

NESTS OF *PHIDIPPUS JOHNSONI* (ARANEAE, SALTICIDAE): CHARACTERISTICS, PATTERN OF OCCUPATION, AND FUNCTION

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ABSTRACT

Phidippus johnsoni constructs tubular nests from silk under rocks, under pieces of wood, inside hollow reeds, etc.; and these are involved in molting, courtship, mating, oviposition, and other aspects of the spider's life history. Relatively large rocks and pieces of wood tend to be chosen for nest sites. Nest length tends to be two to three times greater than the spider's body length. Nests vary in shape, density, raggedness, and the degree to which they are cluttered with debris. Most spiders reside in nests of greater density and lesser raggedness and clutter. Molting and oviposition occur in especially dense nests. Spiders tend to remain inside nests for six days preceding and two days following molting. Spiders enter their nests before dark and remain inside at night. Much time is probably spent spinning. Males are more likely to be found outside nests compared to females and immatures, and the nests they occupy tend to be less dense. Marked spiders in the field employ the same nest sites for prolonged periods (maximum, 28 to 33 days), sometimes making excursions of as far as 1.2 m away from nests before returning. Two adult females in individual terraria each occupied a single nest for 6 to 7 months, sometimes making excursions of as far as 80 cm. Females in nature and the laboratory oviposited repeated batches in single nests. Sometimes nests built by other individuals were employed by spiders.

INTRODUCTION

Although prey capturing devices, such as the "nets" of dinopids, the "purses" of *Atypus*, and especially the "webs" of diverse species of spiders (see, e. g., Levi 1978, Risch 1977, Stern and Kullmann 1975, Witt *et al.* 1968) have received considerable attention, the silken structures of vagabond spiders have received relatively little attention. This paper will deal with the silk nests of *Phidippus johnsoni* Peckham and Peckham, a common salticid species in western North America. The range of this species is from the Great Plains to the Pacific Ocean and from Canada to Mexico, where it occurs in a variety of types of habitats from sea level to timberline.

Possessing one of the most highly developed invertebrate visual systems (Land 1972), the salticids are diurnal predators that use vision to stalk their prey (Gardner 1965). Although silk is not usually employed in prey capture, it plays a role in other aspects of the life of these spiders. The salticids build silken nests (retreats) inside which they molt,

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oviposit, and remain at night and during inclement weather. Also, nests are important in understanding the mating tactics of *P. johnsoni* and probably other salticids (Jackson 1977a, b). A male *P. johnsoni* encountering a female outside her nest employs a type of courtship comprised of vision-dependent displays. However, if the female is inside her nest, the male employs a non-vision-dependent, vibratory courtship. If the female is a subadult inside her nest, the male employs a third tactic involving the construction of a second chamber on the female's nest and cohabitation until she matures. Following each of the latter two tactics, mating takes place inside the nest.

General aspects of the life history of this species have been discussed elsewhere (Jackson 1978). The goal of this paper is to record the characteristics of nests and to investigate specific aspects of life history related to the use of nests by the spiders. Certain information from the life history study will be summarized here, since it will be important for the discussion of specific items in the text. In the laboratory, *P. johnsoni* undergoes 5 to 8 molts before reaching maturity. Adults tend to be approximately 10 mm in body length; males are smaller than females, maturing earlier and after fewer molts. Mature individuals do not molt further, and adults tend to survive 3 to 4 months. Females are iteroparous, ovipositing up to 5 successive batches of fertile eggs after a single copulation. Approximately one month passes between mating and the first oviposition, and the inter-oviposition interval for later batches is approximately one month. Eggs hatch nearly 3 weeks after oviposition. The postembryos remain inside the nest, and the first instar spiderlings tend to disperse from the nest 3 weeks after hatching occurs.

METHODS

General—Data concerning nests were gathered in the laboratory during the course of rearing a set of spiderlings from egg to adult (Jackson, 1978). Data from the field were gathered during censuses (Jackson, 1978) in which each nest in the census area was recorded. The census areas were at Tilden and Mt. Diablo in the Coastal Range, Pt. Reyes and Inglenook at sea level next to the Pacific Ocean, Pothole Dome in the Sierra Nevada, and Whiskey Mountain in the Rocky Mountains. Whiskey Mountain is in Wyoming, and the other sites are in California.

