(iii) An adult female from Tomakin, NSW (CIX) and a juvenile from Merry Beach, NSW (CIX) were placed in a jar together. The next morning the juvenile had been killed and eaten, and the female was missing four legs.
(iv) Two jars containing three and four juveniles from the same colony from Kioloa, NSW (CIX) were kept separate for three months. After this period, the jars were combined. The spiders aggregated, all in physical contact with at least one other individual and no aggressive behavior was observed. After a week, all were still alive.
(v) A juvenile collected from a colony from Kioloa, NSW (CIX) was placed in a jar with three juveniles collected from another colony 20 meters away. It was immediately killed by the three.
(vi) A colony from Greenways, SA (mII) of approximately 50 individuals consisting of four distinguishable cohorts of juveniles and an adult female was maintained in the laboratory for two months. At this point, two juveniles from Glenthompson, Vic (mII), slightly smaller than the largest cohort, were placed in the jar. These remained together but separate from the rest of the colony for about two weeks. After this time they joined the main aggregation and their presence was tolerated. Shortly afterwards, the adult female died (for no apparent reason) and was replaced with an adult female from Glenthompson, Vic (mII). Over the next five days, the new female killed (but did not eat) all of the colony members except for three males; two adults and one subadult. The

four spiders remained together for almost six weeks, when the female laid a small egg sac, and the males were removed. Two weeks later eleven hatchlings emerged, but died within a week.

Despite this strong internest aggression, *D. cancerides* does not seem to have colony-level defence mechanisms against large predators. It is not an aggressive species and when colonies are disturbed for collection purposes, no concerted effort is made to defend the nest. Adult females, particularly those with eggs or hatchlings, may attempt to bite, however.

Population structure

Details on the levels of allozyme polymorphism (# alleles/locus), heterozygosity, and the inbreeding coefficient (F_{is}) observed in the 6 populations of *D. cancerides* surveyed are given in Table 1. Although the observed heterozygosity is slightly lower than expected under Hardy-Weinberg equilibrium, the difference is not significant in any of the populations surveyed. Consequently, no significant inbreeding has been detected in *D. cancerides*. Polymorphism variables are also given for the three nonsocial sparassid species (Table 1) but, given their small sample sizes, the inbreeding coefficient was not calculated and expected heterozygosity levels should be treated with caution. The *D. cancerides* races showed levels of genetic variability within or above the range for the nonsocial Australian huntsman species for number of alleles/locus, percentage of polymorphic loci and observed heterozygosity.

Table 2 shows the results of within-colony variation for cohorts from the three colonies of *D. cancerides* examined. From these data it is clear that none of the cohorts is exclusively the progeny of the adult female collected from the same colony, even allowing for multiple fathers. Incompatible genotypes were seen in 2/10 , 4/9 and 3/8 of the progeny in the three colonies, respectively. Similarly, 4 of the

Table 1. Genetic variability measures and inbreeding index (F_{is}) for the six chromosomal races of *Delena cancerides* and three non-social sparassid species. Average no. of alleles and heterozygosity levels are given with 95% confidence limits. F_{is} was not calculated for the non-social species, owing to the very low sample sizes

Race/Species	Mean Sample size	Mean # Alleles per locus	% Loci Poly-morphic	Heterozygosity		Sig	Inbreeding
				Observed	Predicted	0.05	Index (F_{is})
tII (Nothern)	19.1	1.7 ± 0.4	42.1	0.066 ± 0.041	0.084 ± 0.054	ns	0.214
tII (Southern)	13.7	1.7 ± 0.6	31.6	0.064 ± 0.06	0.088 ± 0.071	ns	0.272
mII	38.8	1.9 ± 0.6	47.4	0.053 ± 0.035	0.058 ± 0.041	ns	0.086
CV	45.7	2.1 ± 0.6	68.4	0.054 ± 0.035	0.08 ± 0.055	ns	0.325
Hybrids	15.4	1.8 ± 0.6	52.6	0.083 ± 0.053	0.094 ± 0.059	ns	0.117
CIX	90.2	2.9 ± 0.8	68.4	0.094 ± 0.056	0.107 ± 0.065	ns	0.121
Isopoda sp.	4	1.2 ± 0.4	11.1	0.014 ± 0.027	0.069 ± 0.098		
Isopoda vaster	4	1.4 ± 0.2	33.3	0	0.159 ± 0.110		
Olios diana	3.9	1.2 ± 0.2	16.7	0.069 ± 0.110	0.075 ± 0.086		

