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BIOLOGY OF *PEUCETIA VIRIDANS* (ARANEAE, OXYOPIDAE) IN SOUTH CAROLINA, WITH SPECIAL REFERENCE TO PREDATION AND MATERNAL CARE

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ABSTRACT

We studied the biology of the green lynx spider, *Peucetia viridans*, in South Carolina, with emphasis on the selection factors that maintain extended maternal care. Nocturnal predation on the clutch was greater than diurnal predation. *Chiracanthium inclusum* (Araneae, Clubionidae) was the primary predator of eggs and emerged spiderlings. After producing a fertile egg sac in the field, female *P. viridans* produced at least three fertile sacs in the laboratory. In the field, females produced a second egg sac if their first sac was lost early in the season. In contrast with other studies, spiderlings were unable to exit from about 74% of the egg sacs without the aid of the mother.

INTRODUCTION

Maternal care in spiders ranges from short-term guarding of egg sacs in solitary species to long-term communal care of young in social species. The most common form of maternal care is a brief guarding period after the spiderlings have emerged from the egg sac (Brach 1976). In most families, this gregariousness is short-lived and usually disappears after the first post-eclosion molt. At this time, maternal behavior often disappears, and conflicts between mother and young can result in spiderlings being eaten (Foelix 1982).

The green lynx spider, *Peucetia viridans* (Hentz), mates only once and guards its egg sac and young until spiderling dispersal. After mating, the female feeds for several weeks, and oviposits 25-600 eggs into an egg sac which she anchors to the vegetation with silk (Whitcomb et al. 1966). Spiderlings emerge from the egg sac as second instars and remain on or around the sacs until dispersal by ballooning.

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The purpose of this study was to examine the biology of *P. viridans*, with emphasis on the role of predation as a selection factor favoring extended maternal care.

MATERIALS AND METHODS

Study site.—The study site is located approximately 2.3 km SE of Clemson University in Clemson, Pickens County, South Carolina. The site consists primarily of grasses and forbs and is bordered on the east by Lake Hartwell and on the west by woody vegetation.

We made observations every day from 25 September through 20 December 1987 and once per week from 21 December through 18 January 1988 for approximately 2-4 h, starting at 1230 EST. In addition, nocturnal observations were made from 28 September through 13 October 1987 for 2-4 h, beginning at 2230 EST. By the latter date, predation ceased because of low nighttime temperatures. The study area was divided into four sections, and a different section was selected sequentially as the starting location each day. Additional field observations were made once per day from 4 September through 6 December 1988.

From 7 October 1987 through 20 May 1988 and from 9 September through 9 December 1988, we conducted laboratory studies in a rearing chamber maintained at 25 ± 2°C and 65 ± 4% relative humidity, with a 14L:10D photoperiod. In experiments lasting longer than 48 h, we fed each green lynx female one muscid fly three times per week.

Natural history observations.—*Laboratory studies*: To determine whether *P. viridans* females could produce more than one egg sac, we removed 46 females from their field sacs in 1987 and housed them individually in plastic containers (6.1 cm deep x 4.0 cm diameter) in the laboratory. We also removed females from sacs produced in the laboratory within one day after spiderlings emerged. For each egg sac, we recorded the date of construction, date of spiderling emergence, number of unhatched eggs, and number of spiderlings. When females died, we counted mature (chorionated) eggs in the ovaries. We recorded how many days spiderlings required to emerge from successive sacs and how many days females required for subsequent oviposition (empty sacs disregarded). To determine whether spiderlings could emerge from egg sacs without the aid of the mother, we removed 43 egg sacs from guarding females in September 1988 and housed the sacs in the laboratory. Sacs were not removed until 24 h after construction to allow time for the silk to harden. When females constructed second egg sacs in the field, we also removed these sacs 24 h after construction. If no spiderlings emerged from egg sacs within 65 days after construction, we opened the sacs to determine the fate of the clutch.