The temperature in the laboratory was maintained at $24 \pm 1^\circ\text{C}$, the light regime was 11L: 13D (lights on, 0900 hrs.; off, 2000 hrs.) for spiders reared from eggs. Each spider was observed for 15 sec at 0930, 1100, 1400, 1600, 1800, 1930, and 2000 hrs, just before the lights went off. The location of each spider and whether it was spinning was recorded. These records were kept for each spider, starting with its first instar and continuing until it died, escaped, or reached its fifth instar. Sometimes, for inadvertent reasons, some observations were missed on certain days. When spiders were checked between 2000 and 2200 hrs, a flashlight was used. The 11 x 8 x 6 cm plastic cages used in the laboratory have been described elsewhere (Jackson, 1974). The light regime for all other spiders was 12L: 12D (lights on, 0800 hrs).

Except where noted otherwise, data will be given as means \pm S.D. All statistical tests are described in Sokal and Rohlf (1969).

Field Procedures For Investigating Prolonged Use of Nests—Spiders were marked at Mt. Diablo by forcing them from their nests under rocks and taking them into glass shell vials, plugged with cotton. The vials were placed inside a thermos bottle containing crushed ice. As soon as the low temperature had made the spiders sluggish, they were

placed on a sheet of white paper and marked with different colors of enamel paint, applied to the dorsal abdomen with an insect pin. A single spot, less than 1 mm in diameter, was made. The spiders were marked in April, at which time all spiders at Mt. Diablo were either adults or large immatures that would mature at their next molt. When spiders were marked in the laboratory, there was no evidence that this procedure impaired their health or diminished their longevity. The spiders were marked in late afternoon (1500 to 1800 hrs), not all on the same day. After marking, each spider was released beside its nest, which it subsequently re-entered, and the rock was returned to its original position. A metal stake bearing a code number was placed beside the rock to expedite locating it on subsequent visits.

Each marked rock was checked at one to three day intervals, usually two days, each time in the late afternoon. Whenever the marked spider was not found at the marked rock, a search was made of an area within a 4 m or greater radius of the marked rock. The search consisted of overturning each rock greater than 5 cm in length. (*P. johnsoni* have not been found in nests under rocks smaller than this.) If the marked spider was located at a new site, this was marked with a new stake and code number. If the spider was not located, the area was searched at 1 to 3 day intervals for at least 2 weeks subsequently. In some cases, marked spiders were found away from the marked rocks; but at the next check they were again at the marked rock. These were recorded as having been at the same nest site at the previous check as well, since it is strongly suggested that the spider returned to its nest before night.

Laboratory Procedures For Investigating Prolonged Use Of Nests--Two adult females, each in a nest with eggs at the time, were collected from Mt. Diablo in late spring. Two days later, each was placed inside a separate terrarium. Beginning the next day, the location of each spider was systematically recorded until it died. However, it did not prove feasible to follow a strict routine for this. Whenever I was in the laboratory, I checked the spiders at 0930, 1100, 1400, 1600, and 2000 hrs, just before the lights went off. Sometimes some of the check-times were missed, and a number of entire days were missed because I was unable to be in the laboratory. However, the longest period I was away at one time was 12 days. Occasionally spiders were observed continuously for up to several hours at a time.

The terraria, made from clear plastic, were 56 cm long, 53 cm wide, and 30 cm tall. There was a 10 cm diameter rock near the center of the floor of each terrarium. Mineral oil rendered the walls of the terraria too slippery for the spiders to climb. Pupae of house flies (*Musca domestica*) were added every two weeks to a glass dish on the floor of the terrarium. As a result, adult flies were continually present, feeding on sugar kept in three other glass dishes. Each 3 cm diameter dish was approximately 8 cm from a different corner of the cage. Moisture was provided by means of a cotton roll that passed through a hole in the wall of the cage, the exterior end situated in a glass beaker filled with water. The lid of each terrarium was fitted with four evenly spaced ventilation holes (7.5 cm diameter), each covered with metal screen. The floor of each terrarium was covered with sand.

RESULTS AND DISCUSSION

Location Of Nests--Most nests were found associated with wooden boards, fence posts, dead trees (Pt. Reyes, Inglenook), or rocks (all other census areas). Many of those on dead trees were under loose bark. They were found underneath, on sides, and inside

crevices of wood and rocks. In the census areas and other locations, occasionally nests were found underneath dried dung (cow and horse), inside tin cans, and inside dry, hollow reeds (standing or lying on the ground).

Since previous collecting indicated that *P. johnsoni* were not found under rocks or pieces of wood with length less than 5 cm, these were checked only sporadically during censuses. All rocks and wood larger than this were checked during each census. Occupied nests tended to be found under larger rocks and wood, even when those less than 5 cm were not considered (Table 1).

