Tolerance, interattraction and co-operation in the behaviour of the social spider *Phryganoporus candidus* (Araneae: Desidae)

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Summary

Experiments and observations were carried out on the behaviour of the social spider *Phryganoporus candidus* (= *Badumna candida*) (L. Koch). The parent female shared food indiscriminately with her own or alien broods, and first instar spiderlings had a poor chance of survival when deprived of this maternal care. Groups of juveniles clustered closer together over time, but tolerance and interattraction changed markedly in subadult and adult females and in adult males. Isolation produced or enhanced a decline in tolerance levels in subadult females and adult males, and these effects were explicable in terms of the spider's life history. The action of pheromones is proposed as a possible explanation for some of these intraspecific interactions. Female spiders that were relatively close to the prey, or those that were larger or hungrier than their siblings (or more familiar with the web), were most likely to contact prey first. Predation was shown to be at least in part co-operative, and co-operation may also be necessary to explain why males tended to avoid contacting prey until it was subdued by females; otherwise, intraspecific tolerance is sufficient to explain those aspects of the predatory behaviour of *P. candidus* reported here.

Introduction

Kullmann (1968) designated three criteria for the recognition of social behaviour in spiders: tolerance, interattraction and co-operation. Although their meanings remain largely intuitive, these terms have persisted in descriptions and interpretations of such behaviour, and seem, moreover, by their generality and simplicity, preadapted to be seminal in the development of a unified theory of animal sociality. More than 50 spider species satisfy one or more of these criteria (D'Andrea, 1987). Those species that exhibit all three through two or more overlapping generations are designated as permanent-social, to distinguish them from periodic-social spiders which exhibit the three criteria only as juveniles and subadults (Kullmann, 1968).

Badumna candida (L. Koch) is a periodic-social spider (Downes, 1993), and is one of three species that together form the *candida* species-group of the genus *Badumna* Thorell (Gray, 1983; Colgan & Gray, 1992). A revision is in progress (M. R. Gray, pers. comm.), proposing that *Badumna candida* revert to *Phryganoporus candidus* (L. Koch), and I have adopted this nomenclature here. *P. candidus* was the least known of the 23 species of social spiders compared in Buskirk's (1981) review. Here I report on a study of maternal care, interattraction, subadult and adult interactive behaviour, and predation, in this species.

Maternal care of the eggs or young is universal among spiders if defined to include furnishing the eggs with a protective silken sac and positioning the sac in some appropriate place. More advanced expressions of maternal care include laceration of egg sacs to enable young to emerge (Kullmann, 1969; Kullmann *et al.*, 1971; Willey & Adler, 1989), regurgitation feeding of the young by the parent female (Kullmann & Zimmermann, 1975; Rowell, 1985) and provision of prey (and trophic eggs) to the young (Tretzel, 1961; Gundermann *et al.*, 1988; Bessekon *et al.*, 1992). Brood care, which can be essential to reproductive success (Gillespie, 1990), is mediated at least in part by discriminatory inhibition of predatory behaviour (Krafft & Horel, 1980), and the necessary mutual tolerance among the spiderlings themselves is a preadaption to sociality (Horel & Krafft, 1986). The questions about maternal care addressed in the present study were whether the young emerged unassisted from the egg sac, whether the parent actively fed or passively tolerated the feeding of her own or alien broods, and whether brood survival depended on the presence of the parent.

The interattractive behaviour of social spiders, itself a necessary component of maternal care, ranges from incomplete aggregation in *Achaearanea disparata* Denis, the spiders rarely touching each other (Darchen, 1968), to tight clustering in *Eriophora bistriata* (Rengger), a typical group of which resembles a "large black mass" (Fowler & Diehl, 1978). It was measured in *P. candidus* by recording the propensity of middle-instar spiders to aggregate over fixed time intervals.

Sex- and age-specific changes in interattractive and interactive behaviour have been recorded for a number of species of social spiders, including *Anelosimus studiosus* (Hentz) (Brach, 1977), *Mallos trivittatus* (Banks) and *M. gregalis* (Simon) (Jackson, 1979a). The life history of *P. candidus*, and in particular the summer dispersal and nest-founding phase, gives grounds to expect similar changes in interactive behaviour between individuals of the same sex as they approach and attain maturity. Most subadult females disperse before their penultimate instar to found nests solitarily; this dispersal may produce, or arise from, a decline in tolerance levels among female siblings. Males often reach maturity together in the home nest, but shortly afterwards disperse to locate females and sometimes compete for them (Downes, 1993). Another aim of the present study, therefore, was to investigate how the onset of maturation affects the high levels of tolerance and interattraction characteristic of *P. candidus* immatures of the same sex. An explanation is offered of the mechanism and adaptiveness of the observed changes.