Field studies: In the field, we determined the percentage of guarding females occupying each species of plant (N = 82) and the height of the egg sacs above the ground (N = 81). Some females pulled leaves around the sacs, and tied the leaves together with silk, which formed shelters that hid the sacs from view. Using two treatments, sheltered sacs (N = 19) and unsheltered sacs (N = 11); we tested the null hypothesis that predation on egg sacs was independent of the presence of a shelter in *Rubus argutus* Link (blackberry), the primary plant used for egg-sac anchorage.

Prey items of females and spiderlings were recorded. Feeding rates of females and spiderlings were calculated by dividing the number of feeding observations on each group (gravid females, females after egg-sac loss, females guarding spiderlings, females guarding egg sacs, and unguarded spiderlings) by the total number of observation periods for each group.

Egg sacs consist of a flat disc attached to a round bowl. Using the bowl as a reference point, we determined the orientation of the egg sacs once every 24 h until the first spiderlings emerged. An orientation change was recorded when the bowl direction differed by one major compass subdivision (22.5°) or more from one observation period to the next. For each female, we calculated the percentage of observation periods during which orientation changed. These percentages were ranked and analyzed with analysis of variance to compare changes in bowl orientation in the absence of the female ($N = 25$) versus changes in orientation in the presence of the female ($N = 53$).

To determine whether females could produce a second egg sac in the field, we located 43 gravid females in September 1988 and tracked them until construction of the first sac, removed the first sac, and noted whether additional sacs were produced. To aid in identification of females, each female was given a unique mark on the abdomen or legs with orange, water-proof enamel.

Predation experiments.—*Field studies*: In the field, we randomly assigned each spider to one of three treatments. Each plant occupied by a female was marked with a numbered ribbon, and the coloration and markings of each female were recorded. In treatment 1, we removed females from their egg sacs on 25 September ($N = 26$). In treatment 2 ($N = 28$), we removed females from spiderlings after approximately 90% of the young had emerged from the egg sac. Treatment 3 served as a control ($N = 29$), with females left to guard both egg sacs and spiderlings. Mortality was only attributed to predation if we observed a predator consuming eggs or spiderlings or if dissection of the predator revealed eggs or young.

Over the course of the study, many of the samples fit the criteria of more than one treatment (e.g., disappearance of a guarding female would move the sample from treatment 3 to treatment 1). Because of this lack of independence between treatments, data were compared on a percentage basis. The total percentage of predation was calculated for unguarded egg sacs, unguarded spiderlings, guarded egg sacs, and guarded spiderlings. These percentages were calculated by dividing the total number of predators for each of the above four groups by the total number of observation periods for each group. When the same species of predator appeared on the same clutch in consecutive observation periods (observation periods began daily at 1230 EST and 2230 EST), it was counted only once. No predators were observed after 18 November, so observation periods beyond this point were not included in analyses.

Percentages of diurnal versus nocturnal predation were calculated for the four groups. Percentages of diurnal predation were calculated by dividing the total number of predators for each group by the total number of diurnal observation periods on that group. Percentages of nocturnal predators were calculated in a similar manner. Diurnal plus nocturnal predators do not always equal the total number of predators because if the same species of predator appeared on the same clutch in consecutive observation periods, it was recorded as a diurnal and a nocturnal predator. A 24-h absence was required between diurnal observations and between nocturnal observations before counting the same species of predator on a particular clutch twice. Egg-sac and female disappearances were also recorded.

We deposited voucher specimens of *P. viridans*, predators, and prey items in the Clemson University Arthropod Collection.

RESULTS

Natural history observations.—*Laboratory studies*: The fertility (number of spiderlings plus number of unhatched eggs) of *P. viridans* decreased with consecutive egg sacs (Table 1). In the laboratory, a second egg sac was constructed by 93.5% of the females (16.3% of the sacs were empty), a third sac by 45.6% of the females (19.0% were empty), a fourth sac by 8.7% of the females (25.0% were empty), and a fifth sac (empty) by 2.2% of the females. Females did not open sacs without spiderlings (N = 22), whereas, females opened sacs with spiderlings (N = 39) except when the females died prematurely (N = 4). Spiderlings in these unguarded sacs were unable to emerge. At death, females (N = 26) contained an average of 11.7 ± 1.9 ($\bar{X}$ ± SE) mature eggs. Spiderling-emergence times from successive egg sacs were relatively constant (21-28 days). The amount of time required for oviposition decreased with successive sacs (Table 2).