The exact locations of 87 nests (each occupied by *P. johnsoni*) were recorded at Tilden. Most (78%) were on the sides of rocks. The remainder were completely under the rocks. Most (53%) of those on sides of rocks were less than 1 cm above the ground, although some were as high as 8 cm above the ground. In virtually every case, another rock, grass, or other vegetation covered the side of the rock, concealing the nest. The nests under rocks were 1.2 ± 0.83 cm from the side of the rock.

In the laboratory, most nests were constructed in corners; i.e., at locations where three (50%) or two (35%) of the six sides of the cage met ($n=241$). Corners may be optimal for building a nest with an adequate degree of three-dimensionality, and a corner may more closely simulate a concealed location on a rock.

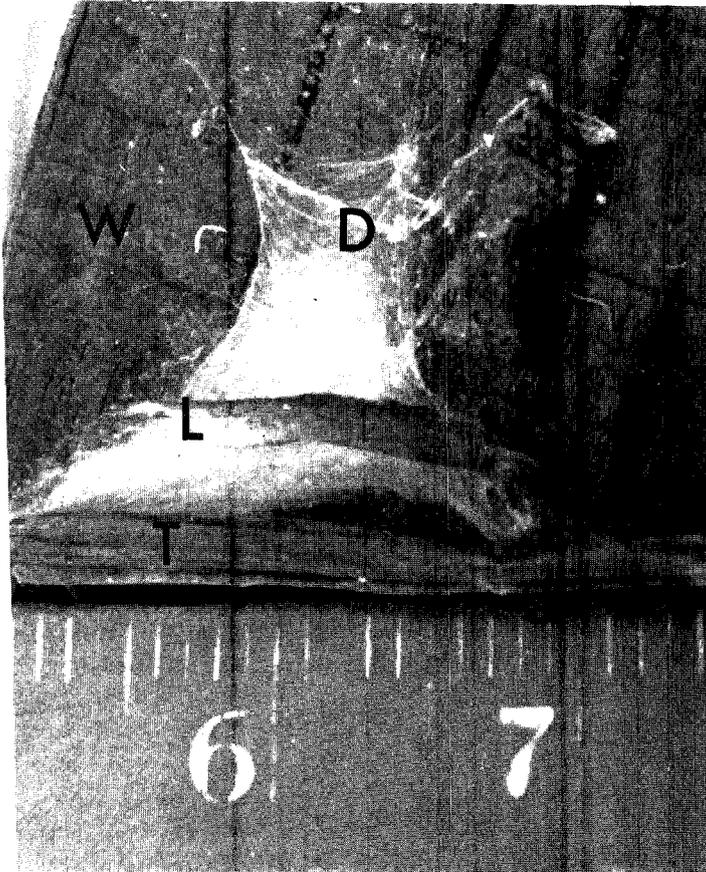


Fig. 1.—Nest of *P. johnsoni*. Shape: T-nest, (see text). D: door. Other two doors obscured by debris (L: leaf; T: twig). Nest fastened to piece of wood (W). Scale: numbers on ruler 1 cm apart.

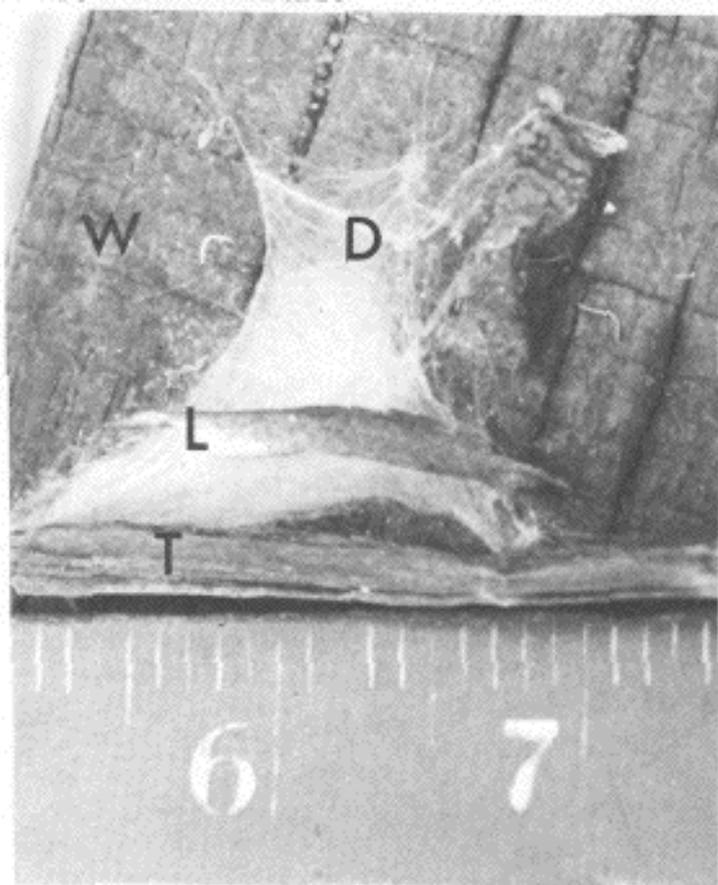


Fig. 1.—Nest of *P. johnsoni*. Shape: T-nest, (see text). D: door. Other two doors obscured by debris (L: leaf; T: twig). Nest fastened to piece of wood (W). Scale: numbers on ruler 1 cm apart.