Hunting in groups, which is characteristic, if not diagnostic, of social spiders, is thought to have two main advantages: a greater chance of detecting and avoiding predators, and an improved harvesting efficiency (Clark & Mangel, 1986). The first of these may apply to foraging groups of orb-weavers (Rayor & Uetz, 1990). The second has been widely demonstrated among social spiders (e.g. Nentwig, 1985; Rypstra & Tirey, 1991). Neither, however, is thought to have been a significant

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factor in the evolution of spider sociality (Seibt & Wickler, 1988a). Indeed, co-operative hunting in general is considered to be more often a consequence of gregariousness rather than its evolutionary cause (Packer & Ruttan, 1988). In kin groups, and with risks of death and injury attendant on subduing prey in the web, the predatory behaviour of non-territorial social spiders is clearly of great theoretical interest. Pasquet & Krafft (1992) report that *Anelosimus eximius* (Keyserling) individuals encircle prey and wait before moving in to subdue it, and that males are less likely than females to be first to engage the quarry. Other than this, little is known of the factors that govern the propensity of individuals to attack prey. The experiments reported here examined the effects of four factors (proximity, size [of predator], hunger and sex) on the likelihood that an individual *P. candidus* would attack a given prey item. The aim was to determine whether group foraging in *P. candidus* depended on co-operation as well as tolerance.

Materials and methods

Specimens of *P. candidus* were obtained from nests collected from a 400 ha area of open dry sclerophyll woodland adjacent to the campus of James Cook University, North Queensland. All observations and experiments were carried out under subdued lighting, a temperature of 22–26°C and a photoperiod of approximately 13 hours light, 11 hours dark. No spider was used in more than one observational or experimental trial. Unless otherwise stated, all specimen selection procedures were randomised.

Maternal care

To determine whether the young could emerge unassisted, 44 unbreached egg sacs were isolated singly in glass containers (50 mm tall, 25 mm diameter) with perforated plastic stoppers, and left without further interference.

Parent-young feeding interactions were investigated as follows: on 18 occasions, the parent female was kept with one of her unbreached sacs (and thus, later, with her newly-emerged brood of young). On other (>50) occasions, the parent female was kept with some or all of the cohort of young that was present in the nest. Observations were made on these groups to determine whether the parent passively allowed her young to feed with her, or actively fed her brood, or neither. A separate series of observations was conducted to determine whether the parent's hunger level or her relatedness to the brood influenced her propensity to share food (Table 1). These observations were carried out in containers (as above) which had been occupied by the females and broods (eight to ten first and second instars) for one to two weeks. Each observation lasted from one to two hours. Prey items used were *Drosophila*, houseflies or cockroaches, distributed as far as possible equally (and in equal amounts) among the replicates.

The effect of the presence or absence of the parent female on spiderling survival was tested by putting groups of ten newly-emerged first instar spiderlings either into glass containers (as above) inhabited by adult females (control, $n=10$) or into similar containers from which the females were removed but whose webs remained (treatment, $n=10$). These experiments depended on the availability of suitable adults and young; randomisation could not therefore be employed, nor were the host females similar in condition or in the age and quality of their webs. In all other respects, however, the experimental conditions were the same for treatment and control spiders. Each group was fed ten *Drosophila* twice a week. Each was terminated when no first instar spiderlings remained, i.e. they had all either moulted or died.

Interattraction

To measure interattraction, 50 pairs of unrelated middle-instar spiders were placed at opposite ends of unwebbed 90 mm petri dishes, one pair to each dish. Their relative positions after 15 minutes, at four hourly intervals thereafter, and at four daily intervals thereafter, were recorded as (i) touching, (ii) close (<20 mm apart), (iii) halfway (20–70 mm apart), (iv) far (70–80 mm apart) or (v) furthest (>80 mm apart). The appropriateness of these distances as measures of aggregative behaviour is based on more than 100 hours of observation of the disposition and behaviour of these spiders in natural nests (Downes, 1994).

