

THE BIOLOGY OF *CLUBIONA CAMBRIDGEI* (ARANEA, CLUBIONIDAE): INTRASPECIFIC INTERACTIONS

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SUMMARY: *Clubiona cambridgei* is a short-sighted hunting spider that lives on bushes of New Zealand flax (*Phormium tenax*) and constructs silken nests within tunnels formed by rolled-up leaves. Intraspecific interactions in this species are integrally related to the use of nests. In laboratory observations, mating was never observed outside nests, although virgin females readily mated while inside their nests. A distinctive courtship preceded copulation in every case, and displays occurred also in other types of interactions. Interactions were more lengthy at than away from nests. Males cohabited in nests with subadult females. After the subadults moulted and matured, the males mated with them inside the nests. Vacant nests of adult and subadult females elicited courtship behaviour from males, and males discriminated between these nests and ones of males, immatures, and another species of spider, never courting at the latter three types. After being washed in ether, nests of females no longer elicited male courtship, suggesting that contact sex pheromones are involved.

INTRODUCTION

Clubionidae is a large, cosmopolitan family of short-sighted hunting spiders. Three genera occur in New Zealand. Two, *Chiracanthium* and *Supunna*, are each represented by a single species, both probably introduced from Australia, while the large cosmopolitan genus *Clubiona* is represented by 12 species (Forster and Blest, 1979).

One common endemic clubionid, *Clubiona cambridgei* occurs in marshy areas of North and South Island. It lives principally on New Zealand flax (*Phormium tenax*), forming silken nests on the dried, rolled-up flax leaves. These nests are a focal point, with the spiders remaining there during periods of inactivity and during moulting. Females oviposit inside nests and remain with their eggs until they hatch and the spiderlings disperse. Some males cohabit with subadult females in their nests awaiting the female's maturity. It has been suggested (Platnick, 1971) that males recognise conspecific females by their nests alone.

By examining the behaviour of spiders at nests this study sought to:

1. describe the sexual behaviour of *C. cambridgei* to determine the extent of their courtship behaviour.
2. to quantify the role of nests in intraspecific interactions.
3. by experiment to determine whether vacant nests of females elicit courtship from males.

GENERAL METHODS

All spiders were collected from flax bushes at Spencer Park (16 km N.E. of Christchurch). In the laboratory, they were housed individually in glass vials and fed on *Drosophila melanogaster*. Within these vials each spider spun a nest and these were used in subsequent experiments.

To determine behaviours involved in intraspecific contacts, one spider (intruder) was introduced into the cage of another (resident). In male-female interactions, the male was always the intruder. Interactions began when the spiders contacted each other or the intruder contacted the nest. All nests were densely spun, almost opaque, and at least 7-10 days old. When contact failed to occur within 30 min, the intruder was removed. Interactions were considered ended when the spiders moved away from each other or one walked away from the nest. The intruder was then removed to prevent additional interactions. No spider was tested more than once on a given day.

Normally and non-normally distributed data will be presented in the text as means \pm standard deviation and median (minimum-maximum) respectively. Statistical tests are described by Sokal and Rohlf (1969).

TERMINOLOGY

Mature spiders will be referred to as simply 'males' and 'females'. 'Sub adults' are females one moult from maturity and can be identified by the outline of the epigynum which is visible beneath the cuticle

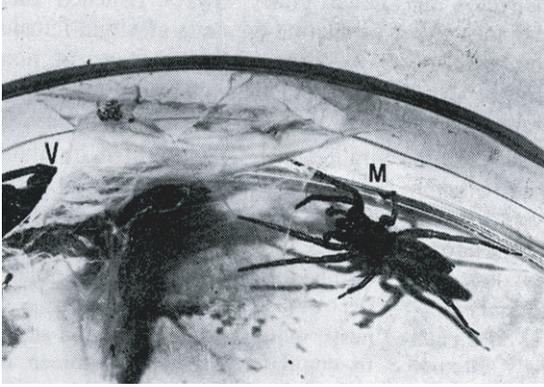


FIGURE 1. Male (M) *Clubiona cambridgei* probing and abdomen twitching on nest of virgin female (V).

of the ventral abdomen. 'Immatures' are spiders at other stages prior to maturity, but excluding post-embryos and first instars still in the maternal nest. A cohabiting pair consisted of a subadult in a nest with a male in an adjoining chamber.