Shape And Size—Nests consisted of sheets of white silk enclosing a hollow interior, usually with two doors (Fig. 1). A door is an elastic opening through which the spider enters and departs. Four shapes were most common, each named for the letter of the alphabet that it most closely resembled. Ones shaped like straight tubes, normally with a door at each end, are called "I nests." Ones with two arms, each approximately perpendicular to the other, are called "L nests." Nests with arms making an angle closer to 45° are called "V nests." On L and V nests there were normally two doors, one at the end of each arm. Nests with two arms at one end, approximately perpendicular to a third arm, are called "T nests." These usually had three doors, one at the end of each arm. In both the laboratory (64%) and the field (89%), I nests were the most common shape; L nests (laboratory, 22%; field, 3%), V nests (14%, 3%), and T nests (0%; 5%) were less common (laboratory, n = 241; field, Tilden, n = 87). In the laboratory, spiders frequently occupied the same nest for prolonged periods, and sometimes they slowly changed I nests into L nests or T nests. In the percentages given here, these were recorded as I nests.

At Tilden, 69 I nests occupied by adult *P. johnsoni* were measured to the nearest millimeter. The distance between the two doors is defined as the length. For width, measurements were made across the nests perpendicular to the axis connecting the doors, at the widest location on the nest. Also, the widest diameter of the widest door was measured. Length was 25.3±6.19 mm; width, 16.4±4.89 mm; door width, 11.1±1.48 mm. Since adult spiders tended to be 8 to 10 mm in length (Jackson 1978), nests tended to be approximately two to three times longer than the spider.

Other Characteristics—Nests vary in density (Table 2), but tended to be at the greater end of the density scale. Nests in which spiders molted or oviposited in the field were usually of density value 5 (87%). In the laboratory normally several days (9.4±6.31, n = 94, min = 1, max = 28) passed between initial construction and the time when nests became of density value 5. Occasionally nests of density value 1 were seen in the laboratory, but never in the field.

In the laboratory, older nests tended to take on a torn or shredded appearance ("ragged"), and these nests were usually abandoned by the spiders in the laboratory. Raggedness of nests was judged on a scale from 1 (not at all ragged) to 6 (ragged to such a degree that it was barely recognizable as a nest). During Census No. 2 at Tilden (Table 1), the raggedness of 112 nests (25 occupied by *P. johnsoni*, 87 not occupied) was recorded. The occupied nests were less ragged (raggedness-value 1, 40%; 2, 40%; 3, 12%; 4, 4%; 5, 4%; 6, 0%) than ones that were not occupied (1, 4%; 2, 22%; 3, 23%; 4, 21%; 5, 15%; 6, 15%) (Mann Whitney U-test, p<0.001).

Nests in ragged condition in nature were frequently impregnated with debris, such as small stones and vegetable matter (Fig. 1). Clutter was judged on a scale from 1 to 5 (1, no debris; 2, ca. 25% of nest surface covered by debris; 3, ca. 50% covered; 4, ca. 75% covered; 5, ca. 100% covered). Considering the same 112 nests from Tilden Census No. 2, occupied nests were less cluttered (1, 44%; 2, 44%; 3, 8%; 4, 44%; 5, 0%) than unoccupied ones (1, 10%; 2, 45%; 3, 30%; 4, 10%; 5, 5%) (Mann Whitney U-test, p<0.001).

Sometimes spiders eventually constructed a second chamber on older nests, usually with the doors of the two chambers superimposed. When a male cohabits with a subadult female (Jackson 1976), he constructs a second chamber on the female's nest, with the doors of his chamber superimposed on those of the subadult's. Occasionally when the nest of the subadult already had two chambers, the male cohabited in the existing second chamber, rather than constructing a new chamber himself.