Subadult and adult interactions

Trials (total: 213) were conducted of behavioural interactions between pairs of spiders of the same sex and stage of maturation: subadult females (i.e. females one or two moults from maturity), adult females, subadult males (i.e. males one moult from maturity), and adult males. Each of these classes was further subdivided into two groups: those that had a history of isolation, i.e. had been isolated from contact with conspecifics for at least one month, and those that had never been isolated from contact with conspecifics, whether or not those conspecifics were their own siblings.

Trials were carried out by placing the two individuals at opposite ends of an unwebbed 90 mm petri dish, observing behaviour for 15 minutes, then rechecking the following day. The behaviour monitored over the initial 15-minute period was recorded as (i) strongly tolerant, strongly interattracted (the spiders readily adopting body-contact positions), (ii) tolerant, not interattracted (keeping apart without aggression), (iii) barely tolerant,

| | Female from field nest | | Lab-reared female |
	With own brood	With alien brood	With field-collected brood
Unfed for one day	10	6	10
Unfed for ten days	7	8	8

Table 1: Experimental design for *P. candidus* parent-young feeding interactions. Numbers given are replicates (observations) for each combination. An alien brood is one from a nest at least 1 km distant from that of the female concerned.

mildly repulsed (slow and stiff in movements, actively avoiding each other), (iv) intolerant, repulsed (constantly moving, retreating on contact, some aggression), and/or (v) strongly intolerant, strongly repulsed (body-contact leading to frenzied behaviour and sometimes lethal aggression).

Observations were also made on the interactive behaviour of groups of spiders kept either in observation boxes (15 × 15 × 10 cm, wooden, glass front and top) or in plastic containers (10 cm tall, 10 cm diameter) in the laboratory, and on spiders in natural nests.

Predation: effect of distance

For each of 20 trials, middle-instar spiders from the same nest and of similar size were fed to satiation for one week. Ten of these were then placed together in a petri dish (60 mm diameter) and left without food for three days, during which time they set their web. A muscoid fly was then introduced at a point opposite the retreat tunnel that the spiders invariably constructed along about 90–140 degrees of one side of the dish. The movement of the dish's lid during the introduction of prey did not appear seriously to disturb the spiders, which were at varying distances from the prey at the moment of its introduction and which were separated by sight into two groups: the five nearest to, and the five furthest from, the prey. If all spiders were together in the retreat, the trial was postponed. The trial was complete when five separate spiders had contacted the prey; the group (nearest or furthest) to which each of those five had initially belonged was noted. Usually the outcomes were unequivocal, only two trial attempts being aborted owing to confusion of identity (previous experience had shown that the use of marking paint was unnecessary). It was assumed that the spiders behaved independently. This assumption, which applies also to the other experiments on predation described here, is discussed below.

Predation: effect of spider size

The only procedural difference was that the ten spiders of each of the 21 trials comprised two groups of five, one consisting of noticeably larger individuals than the other (making observations straightforward). The first five contacts were recorded in sequence as either large or small, not counting second contacts by the same spider (which were few). Before a trial began, there was never any apparent relationship between spider size and location with respect to the retreat. Randomness in this respect was assumed.

Predation: effect of hunger

The experimental procedure was the same, but the preparation of the individuals used in the trials differed. For each trial, two groups of 20 spiders were fed to satiation for a week, then one group was continued on this feeding programme for a further ten days while the other group was kept unfed. Five from each group were then selected to give a group of ten apparently identical

in body and leg length but differing in that one group had fat abdomens, the other thin, making them easy to distinguish. There was never any apparent relationship between physical condition (i.e. state of hunger) and occupancy of the retreat tunnel; as above, initial locations were assumed to be random in this respect.

A further procedural difference in this experiment was that the two groups (five satiated, five hungry) of spiders used in each trial were introduced to separate petri dishes three days before the trial, and the satiated group fed the day before the trial. On the morning of the trial, one of the groups (this was alternated between satiated and hungry) was extracted from its web and put in with the other, relatively undisturbed, group. They were left to settle down with their hosts for six hours before the trial was conducted. This enabled the effects of "prior occupancy" to be detected. There were ten trials in which prior occupancy was held by hungry spiders and ten trials in which prior occupancy was held by satiated spiders. There were no apparent differences in the amount or extent of the webs set by hungry or satiated spiders.