Table 2. Electrophoretic data for colony cohort analysis. Variable loci shown only. The following assessments are made – i) whether an individual male may have fathered the cohort, assuming the adult female is the sole mother of the cohort (if yes, the most probable paternal genotype is given), and ii) whether the adult female could be the mother of the whole cohort, if multiple fathers are permitted. For Colony 3, the possibility that the adult male collected could be the father is also assessed, allowing for multiple mothers

Colony 1	ALD	GPI	PGM	MPI	GOT-1
Adult female	B B	A A	B B	C C	C C
Juv 1	A B	A A	B B	C C	C C
Juv 2	A B	A A	B B	C C	C C
Juv 3	A B	A A	B B	C C	C C
Juv 4	A B	A A	B B	B C	C C
Juv 5	A B	A B	B B	B C	C C
Juv 6	A A	A A	B B	C C	C C
Juv 7	A B	A A	B B	A B	C C
Juv 8	A B	A A	B B	B C	C C
Juv 9	A B	A B	B B	B C	A C
Juv 10	A B	A A	A B	B C	C C
Putative father	×	A B	A B	×	A C
Adult female = mother?	×	√	√	×	√

Colony 2	ALD	IDH-1	GOT-1	MPI
Adult female	A A	A A	A B	B B
Juv 1	A A	A A	A B	B B
Juv 2	A B	A B	A B	A A
Juv 3	A A	A B	A A	A B
Juv 4	A B	A A	A B	B B
Juv 5	A B	A A	A B	B B
Juv 6	A A	A A	A B	B B
Juv 7	A B	A B	A A	A A
Juv 8	A A	A B	A A	A A
Juv 9	A A	A A	A A	A A
Putative father	A B	A B	A –	×
Adult female = mother?	√	√	√	×

Colony 3	PGD	ALD	PGI	PGM	IDH-1
Adult female	C C	B C	F F	E E	B B
Adult male	C C	B B	F F	E E	C C
Juv 1	C C	B C	F F	E E	B C
Juv 2	C C	B B	F H	D E	B C
Juv 3	C C	B C	F F	D D	B B
Juv 4	C C	B B	F F	E E	B C
Juv 5	A C	B C	F H	D E	B B
Juv 6	C C	B C	F F	E E	C C
Juv 7	C C	B C	F I	E E	B B
Juv 8	C C	C C	C F	E E	B B
Single Paternal genotype	A C	B C	×	×	×
Adult female = mother?	√	√	√	×	×
Adult male = father?	√	×	√	×	×

√ = yes
× = no

Table 3. Sex ratios for hatchlings from 3 colonies (the number of individuals sexed reflects the success in distinguishing ovaries from testes at a stage when these organs are still small)

Locality	# Males	# Females	Total
Tamworth, NSW	14	15	29
Kuringai, NSW	4	1	5
Greenways, SA	6	6	12
Total	24	22	46

Heterogeneity G = 3.692 (non significant)
Proportion males = 0.522 ± 0.15 (95% c.i.)

juveniles in colony 3 could not be the progeny of the male collected from the same colony.

Sex ratio

In all, 40 embryos from one egg sac were sexed on the basis of their karyotype. Of these, 21 were male and 19 female (proportion of males = 0.53 ± 0.16, 95% c.i.). Moreover, a significant sex ratio bias in hatchlings was not detected at any of the sites examined (see Table 3) and a sample of individuals with visible secondary sexual characters from a colony near Newcastle still maintained and even sex ratio (6 out of 12 individuals successfully sexed were males).

Discussion

The combination of traits that characterize *D. cancerides* make it unlike any previously described social spider:

(1) it is a hunting rather than a snare building species, so that the hypothesis that the web constitutes a preadaptation for the evolution of social behavior does not apply to this species;
(2) it shows strong aggression among members of separate colonies, suggesting the existence of colony-level recognition mechanisms so far unknown in other species;
(3) its populations exhibit levels of genetic polymorphism consistent with an almost panmictic population structure, in contrast with most species with a similar level of social behavior so far studied; and
(4) its colonies produce an equal number of males and females, again, unlike most of these other highly-social species (reviewed in Avilés, 1995).

