NEST-MEDIATED SEXUAL DISCRIMINATION
BY A JUMPING SPIDER (*PHIDIPPUS JOHNSONI*)

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ABSTRACT

Empty nests of conspecific females elicit courtship behavior from males of *Phidippus johnsoni*. Males discriminate between nests of adult males and adult females and also between nests of subadult males and subadult females.

INTRODUCTION

Spiders are the major example in the animal kingdom of adaptive radiation in the use of silk, and it is not surprising that communication is found among its functions. The salticid spiders, however, are unlike most spiders in having highly developed vision (Land 1972) on which they rely in most aspects of their behavior, and the communicatory behavior most commonly associated with spiders of this family consists of dancing and specialized movements and postures of the legs, pedipalpi, and abdomen (Crane 1949). Communication involving the use of silk in this family has received little attention. However, Bristowe (1958) noted that the males of various salticid species show excited "signs of awareness" when they touch unoccupied nests built by conspecific females.

Males of *Phidippus johnsoni* Peckham and Peckham, a common species in western North America, employ visually mediated courtship when they encounter adult females in the presence of adequate light (Jackson 1977 a,b, 1978 a); however, many salticids, including *P. johnsoni*, build silken nests under rocks, in hollow reeds, and in other dimly lit locations and use these for molting, ovipositing, and passing periods of inactivity (Jackson 1979). If a male *P. johnsoni* encounters an adult female inside her nest, he employs vibratory courtship which does not depend on vision. If the female inside the nest is a subadult, the male first courts, then spins a second chamber on the female's nest and cohabits with her until she matures (Jackson 1977).

Males of various non-salticid spiders have been shown to begin courtship in response to contact with draglines, webs, or nests and to make species- and sex-discriminations on the basis of the silk after contact (e.g. Tietjen 1977, Jackson 1978b). This paper is concerned

with similar adaptations related to communication and the use of silk in *P. johnsoni*. In an earlier study (Jackson 1976a) it was shown that male *P. johnsoni* respond to empty nests of adult females with elements of behavior that normally occur during courtship and that they discriminate between the nests of adult conspecific females and the similarly sized nests of *Herpyllus hesperolus* (Chamberlin), a sympatric gnaphosid spider that is a potential predator of *P. johnsoni*. Two questions will be considered in this paper. Do adult males discriminate between the nests of adult females and adult males? Do adult males discriminate between nests of subadult females and subadult males?

METHODS

Spiders.—Spiders were collected as immatures from Tilden Regional Park, Oakland, California. Each adult male and female was 5 to 30 days post-maturity at the time of the tests. All females were virgins. None of the spiders had been involved in interactions with other spiders in the laboratory previous to the tests.

Maintenance and Apparatus.—Details of maintenance are provided elsewhere (Jackson 1974, 1976b). Each spider was kept individually in a transparent plastic cage (10 x 10 x 6.5 cm) with a ventilation hole covered by a metal screen and two 4.5-cm-diameter holes plugged with corks (see Jackson 1978a, Fig. 1). Each spider spun at least one nest fastened to one of the two corks, and the opposite cork-hole provided access to the interior of the cage without damaging the nest.

Testing Procedure.—All tests took place within the first 4 hr. after the lights came on in the laboratory (12L: 12D, lights on at 0900 hr; temp., 24°C). Each spider was forced from its nest with a camel hair brush and removed from the cage 2 to 8 min before introduction of the test male. Any additional nests and any living flies in the cages were removed. All nests were relatively dense (see Jackson 1979) and were 7 to 30 days old. Time elapsing between introduction of the male and his first touching the nest was recorded. A description of his behavior for 30 min following contact was recorded on a tape recorder with a metronome providing a time base (one beat per sec).

The nest used in each test came from a different spider. Each male was tested with one nest on one day and on the following day with a different one. No male was tested with more than one pair of nests. One nest was from a female and the other from a male, each either adult or subadult. One half of the males were tested on the first day with nests of females; the other half, first with nests of males. Twelve males were tested with nests of adults and 18 with nests of subadults.