Twenty trials were also conducted in which both satiated and hungry spiders were introduced simultaneously into an unwebbed petri dish and left for three days before the trial. This avoided the complications of prior occupancy and unequal disturbance before the experiment, but it did mean that by the time an adequate web had been set, the "satiated" spiders had been without food for three days.

Predation: effect of sex

Procedures identical to those of the experiments on distance and size effects were followed, except that each of the 18 trial groups of ten comprised five subadult females and five subadult males. There was no apparent relationship between sex and location with respect to the retreat tunnel; again, randomness was assumed.

Predation: general observations

As well as the above-mentioned formal observations of natural colonies (Downes, 1994), untimed and irregular observations were made over several years among captive and natural groups of P. candidus.

Results

Maternal care

On two occasions, spiderlings failed to emerge from their egg sacs and starved; none had been cannibalised. On all other (42) occasions when intact, unbreached sacs had been kept in isolation, emergence followed normally.

Females did not actively feed their young, either by seeking to share their food with them, or by regurgitation. However, they typically allowed young to feed with them on the same prey item. If the prey was a single, substantial item, i.e. a housefly or cockroach, all the

female spiders which had been unfed for ten days were intolerant of the young during the early stages of the meal. This was shown by sudden jerking of the body, which kept the young at a distance, and/or by retreating with the prey when persistent young endeavoured to feed. As with some other components of behaviour reported here, jerking and retreating were not discrete, all-or-nothing actions. The parent's tolerance always increased as her meal progressed; usually this ended with several or most of the spiderlings feeding with her, sometimes from between her chelicerae. All of the females which had been unfed for only a single day before the test behaved similarly, but were less reactive to (i.e. more tolerant of) the young supplicants. Usually, but not always, females fed with the young until little but scraps remained; spiderlings that had not fed at the mother's mouth usually scavenged these fragments. In about 10% of cases, females left the meal in progress only to return to it later. When parent and young were feeding together, the digestive juices and partly-digested prey soup surrounding and permeating the prey item formed a largely continuous pool, in which all the spiders' mouths were immersed. Females did not discriminate between their own and alien broods in their levels of tolerance or their propensity to share food.

When prey items were several and small, i.e. *Drosophila*, the same feeding behaviour as described above occurred, but only two to four spiderlings would pester the female (unsuccessfully, since she usually ate the whole of it herself and could easily retreat with it). Other groups of two to six spiderlings, provided at least some were second or later instars, subdued and fed upon prey items of their own, and often retreated with fragments to feed individually.

The survivorship of first instar spiderlings with and without the parent female is shown in Fig. 1. Mortality without further development was 9% and 94% respectively ($t=194.06$, $p<0.001$). Corresponding frequencies of moulting to second instar are also given in Fig. 1.
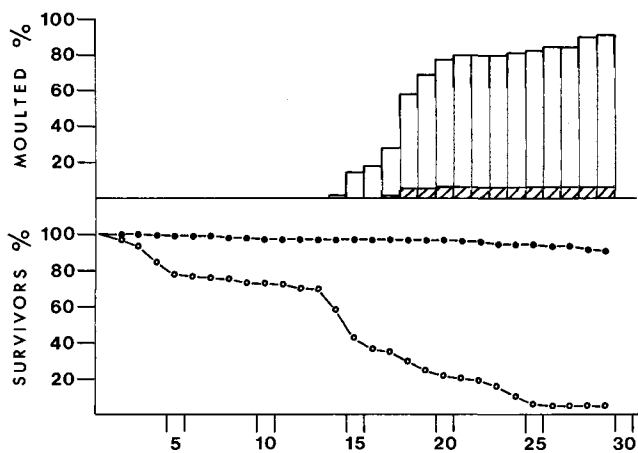

Fig. 1: Survivorship of first instar *P. candidus* spiderlings with the parent female present (closed dots) and with no female present (open dots). Also shown are proportions that moulted to second instar (clear columns, with parent; shaded columns, without parent).

Interattraction

The spiders usually settled into immobility within less than half an hour from the start of the test (often far sooner), and showed very high levels of interattraction (Table 2). More time was spent in body contact than in any other relative position during the resting phase (daytime) of the diurnal activity cycle of these spiders over four days, i.e. over the phase of the cycle when the records were taken. Also, the proportion of time spent either in contact or close together increased over the course of the four days' trial, from 58% for the first 15 minutes to 88% after four days. The spiders were positioning themselves closer and closer to each other as time went by, in conjunction with the establishment of a common web throughout their containers. The frequency distribution of classes of proximity, between the one hour stage (i.e. after the initial settling-down period — see above) and the four day stage, was significantly different ($\chi^2=15.72$, $p<0.005$).