Table 1.—Size of rocks (Tilden, Mt. Diablo, Whiskey Mountain, Pothole Dome) and pieces of wood (Pt. Reyes, Inglenook). Ones with compared to ones without nests occupied by *P. johnsoni* (t-tests; t-values given when significant, * $P < 0.05$, ** $P < 0.001$). All rocks or wood in census area with occupied nests measured. For those not occupied, a sector of the census area was selected randomly. Length: the greatest distance across rock or wood in a plane parallel to ground. Width: distance across in same plane as length but perpendicular to the length. Height: greatest distance across in plane perpendicular to ground. Only rocks and wood with length 5 cm or greater measured.

Census	Area of sector (sq. m)	Rocks or wood with occupied nests	Number	Length (cm)	Width (cm)	Height (cm)
Tilden No. 1	290	Yes	62	42.9 ± 16.71	27.4 ± 10.77	21.3 ± 10.87
		No	143	40.4 ± 21.39	26.7 ± 13.13	20.6 ± 16.61
		t		n.s.	n.s.	n.s.
Tilden No. 2	232	Yes	25	40.6 ± 21.56	33.5 ± 31.80	19.3 ± 12.62
		No	87	30.2 ± 20.54	20.8 ± 14.39	8.6 ± 6.12
		t		n.s.	2.350*	5.816**
Mt. Diablo No. 1	279	Yes	36	20.1 ± 7.34	15.7 ± 5.87	13.2 ± 5.79
		No	108	11.2 ± 5.23	7.9 ± 4.17	4.3 ± 2.72
		t		7.937**	8.817**	12.425**
Mt. Diablo No. 2	186	Yes	31	16.5 ± 5.51	11.7 ± 4.11	8.4 ± 2.46
		No	64	11.4 ± 5.71	8.1 ± 3.58	4.6 ± 3.96
		t		4.108**	4.320**	4.905**
Pt. Reyes No. 1	93	Yes	11	69.6 ± 59.46	10.2 ± 3.76	4.1 ± 1.70
		No	140	42.16 ± 47.19	7.6 ± 4.04	3.3 ± 2.06
		t		n.s.	2.017**	n.s.
Pt. Reyes No. 2	84	Yes	16	87.9 ± 95.55	15.2 ± 11.28	8.1 ± 8.15
		No	192	26.4 ± 23.01	7.6 ± 4.52	3.0 ± 2.64
		t		6.949**	5.514**	5.805**
Inglenook	1510	Yes	20	129.0 ± 64.16	8.6 ± 2.90	3.3 ± 1.45
		No	105	74.7 ± 61.82	11.2 ± 16.97	4.1 ± 10.95
		t		3.583**	n.s.	n.s.
Whiskey Mountain	41	Yes	5	20.8 ± 8.69	12.7 ± 1.80	4.6 ± 2.13
		No	170	20.1 ± 13.56	14.0 ± 9.55	6.6 ± 5.28
		t		n.s.	n.s.	n.s.
Pothole Dome	51	Yes	9	21.8 ± 11.91	16.0 ± 8.03	6.9 ± 3.10
		No	189	18.5 ± 14.91	13.2 ± 10.82	5.1 ± 3.68
		t		n.s.	n.s.	n.s.

Table 2.—Silk density of nests from census areas: 1, very little silk, only minimally structured as a nest (doors not distinct); 2, nearly transparent, but distinctly structured as a nest; 3, translucent; 4, nearly opaque; 5, completely opaque. Data expressed as the percentages of nests of a given category (percentage of N) having the specified densities. Each nest occupied by a living *P. johnsoni*: F, adult female only; M, adult male only; F, M, or I, either an adult female, adult male, an immature spider (exclusive of postembryos and first instars), or an adult male with an adult or immature female. Progeny: mass of postembryos or first instar spiderlings.

OCCUPANTS OF NESTS			SILK DENSITY OF NEST					N
Sex/Age Class	Exuvium	Progeny	1	2	3	4	5	
M, F, or I	No	No	0%	2%	19%	26%	53%	1280
M, F, or I	Yes	Yes or No	0%	0%	1%	17%	82%	136
F	No	Yes	0%	0%	0%	4%	96%	135
F	No	No	0%	3%	24%	20%	53%	205
M	No	No	0%	13%	56%	15%	16%	62

Patterns Of Occupation—Various observations suggest that it is adaptively very important for *P. johnsoni* to occupy nests at night. When censuses were made in the field at sunrise, all the *P. johnsoni* located were occupying nests (Jackson 1978). In the laboratory, when spiders (n = 322) were placed in clean cages, most (89%) built nests within 24 hrs, either before the lights went off or during the dark period in the laboratory.