Virgin females were collected as subadults and permitted to mature in the laboratory. Females collected as adults were assumed to have mated previously. These, along with ones that were observed to copulate in the laboratory, are referred to as non-virgins.

The initial response of *C. cambridgei* upon encountering *Drosophila*, conspecifics, and other similarly-sized objects was to spread apart the basal segments of the chelicerae, extend the fangs, and elevate legs I and II. However, the following behaviours occurred primarily during intraspecific interactions.

Abdomen twitch

Abdomen twitching by males consisted of rapid dorso-ventral movements of the abdomen in bouts usually lasting 1-2 sec. Virgin females twitched their abdomens slower than males and in longer bouts (3-4 sec) (Fig. 1).

Lunge

The spider lunged by suddenly extending legs III and IV and moving the body forward 1 - 3 mm toward the other spider, then back to the original position, with the entire motion taking less than 0.5 sec. As the spider lunged, its fangs were held partially extended and legs I and II were sometimes elevated and extended partially forward. At the most forward point of motion, the other spider was sometimes contacted by the lunging spider's legs or face.

Lunging occurred away from nests only. Non-

virgin females always lunged at males. Also, lunging occurred in all female-female and in eight of 25 male-male interactions away from nests.

Stab

Stabbing spiders were always inside nests. Stabbing resembled lunging except that fangs were fully extended and legs I and II were always elevated. The spider always aimed toward the intruder on its nest, and its fangs often penetrated the silk and extended to the outside of the nest, sometimes making momentary contact with the other spider.

Probe

Spiders probed by slightly moving 1-4 of the legs I and II dorso-ventrally after flexing them from the femur-patella and tibia-metatarsus joints, and keeping the tarsi in constant contact with the silk. Males probed in all interactions with virgin females and subadults and in II of the 47 with non-virgin females in nests.

Tear open and enter nest

After inserting both fangs in the silk, the spider elevated its cephalothorax, causing a hole to form in the nest. There were usually several repetitions, each enlarging the hole. Next the spider walked into the nest through the hole it made. Other times spiders entered nests through the doors.

In all male-subadult and 12 of the 22 male-virgin female interactions, males tore open and entered nests. In the other to male-virgin female interactions, the males entered through doors.

Mount

After entering nests, males contacted virgin females and sub-adults with tarsi I and II. Next the male mounted by walking over the facing female

Stroke

While mounted, the male leaned to one side, and with leg I flexed (left leg I if leaning to his right side, and vice versa), stroked by moving it so that the tarsus moved ca. 1 mm dorso-ventrally over the female's lateral abdomen.

Rotate abdomen

As the male stroked, the female's abdomen rotated 4-50 - 90° with the cephalothorax remaining stationary, bringing the epigynum to the male's palp.

Scrape

With the female's abdomen rotated, the male repeatedly scraped by moving his closer palp dorso-ventrally (amplitude: ca. 1 mm) on the female's abdomen in the vicinity of her epigynum.

Copulate

Copulation or mating was defined as occurring

when the male's palpal organ was pressed against and presumably engaged in the female's epigynum. Each palp was applied once. When the first palp was withdrawn, the female's abdomen rolled back to its original position. The male moved back over the centre of the female's abdomen. Next he stroked, the female's abdomen rotated, and the male applied his other palp. When the second palp was withdrawn, the male walked away from the inactive female.

INTERACTIONS AWAY FROM NESTS

The number of interactions observed are indicated in parentheses: male-virgin female (16), male-non-virgin female (30), male-male (25), male-subadult (20), male-immature (27), female-female (25), female-immature (25).

Results

All interactions were brief: male-virgin female, 17 sec (3-24 sec); male-non-virgin female, 7 sec (2-12 sec); male-subadult, 8 sec (2-21 sec); male-male, 5 sec (2-15 sec); male-immature, 2 sec (1-4 sec); female-female, 9 sec (3-27 sec); female-immature, 2 sec (1-5 sec). (Cases in which cannibalism occurred deleted.)

No responses were evident until, seemingly by accident, one spider touched another with a leg while walking. If initially facing away, often the spiders next oriented toward each other. Males which contacted virgin females sometimes briefly abdomen twitched or lunged before one, or more often, both spiders ran away in opposite directions. Virgin females, subadults, and immatures never abdomen twitched or lunged before decamping. In male-female interactions, males always decamped first. In interactions with adults, subadults and immatures decamped first.