Subadult and adult interactions

Subadult females (siblings) in field nests never fought before dispersal. They subdued prey together and fed without aggression if the prey was too large to be moved from place to place by a single spider; if not, chases, but not fights, sometimes took place. Their behaviour in the laboratory, provided they had been reared in groups (related or unrelated), was no different, and when not feeding they typically settled down in body-contact clusters of a few to many individuals. When extracted from the groups they belonged to, and put together in pairs in unwebbed petri dishes, subadult females, with few exceptions, took up body-contact positions and stayed thus for most of the time in their resting phase (Table 3). The same behaviour occurred when the two test spiders originated from groups reared separately: so long as their history was one of contact with conspecifics since their middle instars, subadult females were mutually both tolerant and interattracted.

Uniting six field-collected subadult founder (i.e. solitary) females in a single unwebbed container in the laboratory produced very different results. One instantly bit and killed another, while others made every effort to avoid body contact. After 10–15 minutes, overt aggression had subsided, but they still behaved frenziedly an hour later if they came into contact. The following day only three were alive, and these were far apart. Two days later they were spaced as far apart as the container would allow. Formal trials in unwebbed petri dishes, using pairs of related or unrelated subadult females with histories of isolation produced similar results (Table 3).

Adult females reared from mid-instars to maturity in batches in the laboratory normally spaced themselves apart from each other; yet it was not uncommon for them to gather in body-contact clusters in their resting phase. When extracted in pairs (from the same, or different, batches, as was done for subadults) and united in unwebbed petri dishes they showed a variety of reactions (Table 3). Their behaviour was thus far less

After	Touching	Close	Halfway	Far	Furthest
15 min	22	36	16	18	8
1 hour	30	22	30	8	10
2 hours	36	24	24	10	6
3 hours	30	32	28	6	4
4 hours	44	28	16	10	2
1 day	42	36	16	6	0
2 days	50	34	14 ˙	0	2
3 days	58	24	14	4	0
4 days	48	40	8	2	2

Table 2: Interattraction in *P. candidus*. Proportions (%) of 50 confined pairs of middle instar spiders showing various degrees of proximity.

predictable than that of subadults, but while they rarely fought or became frenzied when contacting each other, they were unnaturally stiff in their movements and showed a tendency to "freeze" when they touched. On 17 (28%) of occasions, however, pairs of such females settled down in "normal" body contact.

Uniting adult females that had been living alone for a month or more also gave a variety of outcomes (Table 3). Their range of behaviour, however, differed from that of females that had not experienced isolation ($\chi^2 = 42.06$, $p < 0.001$), especially in their tendency to avoid mutual contact. But, like the other adult females, relatively few fought or showed the frenzy characteristic of subadult isolates.

Subadult males, with or without prior isolation, did not differ from earlier instars in their interactive behaviour: tolerance and interattraction were high, most of their resting phase was spent close together or in contact, and aggression was absent (Table 3). The situation was very different with adult males, whose behaviour resembled that of once-isolated subadult females and adult females. The similarity to once-isolated subadult females lay in the way that males with a substantial history of isolation seemed unable to bear contact with males of similar history, displaying, on contact, the same characteristic frenzy and occasional violence. The resemblance in behaviour between adult males and adult females lay in their unpredictability (in contrast to subadults of both sexes, whose behaviour was predictably consistent): whether or not they had a history of isolation, they showed a wide range of levels of tolerance, other than a tolerance of body contact (Table 3). However, their avoidance of body contact and their greater propensity to fight made the range of their behaviour significantly different from that of adult females ($\chi^2 = 35.97$, $p < 0.001$). In general, for adult males reared communally, most were more or less tolerant of each other's presence (i.e. they did not fight), whereas in the case of adult males of solitary background, more than half were intolerant of the presence of conspecific adult males ($\chi^2 = 10.18$, $p < 0.05$).

Predation

The nearer a spider was to an item of prey in the web, the more likely it was that it would contact the prey before more distant individuals did so. Of the 20 spiders

(one in each trial) that were the first individuals to contact their prey, 17 (85%) were initially among those nearest to it, and of the 100 spiders that comprised the 20 groups of five that were the first to contact their prey, 79 were initially among those nearest to it ($\chi^2 = 32.49$, $p < 0.001$).