A random numbers table (Rohlf and Sokal 1969) was used to assign males to groups and particular nests to particular males. No spider provided nests for more than one test. Some of the males were used both for testing and for nest production, but they were never tested with their own nests.

Occurrences of behavior in the pairs of tests were compared using McNemar tests with Yates correction; latencies and durations were compared using two-tailed Wilcoxon signed-ranks tests (Sokal and Rohlf 1969). Latencies were compared only for those males that performed the behavior in question during both tests. Data in text are means ± S.D's when normally distributed; otherwise, medians followed by maxima are provided.

Elements of Behavior.—The behavior of males in the presence of occupied nests has been described elsewhere (Jackson 1977a), and similar behavior occurred at empty nests. Brief descriptions of the important behaviors are provided here.

Twitch abdomen. Rapid, low amplitude, up and down movements of the abdomen.

Table 1.–Number of males of *Phidippus johnsoni* that performed different elements of behavior after contact with empty nests. A: nests of adults. S: nests of subadults.

Behavior		Female only	Male only	Both	Neither
		Nests at which Behavior was Performed			
Abdomen Twitch	A	7	0	3	2
	S	14	0	1	3
Vibrate	A	5	0	2	5
	S	5	1	0	12
Tug	A	2	5	3	2
	S	9	3	2	4
Probe	A	0	0	12	0
	S	3	0	15	0
Enter Nest	A	3	0	9	0
	S	1	1	16	0

Probe. Pushing and pulling on the nest with the first pair of legs.

Tug. Up and down movements of the cephalothorax while the chelicerae grip the silk.

Vibrate. Very rapid, low amplitude, up and down movements with the forelegs on the silk.

In other studies (Jackson 1977a) twitching of abdomen, probing and vibrating were characteristic of interactions between conspecific spiders. Tugging occurred sometimes while spiders were alone and spinning in their own nests, but it was more prevalent in interactions with other spiders.

RESULTS

All males contacted nests 1-28 min after introduction into the cages, and there was no difference in the latency to contact between nests of females and those of males (latency for each male to contact nest of female minus that for the same male to contact nest of male: 1.6 ± 9.16 min for nests of adults; 0.9 ± 10.32 min for nests of subadults), providing no evidence of attraction to nests by airborne pheromones.

Each element of behavior occurred sometimes at nests of each sex-age class (Table 1). However, males more often performed abdomen twitching at nests of females than at those of males (nests of adults: $\chi^2 = 5.143$, $P < 0.025$; subadults: $\chi^2 = 12.071$, $P < 0.005$).

Abdomen twitching, vibrating, tugging and probing tended to occur either soon after the male touched the nest or not at all (latencies in sec from nest-contact until behavior was performed: abdomen twitch, 18, 54; vibrate, 33, 217; tug, 28, 584; probe, 2, 83). The durations (in sec) of these behaviors tended to be brief (abdomen twitch, 14, 144; vibrate, 4, 37; tug, 10, 110; probe, 9, 67; cases in which the behavior failed to occur deleted). Times not engaged in these activities were occupied with grooming, walking, spinning, pivoting, or simply standing inactive.

Spiders that entered nests did so soon (35 sec, 395 sec) after contacting the nest. Sixteen males each entered the nests of both (a) a subadult female and (b) a subadult male, and latencies were greater when the nests were ones of (a) rather than (b) (latency in sec of (a) – (b): 43, 388; Wilcoxon test, T_s = 6, P < 0.01).

Males also probed longer at nests of females than at nests of males (durations in sec of probing at nests of females minus those at nests of males: 10, 41 for nests of adults, T_s = 9; P < 0.02; 10, 64 for nests of subadults, T_s = 11.5, P < 0.01).