These traits make it difficult to place *D. cancerides* within any of the previously recognized categories of social spiders (e.g. Krafft, 1979; D'Andrea, 1987; Avilés, 1995). It cannot be classified as territorial because the spiders share a common space and feed communally on prey that may be captured jointly, unlike, for

instance, the territorial permanent-social (or communal territorial) species, such as *Cirtophora citricola* or *Metepeira spinipes*, that maintain individual foraging territories-usually an orb web (Buskirk, 1981; D'Andrea, 1987; Uetz and Hieber, 1995). Second, because *D. cancerides* colonies may contain several adult females, egg sacs and juveniles of more than one cohort, it is unlike the periodic-social (some also known as subsocial) species that form colonies consisting of one adult female and her developing offspring. Because it lacks individual territories, exhibits extreme tolerance to nest mates, shares its food, and its colonies can contain multiple adult females and multiple cohorts of offspring, *D. cancerides* resembles most the non-territorial permanent-social (also known as quasisocial or cooperative) species such as *A. eximius* or *Stegodyphus sarasinorum* (Buskirk, 1987; D'Andrea, 1987; Avilés, 1995). However, its close to panmictic population structure, 1:1 sex ratio, and extreme intolerance to members of other colonies sets it apart from these other highly-social species. The marked aggressiveness against members of other colonies, in fact, makes *D. cancerides* unique among all spider species thus far studied that exhibit any degree of cooperative behavior.

Most, if not all, of these differences might have their root in the radically different lifestyle of the huntsman spiders which do not rely on a silk snare for prey capture and occupy a habitat – the interstitial space behind tree bark – unlike the habitats occupied by any of the other so far known social spiders. On the basis of our data it would appear that we are faced with a completely different type of social spider for which most of the hypotheses to explain the evolution of sociality in other spider species might not apply.

Preadaptations to sociality

One of the two major preadaptations hypothesized to have facilitated the evolution of social behavior in spiders, the presence of extended maternal care in the ancestral phylogenetic lineage (reviewed in Buskirk, 1981; D'Andrea, 1987; Avilés, 1995), however, does seem to apply to *D. cancerides*. In addition to the construction of incubation chambers in the related genera *Pediana, Isopoda* and *Olios*, where females remain with their egg sacs and newly eclosed young for up to three weeks (see Results section), there is evidence that in *Isopoda immanis* the female opens the egg sac for the young to emerge (Coleman, 1941) and that in a species of *Olios* the female offers prey to her offspring (Tretzel, 1961, cited in D'Andrea, 1987). Extended maternal care has also been documented in huntsman spiders of other genera (e.g. Henschel, 1990). The fact that in these genera the females remain in close proximity to their egg sac, and tolerate the presence of and physical contact with their hatchlings for two to three weeks clearly indicates a degree of intraspecific tolerance beyond that found in other solitary spiders. The more advanced social organization present in *D. cancerides* may have evolved, at least in part, from such mother/offspring associations if the period of tolerance between hatchling sibs and between mother/offspring could have been extended to encompass the entire life cycle of the spiders (Shear, 1970; Kullman, 1972; Burgess, 1978; Krafft, 1979).

The webbing surrounding *D. cancerides* colonies is reminiscent of the web surrounding the incubation cells of *Pediana, Isopoda* and *Olios*. In *Delena*, however, it encloses a much wider area, it is a discontinuous barrier so that entry and egress

are possible, and the colored fibers which span the gap between the exfoliating bark and the tree trunk are considerably tougher. The primary function of the continuous webbing of the non-social species is presumably to exclude predators or parasites for the duration of incubation only. As it prefers dead trees which no longer regenerate their bark, the webbing in *D. cancerides* may also serve to strengthen the attachment between the bark and the tree and prolong the life of the nest, potentially indefinitely. Additional protection from predators and parasites may come from colonial living, itself, as also suggested by the much thinner webbing surrounding the egg sacs of *D. cancerides*, when compared to those of the non-social species. Protection against desiccation of the eggs may also come from the presence of several colony members, though the smaller crevices where *D. cancerides* lives may reduce airflow and thus slow evaporation.

The second major trait considered a preadaptation for the evolution of sociality in spiders, the presence of a silk snare for prey capture, is notably absent among the huntsman spiders. Out of a few dozen spider species with different levels of social behavior (Buskirk, 1981; D'Andrea, 1987), in only one other case, the Australian social thomisids (Main, 1988; Evans, in press), has sociality evolved in a phylogenetic lineage lacking a silk snare. The habitat occupied by *D. cancerides*, however, is not without precedent as leading to the evolution of sociality in other arthropods (e.g. in bark beetles, Kirkendall and Raffa, 1995) and the roots for its social behavior might be related to its under-bark life style.

D. cancerides appears to be more of a host specialist than the other Australian huntsman species; its extreme dorsoventral flattenings well suited to the bark crevices found on dead trees of the genera *Banksia, Acacia, Casuarina* and *Callitris*, and the nature of its webbing specifically suits it to hosts in which bark regeneration has ceased. Thus *Delena*'s Australia-wide distribution may have been attained when banksias and acacias first became widespread in the Eocene and Oligocene, respectively (Trusswell, 1993). When the eucalypts (which now comprise 75% of the Australian vegetation – Lange 1980) expanded at the expense of the drier rainforests and Casuarinaceae woodlands (an event dated to 128,000 years ago in certain regions, Trusswell, 1993, p. 554; see also Singh, 1982), *Delena* might have seen its habitat fragmented and reduced.