Spider size had a significant effect on the relative propensity to contact prey. Of the 21 spiders to make first individual contact, 19 (90%) were large, and of the 105 spiders that were the first to make group contact, 68 (65%) were large ($\chi^2 = 8.57$, $p < 0.005$).

Hunger level had a marked effect on readiness to contact prey, when prior occupancy of the test container was not held by either category of spiders (hungry or satiated). In this case, 85% of first individual attackers, and 86% of first group attackers, were hungry spiders ($\chi^2 = 50.41$, $p < 0.001$). When prior occupancy was held by hungry spiders, the proportion of hungry spiders among the first five to contact prey was 100%. However, when prior occupancy was held by satiated spiders, that proportion was 52% ($\chi^2 = 0.02$, $p > 0.75$), and only 20% of first individual attackers were hungry spiders. The evident interaction between hunger level and prior occupancy was confirmed by tests of association: the readiness of hungry spiders to contact prey depended on whether prior occupancy was held by hungry or satiated spiders ($\chi^2 = 29.00$, $p < 0.001$). Similarly, their readiness depended on whether there was no prior occupancy or some prior occupancy (when held by satiated spiders, $\chi^2 = 18.48$, $p < 0.001$).

Subadult males made up 24% of first individual attackers and 34% of first group attackers, and were thus significantly less inclined than subadult females to contact prey ($\chi^2 = 8.1$, $p < 0.005$).

In captivity and in natural nests, when subduing prey too large to be despatched rapidly by a single spider, *P. candidus* individuals, after probing for suitable locations, typically retained the first biting position with which they engaged the prey. In particular, they tended to hang on tenaciously to detached limbs of insects, while their siblings were dealing with the insects themselves. The

	Females				Males			
	Subadult		Adult		Subadult		Adult	
	+	−	+	−	+	−	+	−
Number of trials:	18	30	25	30	20	30	30	30
Strongly tolerant and interattracted		29		17	20	30		
Tolerant, not interattracted		2	10	9	3		6	6
Barely tolerant, mildly repulsed			19	28			8	22
Intolerant, repulsed			23				11	14
Strongly intolerant, strongly repulsed	18		8	6			27	15

Table 3: Levels of tolerance and interattraction in *P. candidus* subadults and adults with (+) and without (−) a history of isolation. Values are frequencies for each of five categories of behaviour exhibited in the first 15 minutes of contact; totals of frequencies exceeded numbers of trials because some trials exhibited more than one category of behaviour.

former spiders gripped the detached limbs for up to ten minutes.

Discussion

Maternal care

Without ruling out an active parental role, it seems very likely that *P. candidus* spiderlings normally emerge unassisted from the egg sac.

Maternal feeding of young in *P. candidus* was passive, as it is in *Agelena consociata* Denis (Krafft, 1966, 1969), so the topic of regurgitation and other active feeding will not be taken up here, except to say that in so far as regurgitation feeding sometimes distributes substances such as endothelial gut secretions (Stern & Kullmann, 1975), it is a potential or actual source of distribution of factors that may influence development and/or behaviour. The same potential should not be overlooked in the case of the "common drinking pool" version of trophallaxis shared during a feed by a parent and young (or, for that matter, any group of individuals) of *P. candidus*. This way of feeding is an effect of tolerant social interactions and a preadaptation for the further evolution of a more advanced social organisation and communication capability.

P. candidus females did not distinguish between their own and alien broods in their feeding behaviour, and this apparent absence of unique colony discrimination probably reflects both the rarity with which adult females encounter offspring other than their own (restricted to occasions when two closely-adjacent, solo-founded nests intermesh their capture webbing during growth), and the rarity with which unrelated individuals ever feed together naturally (Downes, 1993). Similar findings, and a comparable interpretation, are reported by Gillespie (1990) for *Theridion grallator* Simon. In the genus *Stegodyphus* Simon, acceptance of alien broods for feeding by adult females even extends to spiderlings of a different species (Seibt & Wickler, 1988b).

The presence of the female was not always necessary for spiderling survival, but the chances of survival of an orphaned brood were only one-fifteenth those of survival of a brood with a parent. The possibility of trophic egg production by the parent female, as demonstrated in the agelenid *Coelotes terrestris* (Wider) (Gundermann *et al.*, 1991), cannot be discounted, but does not materially affect the present results or their interpretation.