Twelve males each first touched one of the two nests with which they were tested in the vicinity of the door (an elastic slit-like opening to the nest) and the other nest elsewhere; and latencies to probe for these males were less when first contact was near the door (latency to probe in sec after contact away from door minus latency after contact near door: 3, 28; T_s = 0, P < 0.01). Also, whenever probing occurred, it was concentrated in the vicinity of the door (duration of probing near door/total duration of probing x 100%: 64% ± 41.3%).

DISCUSSION

The behavior of male *P. johnsoni* is adapted to mating with females that they locate in nests. One line of evidence for this is the different motor patterns and sensory modalities involved depending on whether the female is inside or outside her nest (Jackson 1977a, b). The present study provides further evidence. The nest alone elicits courtship from the male and provides the male with information concerning the sex of the previous occupant.

Although empty nests elicit brief courtship behavior, probably the presence of the nest occupant is necessary in order to sustain the male's behavior for more than a few minutes, since courtship tended to last many minutes (mean, 16 min; max., 3 hr 44 min; Jackson 1978a) when females were inside nests. Males seem to be adapted to briefly "announcing" themselves (courting) when they contact nests of conspecific spiders and to desisting when they do not receive an "answer" (response of the female).

It seems likely that chemical stimuli were involved in the discriminatory behavior of male *P. johnsoni* since in other groups of spiders there is evidence of pheromones associated with silk (Kaston 1936, Millot 1946, Tietjen 1978). There were no obvious differences in the shape, size, or other gross structural characteristics of the nests used in this study, suggesting that tactile discriminations of gross structural differences were not involved. Visual discrimination of either gross or fine differences also seems unlikely as an important factor since nests in nature were located in places with little ambient light; but it is possible that males discriminated fine tactile differences upon contact with nests.

In this study and in ones in which the nests were occupied (Jackson 1977a), probing was concentrated in the vicinity of the door; and probing occurred more quickly when males contacted nests near the doors. Perhaps tactile stimuli associated with the opening in the nest facilitate probing, although concentration of pheromones around the door is another possibility.

The communicatory behavior of *P. johnsoni* is more complex than that normally associated with spiders. One aspect of this complexity is the use of alternative tactics for females inside vs outside nests and for adults vs subadults. Another factor is that the rules describing when different behaviors occur do not seem simple. For example, some behaviors performed by males are also performed by females and immatures, and some of

the male's behaviors are the same when interacting with males or females encountered in nests. Since the manner in which behaviors are segregated according to sex-age class is quantitative rather than qualitative (Jackson 1977a), the task of determining the functions and the message-meaning relationships of the displays exchanged between spiders and the signals associated with nests will be difficult.

The fact that the nests of the sympatric gnaphosid spider *H. hesperolus* failed to elicit vibratory courtship behavior from males of *P. johnsoni* (Jackson 1976a) indicates that reliable species-identifying information is provided through the nests, at least with respect to these two species. The occurrence of many of the same elements of behavior at nests of both males and females of conspecifics, however, might be related to the presence of less reliable sex-identifying information or to behaviors having adaptive significance during both male-male and male-female interactions.

Entry into the nest by a male is likely to elicit departure by a subadult female and decrease the male's chances of cohabiting (Jackson 1977a). The adaptive significance of the longer latencies before entering nests of subadult females compared to subadult males may be related to this.

Crane (1949) found evidence suggesting that airborne pheromones emanating from females of *Corythalia, Phiale*, and other neotropical salticids lowered the males' thresholds for performance of displays. This raises the possibility that residual airborne pheromones in the cage after removal of the females might have affected the manner in which males of *P. johnsoni* responded to nests since the maximum time that elapsed between removal of spiders from their nests and when the test males touched the nests was 22 min in this study. However, in the earlier study (Jackson 1976a), a full day elapsed between removal of the females and testing. Also, the cages had ventilation openings. Consequently, chemotactic or tactile stimuli would seem more important than residual airborne pheromones in eliciting responses from males in this study.

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