INTERACTIONS AT NESTS

The number of interactions observed are indicated in parentheses: male-virgin female (22), male-non-virgin female (47), male-male (25), male-subadult (21), male-immature (20), female-female (25), female-immature (20).

Results

These interactions were often more lengthy than ones away from nests: male-virgin female, 2 ± 0.9 min; male-subadult, 7 min (4-11 min); male-non-virgin female, 27 sec (11-127 sec); male-male, 32 sec (15-174 sec); male-immature, 11 sec (5-47 sec); female-female, 19 sec (4-63 sec); female-immature, 9 sec (4-36 sec). (Cases in which cannibalism occurred deleted.)

There were no responses evident until spiders

contacted the nests. Males always twitched their abdomens after contacting the nests of virgin females and usually did so after contacting nests of non-virgins. Usually abdomen twitching occurred almost immediately, before the female became noticeably active. All the virgin females reciprocated by abdomen twitching from inside their nests, and the males eventually entered the nests and mated with the females for 44 ± 29.5 min. In contrast, non-virgin females always stabbed and the male eventually decamped.

Males entered nests, mounted subadults, and seemingly attempted to copulate. With the abdomen of the subadult rotated, the male scraped in the region of the subadult's undeveloped epigynum. Eventually he left the nest and began spinning. At this point, the pair was separated, but presumably the male would have spun a second chamber and cohabited. (Interaction durations given above measured until the males exited from the nests).

In male-male and female-female interactions, there were short episodes of abdomen twitching and stabbing, respectively, before the resident left the nest or the intruder decamped. In interactions between adults and immatures, the resident immatures soon decamped.

CANNIBALISM

Intraspecific predation occurred during 35 of the 348 interactions observed. Non-virgin females killed males in four of the 30 interactions away from, and seven of the 47 at nests, but virgin females never killed males. Cannibalism occurred also in four of the 25 female-female interactions away from nests and four of the 25 at nests. All other cases of cannibalism involved adults killing immatures: away from nests-male (seven of 27), female (nine of 25); at nests-male (four of 20), female (five of 20).

In each case in which cannibalism occurred away from nests, while the two spiders faced each other, one rushed forward, moved over the other spider, and inserted its fully extended fangs into its partner. At nests, cannibalism occurred either when the resident rushed out of the nest and inserted its open fangs into the intruder or when the intruder grabbed the resident from behind as the latter exited from the nest and began to decamp.

EXPERIMENTS WITH VACANT NESTS.

Methods

A test consisted of dropping a male or female onto a vacant nest and recording its behaviour for the next 15 min. Each spider was tested with a pair of nests, one on each of two successive days. In

each test-sequence nest 1 was built by a male, nest 2 by a female, a subadult or an immature. Each spider was assigned a time slot and tested at the same time on both days. One half of the spiders were tested on the first day with nest 1; the other half, with nest 2. For 10 females, nest 2 was one of another female; the numbers of males indicated in parentheses were tested with nests 2 built by: female (25), subadult (20) and immature (15).

Although spiders that provided nests were often used as test-spiders, they were never tested with their own nests. The same spider was never used in more than one test-sequence of a given type, although it might be used in more than one type of test. No spider was tested more than once on a given day, and no nests were used in more than one test.

Nests built by the males and immatures sometimes consisted of considerably less silk than those of females. In order to determine the influence of this variable, 10 males were tested with nests (nest 2) built by females that had been left in clean vials for only 24 hr. The resulting nests consisted of much less silk than any others in the study, some being only barely recognizable as nests. As before, nests 1 were built by males.

Ten males were each tested with a washed nest 1 (immersed in ether for 60 min and left to dry for 24 hr) and an unwashed nest 2 of a female.

Ten males were each tested with a vacant nest of *Trite planiceps* (nest 1). Nests 2 in these tests were ones of conspecific females.

Results

Females walked over nests of both males and females, but rarely remained on them for more than a few seconds. No abdomen twitching occurred, nor were there any other distinctive responses.

Abdomen twitching never occurred when males contacted nests of other conspecific males or of immatures. However, 21 of 25 males twitched their abdomens after contacting nests of females (McNemar test of significance of change, with Yates' correction; $X^2 = 19.048$, $P < 0.005$), and 16 of 20 males twitched their abdomens on nests of subadults ($X^2 = 14.062$, $P < 0.005$). At 24-hr-old nests of females, eight of 10 males twitched their abdomens ($X^2 = 6.125$, $P < 0.025$).