Of the 43 egg sacs (second sacs excluded) taken into the laboratory in 1988, 27.9% of the sacs had spiderlings emerge without maternal aid. An average of 81.1 ± 22.4 spiderlings (53.9 ± 12.6% of the total number of spiderlings in these sacs) emerged. Spiderlings made no exit holes in 27.9% of the sacs, whereas 62.8% of the sacs had one exit hole, and 9.3% of the sacs had two exit holes. Of the sacs with single exit holes, 29.6% had spiderlings lodged in the holes; 77.8% of spiderlings trapped in the holes failed to complete ecdysis. No spiderlings were lodged in the exit holes of sacs with two openings. Of the 6136 spiderlings trapped in the 43 egg sacs, 763 (12.4%) were trapped in their exuviae while trying to molt (Table 3). After 65 days, an average of 3.0 ± 1.3 live spiderlings was found in six of the egg sacs (range = 1-7 spiderlings/sac), and three of these sacs had exit holes.

Table 1.—Clutch sizes and spiderling emergence times from consecutive egg sacs constructed by *Peucetia viridans* in 1987 and 1988. a = after spiderlings hatched, shed chorions were counted; sacs were not included in the analysis when spiderling number was greater than the number of shed chorions or when eggs were oviposited without the protection of an egg sac, b = sacs were constructed in the field; all others were constructed in the laboratory, c = sacs were constructed September-October 1988. (SE = standard error). NA = not applicable because spiderlings did not emerge from sacs.

	No. spiderlings ($\bar{X}$ ± SE)	N[a]	No. unhatched eggs ($\bar{X}$ ± SE)	N	Emergence times (days) ($\bar{X}$ ± SE)	N
Sac #1[b]	144.7 ± 10.04	34	5.7 ± 3.19	46	—	—
Sac #2	18.2 ± 2.19	42	5.6 ± 1.40	43	27.0 ± 0.28	31
Sac #3	11.6 ± 3.79	19	12.2 ± 3.24	20	27.8 ± 0.70	8
Sac #4	2.0 ± 2.00	4	7.2 ± 6.59	4	21.0	1
Sac #5	0.0	1	0.0	1	NA	0
Sac #1[b,c]	165.3 ± 8.68	43	7.7 ± 10.98	43	24.8 ± 1.50	12
Sac #2[b,c]	57.2 ± 33.28	4	52.2 ± 25.32	4	28.0	1

Table 2.—Interval between sequential ovipositions of *Peucetia viridans*. a = egg sacs were constructed in the field; all others were constructed in the laboratory, b = sacs were constructed in 1987, and females were allowed to guard until spiderlings emerged, c = sacs were constructed in 1988, d = value is a minimum, as determined from the first day each field sac was located. (SE = standard error).

	No. days between oviposition events ($\bar{X} \pm$ SE)	N
Sac #1[a,b]-Sac #2[b]	73.8 ± 7.84[d]	9
Sac #2[b]-Sac #3[b]	45.8 ± 2.05	16
Sac #3[b]-Sac #4[b]	40.0 ± 3.46	3
Sac #1[a,c]-Sac #2[a,c]	27.2 ± 2.50	4

Only two of the second egg sacs ($N = 4$) from 1988 contained spiderlings (two contained only eggs) (Table 1); 120 spiderlings (96.8% of the total) emerged from one sac, whereas all 105 spiderlings failed to emerge from the other sac despite the fact that this sac had three exit holes.

Field studies: Females used seventeen species of plants for oviposition (Willey 1988), with one female per plant. *Rubus argutus* ($N = 30$) and *Eupatorium hyssopifolium* L. ($N = 13$) predominated. The average egg-sac height was 73.8 ± 3.0 cm above ground (range = 21.5-161.5 cm), which represented the top 1/4 of all plants. When females constructed shelters, they placed their sacs inside the shelters and remained in direct physical contact with the sacs until spiderlings emerged; they then moved to the outside of the shelters to guard. Predation on the sacs was independent of the presence of *R. argutus* shelters ($\chi^2 = 0.151$, $df = 1$, $P = 0.6979$).