Interattraction

There are at least three possible explanations for the progressive increase in interattraction with time in *P. candidus*. One is that the spiders have body-centred recognition pheromones that differ increasingly with the distance of separation of colonies (i.e. with their history of relatedness), and familiarity with these substances grows with time. Another is that the spiders lace their silk with pheromones that suppress xenophobia, consistent with the fact that the common web was added to daily over the period the spiders were confined together.

A third is that the physical characteristics of the web itself promote aggregation, for an aggregated group occupied only a small portion of a non-homogeneous web. These suggestions are not mutually exclusive, and all are potentially testable by future experiments.

Information hitherto varies on whether social spiders' levels of tolerance and interattraction decrease with distance between colonies. *Agelena consociata*, for instance, shows no different reactions to individuals from nests 50 km away than it does to its own nestmates (Krafft, 1971a), and *Mallos gregalis* from colonies separated by several km behave similarly (Burgess, 1976). Lack of separate colony identity is a consistent feature of the biology of most social spiders (Buskirk, 1981). However, Wickler (1973) noted that when individuals of *Stegodyphus mimosarum* Pavesi are transferred between nests several km apart, the newcomers are "very still" at first, despite there being no evident agitation, nor any aggression. *Coelotes terrestris* was observed to behave in the same way by Tretzel (1961).

Subadult and adult interactions

P. candidus subadult females with a history of isolation were universally intolerant of each other, in marked contrast to those without such a background and also in marked contrast to subadult males with a similar background. The degree of intolerance between subadult female isolates even exceeded that displayed by adult females. Of these three contrasts, that between the sexes relates most directly to the life cycle, since subadult females almost invariably disperse annually from natural nests to found new independent nests, while subadult males normally remain to coexist until they reach maturity in late-cycle nests in February and March (Downes, 1993). The difference in behaviour between subadult females with and without a history of isolation suggests that dispersal produces, rather than arises from, a marked decline in tolerance levels in this sex. However, a decline in tolerance was also apparent in adult females that had not lived alone (as well as in those that had), so intrinsic (hormonal?) changes seem to be operating at maturity if not before. It seems therefore that a decline in tolerance and interattraction among females is largely latent among communal subadults, is fully manifested in them only after they disperse from the nest, and loses its intensity after the maturation moult, apparently because adult females rarely if ever meet in natural circumstances, and probably moult to maturity only in nests established and defended in their subadult stage (Downes, 1993).

For the males, there was no evidence of an expressed or latent decline in tolerance in the subadult stage, but adults did not need to be isolated in order to lose some of their tolerance. Dispersal behaviour of males might therefore be influenced more by intrinsic changes in tolerance levels than it is in females. Nevertheless, the difference between adult males with and without isolation histories suggests that, as with subadult females, a decline in tolerance and interattraction is enhanced by isolation. This might be explained if the levels of these

attributes in subadult females and in adults of both sexes were suppressed by silk-borne pheromones (another testable hypothesis for future work). Pheromones are known to mediate sexual activity (e.g. Rovner, 1968; Jackson, 1981, 1987) and discriminatory behaviour (Jackson, 1982) in spiders, and Wickler (1973) speculated that a chemical signal will be found to mediate spider sociality.

In contrast to the behaviour of *P. candidus* subadult females and adults, Krafft (1970, 1971b) reported that *Agelena consociata* individuals group together more readily after a period of isolation, and when united in groups in unwebbed containers group together before spinning silk. Moreover, this tendency to grouping increases with age, being most pronounced among adult females. However, unlike *P. candidus* which invariably disperses annually, *A. consociata* exhibits a continuity of generations (Krafft, 1971b; Riechert *et al.*, 1986), so a corresponding continuity of levels of tolerance and interattraction, through the adult stage, is not unexpected. The high levels of tolerance characteristic of adults as well as juveniles in permanent-social spiders extends even between species: *Stegodyphus mimosarum* and *S. dumicola* Pocock adult females mix and cooperate with each other as readily as they do with conspecifics (Seibt & Wickler, 1988b).