Although nine of the 10 males twitched their abdomens after contact with unwashed nests of females, each failed to do so on washed ones ($X^2 = 7.111$, $P < 0.005$). Also, although eight of the 10 males twitched their abdomens with nests of conspecific females, each failed to do so with the nests of female *T. planiceps* ($X^2 = 6.125$, $P < 0.025$).

LONG TERM OBSERVATIONS

Methods

Long-term observations were carried out with male-subadult and male-immature pairs. Twenty subadults and 10 immatures were each maintained individually in transparent plastic cages (190 x 120 x 120 mm) and supplied with moisture and *Drosophila* as described by Jackson (1974). After three days a male was introduced into each cage and observations were carried out during both the dark and light phases of the laboratory photoperiod (during the former by briefly shining a light on the spiders). Each pair was checked at least four times a day until moulting or cannibalism occurred.

Results

All 20 males built chambers adjoining the nests of the subadults (Fig. 2) and remained in residence until the subadults moulted. When first observed after moulting, two pairs were in the females' chambers mating; the others had separated. Subsequently, the females were kept isolated. One died a few days later, but each of the others eventually oviposited fertile eggs, indicating that all had copulated after moulting. (Virgin females never oviposited fertile eggs in the laboratory, and parthenogenesis is unknown in the Clubionidae and most spiders.) Cohabitation duration was 9 ± 5.4 days. All males killed and ate the immatures.

DISCUSSION

Display repertoire

Platnick (1971) considered clubionids to have poorly developed courtship and Bristowe (1958) referred to *Clubiona* as having "no marked courtship". This is incorrect for *C. cambridgei*. This species had

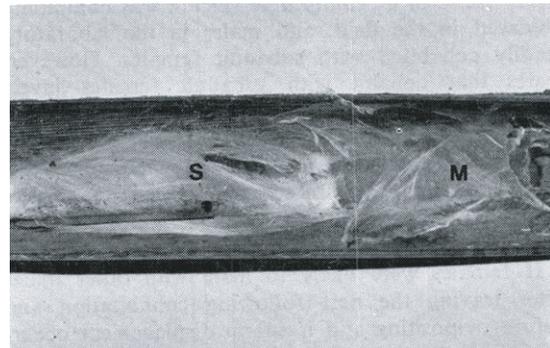


FIGURE 2. Double nest of cohabiting pair of *Clubiona cambridgei*. M: Chamber of male. S: Chamber of subadult female.

a distinctive courtship that preceded copulation in every case, as well as displays that occurred in other types of interactions. Before entering nests of females, males always abdomen twitched and probed; and after mounting, they stroked and scraped before copulation began.

Considering the behaviour of both males and females, abdomen twitching, probing, stroking, scraping, lunging and stabbing are probably displays. Stabbing was sometimes elicited from females when a *Drosophila* walked across their nests. Otherwise, each of these behaviours occurred only during intra-specific interactions.

Considering that their vision is poorly developed, the detection of vibrational stimuli is likely to be of primary importance in the communicatory behaviour of clubionids. Abdomen twitching may convey vibratory stimuli through the substrate, usually a flax leaf when outside nests, and through the silk when at nests. Probing and stabbing may also convey vibrational stimuli across the silk in interactions at nests. Sometimes spiders came into contact with their partners when lunging or stabbing, in which cases tactile stimuli may be important. Stroking and scraping probably convey tactile and/or chemotactic stimuli from the male to the female.

During male-female interactions, virgin females in nests always twitched their abdomens but never stabbed; non-virgins always stabbed but never abdomen twitched. These behaviours have the potential of conveying unambiguously to the male the female's receptivity (abdomen twitch) or non-receptivity (stab).

The relationship between female receptivity and cohabitation

Evidently cohabitation is an important precopulatory tactic of *C. cambridgei* since it was commonly observed in the field, and males in the laboratory readily cohabited with subadult females. However, males that cohabit with subadult females invest considerable time that otherwise might be used in searching for additional mates. In the laboratory, virgin females at nests mated readily, but non-virgin females were always unreceptive to courting males, and this seems significant in understanding the adaptive significance of cohabitation for males.