Adults fed on prey items in five insect orders, and spiderlings fed on insects in three orders and cannibalized conspecifics (Willey 1988). Hymenoptera ($N = 32$) were the primary prey of adult females. We observed 15 females feeding in the presence of spiderlings, but the females moved at least 3 cm away from the clutch and did not share the prey. We observed six spiderlings feeding on small insects; two fed simultaneously on the same ant. Gravid females had the highest feeding rate (10.6%), followed by females after egg-sac loss (6.2%), females guarding spiderlings (3.8%), unguarded spiderlings (1.2%), females guarding egg sacs (1.1%) and guarded spiderlings (0.0%).

Guarded egg sacs were reoriented significantly more often than unguarded sacs ($F = 56.70$, $df = 1$, $P = 0.0001$). Of the 53 guarding females, 51 reoriented their egg sacs an average of 67.7 ± 2.8% of the time; the remaining two sacs had spiderlings emerge on 28 September and 5 October, so reorientation may have occurred prior to initiation of the study. Of the 25 unguarded egg sacs, eight showed no reorientation, and the remaining 17 had orientation changes of $<$

Table 3.—Fate of *Peucetia viridans* spiderlings in unguarded egg sacs in 1988. a = calculated using total spiderling number, b = calculated using number of spiderlings trapped in egg sacs, c = egg sacs containing no spiderlings were omitted from analyses. (SE = standard error)

	N	None trapped in egg sacs ($\bar{X} \pm$ SE)	% trapped in egg sacs ($\bar{X} \pm$ SE)[a]	None trapped in exuviae ($\bar{X} \pm$ SE)	% trapped in exuviae ($\bar{X} \pm$ SE)[b]
Sac #1	43	142.7 ± 11.24	84.9 ± 5.06	17.7 ± 4.49	12.4 ± 2.80
Sac #2	2[c]	54.5 ± 50.50	51.6 ± 48.38	0.0 ± 0.00	0.0 ± 0.00

22.5°; these changes were probably due to a gradual weakening of the silk attachment lines from wind and rain.

The earliest egg sac was constructed on 8 September 1988; in 1987, the first egg sac was located on 10 September. After losing their first egg sac, all 43 females relocated to different plants. We were able to find and follow only four of these females until they constructed second sacs. Oviposition into second egg sacs required less time in the field than in the laboratory (Table 2).

Predation experiments.—*Field studies*: Predation was greater when the female was absent (Table 4). The total percentage of predation was greatest for unguarded egg sacs (6.5%), followed by unguarded spiderlings (1.2%), guarded egg sacs (0.1%), and guarded spiderlings (0.0%).

Chiracanthium inclusum (Hentz) was the most frequently observed predator of unguarded egg sacs and spiderlings, and secondarily used the sac as a retreat. This predator commonly constructed a silk retreat against the egg-sac disc, chewed a hole through the disc, and fed on the clutch from the protection of its retreat. *Chiracanthium inclusum* was observed inside egg sacs where it presumably fed on the sac contents. This predator was seen only once in the presence of a guarding female, but was not observed feeding.

In contrast, we observed *Cesonia bilineata* (Hentz), a gnaphosid spider, remain undetected within a clutch of guarded spiderlings for 15 h. Although the predator was never observed eating spiderlings, it was surrounded by dead spiderlings and moved within the clutch until the guarding female approached, at which time it ceased movement until the female moved away.

The female also was unable to protect the clutch from ants when large numbers were present. We observed a colony of *Crematogaster* sp. swarm over a guarded egg sac. The female moved 6 cm from the egg sac while ants entered the sac and carried spiderlings away. Approximately 12 h later, the female relocated her egg sac. At this time, the egg sac contained two holes, and *Crematogaster* sp. were still detectable within the sac.