The associated fragmentation of *D. cancerides* populations and hence reduced gene flow may have led to the divergence of the various chromosomal races. Moreover, a decrease in density of host trees may have resulted in selection for colonial living since only spiders able to tolerate the presence of other individuals in the increasingly fewer nesting sites would have been able to survive and reproduce. Coloniality would then have also allowed the species to maintain viable population sizes. Prey sharing could have evolved as a means of survival during times of short food supply or as a means of attaining larger colony sizes. The participation of several individuals in prey capture (a behavior observed in the laboratory, but not yet confirmed in the field) could also increase capture efficiency, as shown to occur in other social spiders (Nentwig, 1985; Ward and Enders, 1985; Pasquet and Krafft, 1992). Thus, the development of social behavior in this species may be partly attributable to its strong host species preferences associated with specialized nesting site requirements, in contrast with web-living species which are able to construct their own nesting sites and prey snares.

Intraspecific interactions

The under-bark as opposed to web-bound life style of *D. cancerides* may also be responsible for its extreme intolerance to members of other colonies, a trait unique among social spiders. At least two factors may be involved: (1) a need to find and recognize one's own nest when returning from foraging expeditions, a need not present in web-bound species that simply sit and wait for prey; and (2) a need to exclude wandering individuals from foreign colonies, since dead trees of the appropriate kind are most likely a limiting resource while silk snares can be built almost anywhere. How this strong internest aggressiveness has evolved in connection with the remarkable degree of tolerance and physical contact among individuals within colonies is an issue that will need to be addressed in the future.

The nature of the colony recognition mechanisms employed by *D. cancerides* remains to be determined. Some of the observations reported here suggest that they may be based on a colony "smell" rather than on a kin-recognition system: (1) the electrophoretic evidence (see below) suggests that individuals in a colony are not necessarily close relatives, and yet they are tolerated; (2) individuals collected from nearby trees (e.g. iv, in results section) are equally attacked as are individuals from far away areas; (3) the successful integration into the Greenways colony of the two juveniles from Glenthompson (vi), clearly unrelated because of the distance between the two sites, may have occurred because the size of the jar allowed them to escape detection for long enough to acquire the colony "smell". The fact that the female from Glenthompson killed all but three males of the colony into which it was introduced, on the other hand, may be associated with the mate tolerance observed in the nonsocial huntsman species.

Population structure and sex ratio

The levels of polymorphism and heterozygosity exhibited by *D. cancerides* are considerably higher than those found in most spiders of a comparable level of sociality, such as *A. eximius* or *S. sarasinorum*, which typically exhibit levels of polymorphism of the order of 5–8% (for reviews, see Riechert and Roeloffs, 1993; Smith and Engel, 1994; Avilés, 1995). Indeed, with polymorphism levels ranging between 32 and 68%, *D. cancerides* exhibits similar or higher levels of polymorphism than the nonsocial Australian species analyzed (although the sample sizes for the latter are small, Table 1) and its levels of heterozygosity are close to those predicted under the assumption of random mating. Thus, it would appear that sociality in *D. cancerides* has not led to the formation of closed, inbreeding colonies and the consequent loss in genetic variability seen in these other species.

The only other cooperative spider thus far studied where inbreeding is not the rule is the social lynx spider *Tapinillus* sp. from Ecuador (Avilés, 1994). In this species, as in *D. cancerides*, the sex ratio is not female biased, as it is in the inbred cooperative spiders that have sex ratios of the order of 4 to 25 females per male (reviewed in Avilés, 1995). The fact that an equal number of males and females are produced in *D. cancerides* constitutes indirect evidence of its outbred breeding system and lends support to the notion that, in a broad sense, population structure

and sex ratio may have a mutually predictive power (e.g. Williams, 1966; Hamilton, 1987; Avilés, 1993).

The inference of outbreeding in *D. cancerides* is also supported by the within-colony data which show that juvenile from a single cohort do not necessarily share the same parents, or even have one parent in common. This indicates that migration must occur regularly, or that trees are often colonized by unrelated mothers, or both. As the solitary individuals collected are more commonly females, it is possible that female migration forms the basis for the gene flow apparent. How this is accomplished in the presence of the strong intercolony aggression observed is an issue that will need to be addressed in the future.

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