Predation

The assumption that the test spiders of a given trial acted independently does not imply that interactive influences are unexpected in the group foraging of *P. candidus*, but that the effects of these influences would not materially alter the results of the experiments. The assumption relies on the magnitude of the vibratory signals generated by the prey being great enough to carry to all parts of the 60 mm diameter arena. Because the sounds of those vibrations carried to the ears of the experimenter some 400 mm away, this seems a valid assumption. Recent work has, however, shown that the pursuit of prey by groups of the social theridiid *Anelosimus eximius* is both synchronised and rhythmical, facilitating prey localisation (Krafft & Pasquet, 1991). Whether such co-ordination occurs in *P. candidus* is unknown.

That those individual spiders nearest to a prey item are usually the first to react to it and the first to contact it is an impression almost universal among those who have observed natural colonies of social spiders, though the encircling and waiting behaviour of *Anelosimus eximius* described by Pasquet & Krafft (1992) may obscure or negate that tendency in that species. This effect of proximity on the reaction to prey was confirmed here for *P. candidus*, suggesting that there is no predatory "caste" among the colony members.

Larger spiders tended to be slightly less hesitant than smaller ones in predation, but this tendency need not reflect any division of labour; it is not peculiar to communal feeders and is readily explained in terms of the risk thresholds involved in predator/prey size relationships.

Provided that their familiarity with the web did not differ, hungry spiders were far more inclined than well-fed ones to move quickly to contact and subdue prey. But spiders with limited experience of the web were clearly inhibited, hungry or not, from expending energy and/or taking risks to subdue prey. The risks are potentially serious: mantids and grasshoppers, for instance, are among the insects that pose a marked threat to spiders when caught in their webs (Breitwisch, 1989; Pasquet & Krafft, 1992).

Subadult males showed more caution than females in approaching potential prey, perhaps because they could ill afford loss of, or damage to, one or more pedipalps. Pasquet & Krafft (1992) observed that males of *Anelosimus eximius* were attracted to struggling prey but were never seen to take part in its immobilisation. *P. candidus* males are smaller than females, and, apart from the direct influence of size on predation propensity, it is likely that their relative reticence to engage with prey reflects their relative body sizes and levels of reproductive investment, and hence their relative energy requirements.

When a prey item became available in the web, the spider that made first contact with it was likely to be the nearest, largest, hungriest female. This otherwise unexceptional result implies that group foraging in *P. candidus* depends more on tolerance than on co-operation. Tolerance is the most parsimonious of Kullmann's (1968) three criteria of sociality, because while tolerance is necessary for interattraction and most forms of co-operation, the latter phenomena are not necessary for tolerance. Of the three criteria, tolerance alone is necessary to explain the present experimental results, other than the unequal sharing of the efforts and risks of predation by males and females. Similar conclusions have been drawn for other social spiders, e.g. *Mallos gregalis* (Burgess, 1979). However, *M. gregalis* may sometimes invest energy and materials in subduing and perhaps injecting venom into prey, then leave other (related) conspecifics to gain the benefits of feeding (Jackson, 1979b). Also, the number of social spiders feeding on a prey item often exceeds the number that were involved in killing it (Kullmann, 1970), and *Anelosimus eximius* individuals sometimes participate in kills but do not feed, leaving the prey to others (Brach, 1975).

Darchen (1965) noted the propensity of *Agelena consociata* to grasp a limb of its prey and hang on until the prey is immobile, rather than move to bite it elsewhere. This kind of behaviour, which was observed for *P. candidus* in the present study, differs from that of most solitary web-spiders, and it can be considered a distinctly co-operative way of subduing prey, because the individual spider is relying on similar behaviour by other conspecifics. Group efforts of wrapping and dragging prey items, displayed by *Achaearanea disparata*, have also been interpreted as distinctly co-operative (Darchen, 1968).

It has been pointed out by Jackson (1979b), that since the web contributes so much to the subduing of prey it is presumptuous to call the predatory behaviour of social spiders co-operative, although it might be so indirectly,

because a number of spiders will have contributed to the web. This difficulty is enhanced by the fact that many spider webs direct, amplify and otherwise modify vibratory signals in unexpectedly subtle ways, for instance by filtering frequencies to optimise predation of dipterans (Witt, 1975, 1982; Burgess, 1979).

Concluding remarks

In conclusion, tolerance is necessary for all four kinds of behaviour discussed above, other than the interactive behaviour of some categories of subadult and adult females and of adult males, and is sufficient to explain most of the aspects of predation that came under experimental investigation here. Interattraction is not sufficient to explain maternal care or group foraging but would seem to promote their effectiveness. And cooperation is necessary for maternal care and enhances the success of predation.

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