Spiders with nests were only very rarely found outside their nests during the dark period in the laboratory; and in each case, the spider was inside its nest by morning. Nest departure occurs soon after the lights come on in the morning. However, observations in the field suggest that this is an artifact related to the constant warm temperature in the laboratory. In the field, spiders evidently depart nests later in the morning, after the ambient temperature has risen (data not collected). During the afternoon, the spiders gradually enter their nests in the laboratory (Table 3). Thirty minutes before the lights went off in the laboratory, fewer than 10% of the spiders were generally outside their nests, and most of these usually entered their nests by the time the lights went off, suggestive of a circadian rhythm.

In the laboratory, the total amount of time that spiders remained in their nests was rather large, and this may be partly an artifact related to the continual supply of food (2 to 8 living flies maintained in each cage at all times). A major internal factor influencing the spider's tendency to depart may be hunger, and in the laboratory spiders may remain satiated most of the time. This could be easily tested by maintaining spiders on differing feeding schedules.

Spinning Inside Nests—Spiders apparently spend much time spinning while occupying their nests. The data in Table 3 probably underestimate the percentage of the spider's time occupied with spinning each day, since each spider was observed only briefly and spinning was not recorded unless it happened to occur at the time of observation. Spinning was seen especially in the late afternoon and early morning. However, relatively little spinning occurred at the time just before the lights went off and in the dark. The majority of spinning that was seen took place in old nests; i.e., ones that had been present from a previous day. However, of those spiders spinning at the time the lights went off and in the dark, relatively many were spinning in new nests. Possibly the number of spiders spinning in the dark was particularly subject to underestimation by the methods employed here, since turning the flashlight suddenly on the spiders may have caused startle responses in which they ceased to spin.

Nest Occupation And Molting—Very likely, spiders are especially vulnerable to predation at the time of molting. At least during the molting process itself, the spider is unable to actively defend itself, and possibly it has reduced mobility, sensory acuity, and

Table 3.—Nest related behavior of spiders reared in the laboratory. N: total number of observations made at the indicated times. Inside nest: percentage of the total number of observations during which spiders were located inside nests. Spinning: percentage of the observations of spiders inside nests during which the spiders were spinning. Spinning in Old Nest: percentage of observations of spiders spinning during which the nest was an old nest (present from a previous day). Lights on: 0900; lights out: 2000 hr. See text for details.

Time (hr)	0930	1100	1400	1600	1800	1930	2000	Dark
INSIDE NEST	72	68	72	81	92	92	97	100
SPINNING	6	2	1	2	5	6	2	1
SPINNING IN OLD NEST	95	100	89	96	92	94	83	60
N	1583	1804	2044	1623	1722	617	1580	380

other functions. In the laboratory, spiders remained in their nests for a number of days preceding (5.9 ± 3.35 days, $n = 95$) and following (2.3 ± 1.67 days, $n = 156$) molting. The postmolt period may be related to inactivity by the spider as its cuticle hardens, and the premolt period may be a period of inactivity by the spider as it makes physiological preparations for molting. Comparing (t-tests) the premolt period for the molt on which spiders became mature (prematurity molt) to all previous molts and comparing the premolt period at the prematurity molt for males and females, there were no evident differences. This was also true for postmolt periods.

Nomadic Males And Sedentary Females—Previously (Jackson 1978) the hypothesis was put forth that males of *P. johnsoni* are adapted to a life style that emphasizes searching for females and mating at the expense of maintenance and survival. Consistent with this, males in the field were found in nests of lesser density than those of females (Table 2, Mann Whitney, $P < 0.001$). Also, disproportionately many males were located outside nests compared to females and immatures (Table 4).

Location Of Spiders When Not Occupying Nests—A total of 150 individuals were located outside nests in the field. Half (75) were not near a nest; 7 were on a rock or piece of wood with a nest underneath or on the side; 16 were under a rock or piece of wood with a nest present; 8 were standing on a nest; and 44 were standing beside (within 1 cm) of a nest. From these data and from observing spiders in the field and the laboratory, it seems that when spiders depart their nests they often remain quite near the nest, although at other times they go considerable distances from the nest. Further information was provided by observations on marked spiders.

Marked Spiders In The Field—At Mt. Diablo marked spiders frequently remained at the same nest site for a number of days (minimum estimate, 7.1 ± 10.40 days; maximum estimate, 10.1 ± 10.89 days; $n = 16$). When spiders were not found, predation may have occurred or they may have moved outside the area searched. In three cases spiders were found at nests other than the ones at which they were marked. 1. An adult female that was not found on the day after marking was located in a second nest under a different rock, 0.6 m away, 3 days later. 2. Another adult female that was not found on the day after marking was found 14 days later in a second nest under a rock 4 m away. 3. An adult male was initially found inside a nest with an exuvium (large palps on exuvium), presumably having recently molted. He was not found the next day, but 4 days later he was located in a second nest, touching the old nest, under the same rock. Twelve days later, this male was not present; but an adult female was inside the nest. She was marked, re-located at the same nest on the next check-day (2 days later), then not seen again.