Unguarded clutches attacked by orthopterans and hymenopterans (with the exception of *Vespula* sp.) were completely destroyed. Orthopterans consumed entire clutches plus the sac in less than 30 min; ants carried away whole clutches overnight. In contrast, predators such as *C. inclusum, Cesonia bilineata*, and larvae of *Chauliognathus pennsylvanicus* (De Geer) (Coleoptera, Cantharidae) spent several days feeding on a clutch without consuming all of the eggs or young. Gagrellids fed at sacs for less than 1 h and consumed from one to two eggs.

The percentage of nocturnal predation was greater than diurnal predation in all treatments but one (Table 5). Both diurnal and nocturnal predation were greater in the absence of the female. We observed 17 incidents of diurnal predation and 21 incidents of nocturnal predation (Table 4). *Chiracanthium inclusum* was the most common diurnal and nocturnal predator.

During the study, 15 unguarded egg sacs disappeared, presumably from rain, wind, or predation, and 10 sacs disappeared simultaneously with their guarding females, presumably because of relocation or predation. Nine egg sacs disappeared from guarding females, although the females remained. In six instances, guarding females disappeared from their egg sacs, presumably because of predation; the remaining clutches eventually disappeared or suffered mortality from predation.

Table 4.—Predators of *Peucetia viridans* clutches. a = total predation does not always equal diurnal plus nocturnal predation (see text).

	Number of predators		
	Diurnal	Nocturnal	Total[a]
UNGUARDED SACS			
Opiliones, Gagrellidae, undet.	—	3	3
Araneae			
Chiracanthium inclusum (Hentz)	3	6	8
Orthoptera			
Campylacantha olivacea olivacea Scudder	1	—	1
Melanoplus sp.	1	—	1
Oecanthus sp.	1	2	3
Coleoptera			
Chauliognathus pennsylvanicus (De Geer), larval stage	2	5	6
Hymenoptera			
Crematogaster clara Mayr	1	—	1
Crematogaster minutissima Mayr	—	1	1
Crematogaster sp.	1	1	1
Paratrechina parvula (Mayr)	—	1	1
UNGUARDED SPIDERLINGS			
Araneae			
Chiracanthium inclusum	2	1	3
Cesonia bilineata (Hentz)	1	—	1
Orthoptera			
Campylacantha olivacea olivacea	1	—	1
Hymenoptera			
Paratrechina parvula	1	—	1
Vespula sp.	1	—	1
GUARDED SACS			
Hymenoptera			
Crematogaster sp.	1	1	1

DISCUSSION

In South Carolina, the most frequent predator of *P. viridans* eggs was *C. inclusum*, followed by *Ch. pennsylvanicus* larvae, Orthoptera, and gagrellids. In northern Florida, Fink (1986, 1987) found that the two major sources of mortality of *P. viridans* egg sacs were ant predation, and parasitism by *Mantispa viridis* Walker (Neuroptera, Mantispidae); however, ants were the primary factor favoring maternal care of egg sacs because the female's presence did not significantly reduce mantispid parasitism. We did not observe mantispid parasitism in South Carolina and, although mantispids are common in the area,

Table 5.—Diurnal and nocturnal predation (%) on *Peucetia viridans* clutches (% = No. predators / No. observation periods). a = no. of observation periods.

	Diurnal predation (N)[a]	Nocturnal predation (N)
Unguarded sacs	3.8 (262)	13.8 (138)
Unguarded spiderlings	1.3 (470)	1.0 (98)
Guarded sacs	0.1 (865)	0.2 (577)
Guarded spiderlings	0.0 (325)	0.0 (65)

Brushwein (1986), in 4 years, located only two sacs that contained mantispids. In eastern Texas, mantispid parasitism did not constitute a significant source of mortality of *P. viridans* eggs (Killebrew 1982).

In South Carolina, the most frequent predator of emerged spiderlings was *C. inclusum*. In northern Florida, *C. inclusum* was observed in or on five unguarded egg sacs (10.9%), but Fink (1987) stated that *C. inclusum* was not observed feeding on eggs or spiderlings and might be using empty sacs only as a retreat. Fink (1986) concluded that in northern Florida, salticids were the major predators of emerged spiderlings; however, Fink (1986, 1987) made only diurnal observations, so nocturnal predators were not detected.