If females were likely to mate with other males after leaving the nest following cohabitation and before ovipositing and if sperm displacement occurred, as it does in most studied insects that mate more than once (Parker, 1970) and in the two spider species that have been studied (Jackson, 1980a; Vollrath, 1980), then the adaptive significance of cohabi-

tation would be difficult to understand. Since female *C. cambridgei* evidently mate only once, sperm displacement is unlikely to occur in this species. Also, since virgin females are likely to be a limited resource for males (Bateman, 1948; Trivers, 1972), it may be optimal for males to invest time waiting for subadults to moult to adult virgin status rather than searching for adult virgin females (Jackson, 1980b; Parker, 1974); very few of the latter may be present. Also, possibly the risks of predation are less for males who cohabit and remain in nests than for ones who actively search for virgin females in the open (Jackson, 1976).

In contrast to *C. cambridgei*, female *Dysdera crocata* (C. L. Koch) (Oysderidae), a haplogyne short-sighted hunting spider, have been observed to mate with as many as four different males per day (Jackson and Pollard, 1982). It is noteworthy that cohabitation was not observed in *D. crocata*. A male of this species that might cohabit with a subadult would invest time that could be spent searching for females that are likely to be receptive, even if non-virgin. Also it seems likely that sperm displacement might be relatively unimportant in *D. crocata* since the female's spermathecae have space for more sperm than a single male at a single copulation can transfer (Cooke, 1966). Because of these factors, cohabitation seems unlikely to evolve as a precopulatory tactic in this species.

Mechanism by which males determine female maturity

The mechanism by which males determine that females are subadult can be proposed. If the female does not persistently resist the male's entry into her nest by stabbing, then he eventually mounts her in the nest. Males succeed in mating with virgin adult females and attempt to do so with subadults. However, subadults lack functional epigyna, and perhaps it is the failure of attempted copulation that informs the male that the female is subadult. Whether males would mount and attempt to copulate with females more than one moult from maturity is not known because the immatures always decamped soon after the males contacted their nests. However, abdomen twitching was never observed on the nests of immatures.

Cohabitation has been investigated in a salticid species, *Phidippus johnsoni* (Jackson, 1977), but the mechanism by which males of this species determine that females are subadult is unclear. Males of *P. johnsoni* almost never mount subadults.

Nest mediated discrimination

Empty nests of conspecific females, both adult

and subadult, elicited courtship from males. Furthermore, males were able to discriminate between these nests, those of conspecific males and immatures and those of a sympatric jumping spider, never courting at the latter three types. Platnick's (1971) suggestion that male clubionids recognize conspecific females by their nests alone is supported.

Washed nests of females failed to elicit male courtship behaviour, suggesting the presence of contact sex pheromones on non-washed nests. There is evidence of sex pheromones in several other families of spiders (Tietjen and Rovner, 1982), and similar nest-mediated sexual and species discriminations are made by males of a salticid, *P. johnsoni* (Jackson, 1976, 1981). However, this is the first experimental study of this sort to be reported for a clubionid.

Although juveniles do not produce sex pheromones in most species of arthropods (Shorey, 1976), nests of subadult *C. cambridgei* readily elicited male courtship. This is consistent with cohabitation being an important mating strategy in this species.

Mating strategy

Females did not court on nests. This is consistent with a mating system in which males are the ones that search actively for females, and females tend to be more sedentary. This system seems to be widespread in spiders and other animals (Bristowe, 1941; Gertsch, 1949; Jackson, 1977; Daly and Wilson, 1978). Independent evidence of this in *C. cambridgei* was obtained from a life history study (Pollard, unpublished data) in which 13 % of the males but only 4 % of the females were found outside nests.

Although *C. cambridgei* is a vagrant spider that does not use silk in predation, use of silk is integral to the reproductive biology of this species. Copulation occurred inside but never outside nests. During courtship at nests, males probed and abdomen twitched, and females sometimes stabbed. Interactions away from nests were more brief and involved fewer distinctive behaviours than ones at nests. During cohabitation, males remained in nests adjoining those of subadult females. Males were able to discriminate between the vacant nests of conspecific adult and subadult females and those of other sex/age classes of conspecifics and between nests of conspecifics and those of another sympatric species. The presence of contact pheromones on the silk was suggested by these observations. Intraspecific interactions in this species seem to involve behavioural and other adaptations integrally related to the use of silk.

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