Three marked spiders were observed to depart and return to the same nest. 1. An adult female was found 3 cm from her nest, but under the same rock, on the fifth day after marking. Later in the day, she was found inside her nest again. Incidentally, this spider

Table 4.—Comparison of frequencies with which spiders of each sex/age class were found inside versus outside nests. Summed data from all censuses in which at least one male, one female, and one immature were found. Data for males compared to summed data for females and immatures indicate that males were found more often outside nests ($G = 37.634$, $P < 0.005$).

	PERCENTAGE INSIDE NESTS	PERCENTAGE OUTSIDE NESTS	NUMBER
ADULT MALES	68.93	31.07	103
ADULT FEMALES	92.25	7.75	284
IMMATURES	92.58	7.42	283
ALL SEX/AGE CLASSES	88.81	11.19	670

remained at the same nest for one month (maximum estimate, 33 days; minimum, 28 days), the greatest period in this study. 2. Another adult female was located on three different days outside her nest. Each time, she was found inside her nest again at the next check. Five days after marking, she was under a rock 30 cm away from the one with her nest. There was no nest under this rock. Once on the second day and again on the eighth day after marking, she was found 1 cm from her nest but under the same rock. 3. A subadult female was found under a rock 1.2 m from her nest on the fifth day after marking. There was no nest under this rock. At the next check, 2 days later, she was inside her nest again. This spider remained at the same nest for 3 weeks (maximum, 24 days; minimum, 22 days). On the 24th day after marking, an exuvium with paint marks was inside the nest, but the spider had departed. Another subadult female also remained at the same nest for 3 weeks (maximum, 23 days; minimum, 21 days). On the 21st day after marking, an exuvium with paint plus an adult female was found in the nest. Two days later, the female had vanished. Another subadult female remained at one nest only briefly (maximum, 3 days; minimum, 1 day). Three adult males and one adult female were not found again after marking. Another five adult females were found at the same nest for only 1 to 6 days.

In the laboratory and the field (Mt. Diablo and Tilden), males were found to cohabit with subadult females for as long as 2 weeks (Jackson, 1976a). The two subadult females in this study that remained at single nest sites for 3 weeks each before molting, with no males present, demonstrate that prolonged residence by subadult females at single nests is not unique to situations involving cohabitation.

Spiders In Terraria—Each female constructed two nests, each in a corner of her terrarium (i.e., where two walls and the floor came together). The rock was not used as a nest site by either spider, and it was generally observed in the laboratory that when spiders were provided rocks inside terraria and plastic cages, they nevertheless built their nests on the walls of the container rather than on the rocks.

Each spider built its first nest by the first evening, later abandoned this nest, and did not subsequently use it. In the discussion that follows, all references to the spiders' nests refer to the second nests. One spider built its second nest four days after being placed in the terrarium; and the other spider, after five days. One spider oviposited two batches of fertile eggs, followed by an infertile batch. The other spider oviposited three batches of fertile eggs. Each batch was oviposited at approximately one month intervals in the same nest. In effect, each spider had a nest containing either eggs, spiderlings, or both during the entire summer and early fall. Assuming that the same nests were used on days when observations were not made, each spider used a single nest for 6 to 7 months.

Although the two females spent a great deal of their time inside their nests (Table 5), they sometimes departed the nest, usually remaining in the close vicinity of the nest; but sometimes they were seen as far away as the opposite side of the terrarium. Each time, after departing, the female returned to her nest by evening. This behavior persisted after oviposition ceased; and in each case, after the female died, her corpse was found outside but near her nest. The data for the females are consistent and they are pooled in Table 5.

As mentioned earlier, the continual supply of prey in the laboratory may have resulted in the spiders remaining inside their nests a disproportionately greater time than would have been the case in nature.

Field Observations Concerning Multiple Batches In Single Nests—In the field, more than one batch was found in a single nest on seven occasions, each time with an adult female inside the nest. Nests containing both eggs and a set of spiderlings were found five

times. On three occasions, two sets of egg shells were found inside single nests. Most likely, these were cases in which females remained at the same nest at least long enough to produce two batches.