Although predation on egg sacs was independent of the presence of *R. argutus* shelters, this is the first report of *P. viridans* females constructing foliage shelters for their young. It is possible that the shelters protect the egg sacs from predation by making the sacs difficult to locate. Conversely, if a predator finds the sac, it may be protected while it forages. *Pisaurina* spp. and *Dolomedes* spp. (Araneae, Pisauridae) also construct shelters by pulling leaves over the sacs and tying them together with silk (Gertsch 1979).

Although females fed in the presence of spiderlings, we found no evidence that they directly provided food for the young, as reported by Whitcomb et al. (1966). However, spiderlings did feed on small insects that became trapped in the female's silk. We observed two cases of cannibalism among spiderlings in the field, whereas Fink (1984) did not observe any aggression among the young.

In the field, *P. viridans* females consistently reoriented their egg sacs throughout the guarding period. This behavior may regulate temperature of the sac contents and ensure that the eggs develop at the same rate. Randall (1977) found that the adaptive significance of maternal care in *P. viridans* was directly related to the female's role in reorienting the egg sac; when sacs were prevented from being reoriented, spiderlings emerged approximately four days late, which resulted in reduced clutch sizes because of cannibalism within the sacs.

Unguarded spiderlings failed to emerge from 74% of the egg sacs, and subsequently died within the sacs, suggesting that opening the sac might be an important component of maternal care in *P. viridans*; however, low laboratory humidity (65%) might have adversely affected the ability of spiderlings to emerge. In contrast, Randall (1977) and Fink (1986) found that spiderlings were able to emerge from unguarded sacs. Our 1987 results indicate that females need a cue from inside the egg sacs in order to open them, because guarded sacs with no spiderlings were never opened, and guarded sacs with spiderlings were always opened. Randall (1977) also found that females received cues from within the sacs when it was time for the spiderlings to emerge.

Laboratory females in South Carolina produced up to three fertile egg sacs after producing a fertile sac in the field, but clutch size decreased in successive sacs. This decline could be due to sperm depletion, decreased egg production, or an inadequate food supply. The latter is likely because second egg sacs produced in the field in 1988 had a clutch size approximately 2.5 times greater than second sacs produced in the laboratory. Over half of the South Carolina females were gravid at death, so, physiologically, it was possible to produce more eggs, although other factors might have been limiting. Whitcomb et al. (1966) reported that females in the laboratory in Arkansas constructed up to six egg sacs, and that successive sacs contained fewer eggs. Fink (1984) also reported a decrease in egg number in second egg sacs in northern Florida.

In South Carolina, oviposition into second egg sacs in the laboratory occurred after a minimum of 74 days and oviposition into second egg sacs in the field occurred after an average of 27 days; the difference may reflect food availability. Spiderlings in the laboratory required approximately 27 days within the egg sacs prior to emergence. Therefore, unless the first egg sac was lost early in the season, low temperatures, decreased foliage for sac anchorage, scarcity of prey items, and female mortality would lower the probability of a second sac being successful. Whitcomb et al. (1966) reported that in the laboratory in Arkansas (20-24°C), females constructed second egg sacs one to two months after construction of the first sac. These authors, therefore, hypothesized that in Arkansas, *P. viridans* did not have time to produce a second sac before the first frost. Fink (1984) noted that in north Florida, females constructing second sacs would not live long enough to guard them successfully, and she (1986) presented a detailed discussion of the adaptive significance of guarding the first egg sac in northern Florida. Second egg sacs have been reported in the field in southern California (Turner 1979; Polis in Fink 1986) and southern Florida (Fink 1986). We suggest that production of successive egg sacs at higher latitudes, such as in northern South Carolina, is adaptive only when the original sac is lost early in the season.

In *P. viridans*, maternal care reduces clutch mortality from predation; however, our observations indicate that predation pressures in South Carolina differ from those in Florida, and that protection from nocturnal predation and possibly aiding the young in emergence from the egg sac are important factors influencing the retention of maternal care.

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