Use Of Nests Built By Other Individuals—On four occasions, two exuvia of different sizes were found inside the same nest. Possibly, the same spider remained at the nest long enough to molt twice. However, individuals of *P. johnsoni* will occupy nests that they do not construct, as has been noted for other salticid species as well (Crane 1949, Gerhardt 1921, Plett 1962). In the laboratory, when a spider was removed from its cage and a different spider was placed inside the cage, the new spider frequently employed the previous spider's nest. They occupied these overnight, sometimes longer, and occasionally molted or oviposited inside them. There was evidence that this occurred in the field also. Once a large exuvium was found in a nest containing eggs. There was no spider present. One possibility is that a subadult molted and matured in this nest, mated, and finally oviposited in the same nest. Another possibility is that an immature used this nest as a molting site after a previous female had oviposited here, or vice versa. On three occasions, relatively large exuvia were found inside nests with egg shells. In one case, the exuvium came from a male, as indicated by the enlarged palps. Twice exuvia were found that were considerably larger than the spider that occupied the same nest at the time, indicating that these nests had been previously occupied by different spiders.

Plett (1962) found that large individuals of the salticid *Salticus scenicus* will take over the nests of other individuals. This has not been seen in the field for *P. johnsoni*, although aggressive interactions leading to this result have been witnessed in the laboratory (Jackson 1976a).

GENERAL DISCUSSION

Homing Behavior—When Plett (1962) marked *Salticus scenicus* Clerck in the field with colored dots, he found no evidence of homing behavior or a tendency to repeatedly use the same nest. In contrast, *P. johnsoni* seems to make prolonged use of single nests. They depart and return to the same nest site after excursions of as far as 1.2 m. It would be valuable to investigate potential homing mechanisms, including kinesthetic mechanisms and visual orientation by means of landmarks, sun position, and the plane of polarization of sunlight. Chemical trail following, perhaps associated with draglines, might be con-

Table 5.—Pooled data for two adult females kept in individual terraria. The number of days on which observations were made at each time was one-half the number of observations, because 2 observations (2 spiders) were made at each check-time. Considering only those observations during which spiders were outside nests, the percentages at different locations are provided in the last 4 rows: A, on nest; B, within 2 cm of nest; C, more than 2 cm from nest but on same side of terrarium; D, on other side of terrarium. Lights on: 0900, lights out 2000 hr. See text for details.

Time (hr)	0930	1100	1400	1600	1800	2000
No. of Observations	356	332	340	320	308	352
Inside Nest	97%	92%	93%	94%	97%	100%
Outside Nest	3%	8%	7%	6%	3%	0%
A	60%	38%	50%	44%	60%	---
B	20%	15%	8%	33%	20%	---
C	20%	32%	17%	11%	20%	---
D	0%	15%	25%	11%	0%	---

sidered, although this seems a less likely possibility. Orientation by sun position and by plane of sunlight polarization have been demonstrated in agelenid (see Schoer 1974) and lycosid (see Magni *et al.* 1965) spiders, and Land (1969) discussed morphological features that might be related to discrimination of the plane of polarization in the eyes of *P. johnsoni* and other salticids.

Function Of Nests—Adaptive radiation in a group of animals can be viewed as the product of an evolutionary lineage entering a new adaptive zone (Simpson 1953). In the case of spiders, the adaptive zone is probably somehow related to the use of silk. Some of the web building spiders are extremely dependent on silk, with almost every event in their lives involving silk in some intimate manner. Although the salticids are not so extreme, the construction and use of silk nests is integral to understanding the adaptations of *P. johnsoni* and no doubt other salticids.

The daily routine and life history of the spider is very much centered around the nests, which are occupied each night, and in which molting, mating and oviposition take place. Courtship behavior is adapted to nests. Nests, in the laboratory and nature, are used repeatedly over a period of days, with the spider departing and returning to the same nest. Although the time and energy investments put into nests have not been measured, they may be considerable. Much time seems to be spent spinning and most spiders in the field were found occupying relatively dense nests. Nests occupied by spiders in the laboratory acquired comparable density only after several days of occupancy. These factors may favor individuals that make more or less prolonged use of their nests.

One major function of nests is probably protection from predators during periods, such as at night and during molting, when the spider is inactive and probably especially vulnerable. Females remain with their eggs inside nests, and perhaps protect the eggs from predators and parasites. Mating often occurs inside nests, and the spiders are probably safer from predation inside compared to outside nests during courtship and copulation (Jackson 1976b).

Nests might function in keeping the occupants dry. Often after a heavy rain, drops of water were seen on the exterior of nests in the field, and the surroundings of the nests were sometimes very wet. However, the occupants of nests rarely showed signs of having become wet. At most there might be a few drops of water on their bodies and legs. Another possibility that has not been explored is that the interiors of nests remain at more constant temperature and humidity than the surroundings.

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