Fink, L. S. 1987. Green lynx spider egg sacs: sources of mortality and the function of female guarding (Araneae, Oxyopidae). J. Arachnol., 15:231-239.

GREEN LYNX SPIDER EGG SACS: SOURCES OF MORTALITY AND THE FUNCTION OF FEMALE GUARDING (ARANEAE, OXYOPIDAE)

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ABSTRACT

Guarding green lynx spiders reduce egg sac mortality from two major sources, ants and sac dislodgement, using specific behavior patterns. However, they do not discriminate against egg sacs parasitized by mantispids, which are a third important mortality source. When ants are placed on egg sacs females attack, relocate the sac, or cut attachment lines so that the sac hangs from a minimal number of threads. Egg sacs are also relocated in response to other disturbances. The method of moving the egg sac relies heavily on silk lines and is distinct from that of lycosids and pisaurids.

INTRODUCTION

Numerous functions for female guarding of spider egg sacs and spiderlings have been demonstrated or proposed (Table 1), but the relative importance of these factors for any single species has not been assessed. Many previous observations of maternal behavior, especially in the Lycosidae, have been under laboratory conditions (Bonnet 1947; Higashi and Rovner 1975 and references therein). These studies have uncovered details of egg sac construction, maternal transport of eggs and spiderlings, and feeding of spiderlings. They cannot tell us, however, which of the numerous postulated and demonstrated functions of attending females are the most important under natural conditions. This paper describes the natural sources of egg sac mortality over one reproductive season and the maternal behavior patterns which are variously effective against them, for the green lynx spider *Peucetia viridans* (Hentz) (Oxyopidae) in north Florida.

METHODS

Populations of green lynx spiders in three open fields in Alachua Co., FL were censused at 3-day intervals from July through December 1983 (Fink 1984a, 1986). I followed the fates of 199 females and egg sacs. Egg sacs were marked with plastic flags staked nearby, and females were individually identified with dots of Testor's brand enamel paint. All censuses and observations were made during daylight hours.

The green lynx spider attaches her egg sac to low vegetation and guards the sac and emerged offspring for six to eight weeks until they disperse by ballooning

Table 1.—Presumed or demonstrated functions of the presence of female spiders at egg sacs. Proposed function based on: A = anecdotal field observations, F = field experiments, L = laboratory experiments, H = no data, only hypothesized.

Function		Species (Family)	Reference
Anti-predator	A	*Lyssomanes jemineus* (Salticidae)	Eberhard 1974
Anti-parasite	A	*Cyrtophora moluccensis* (Araneidae)	Lubin 1974
Thermoregulation or humidity regulation	A	*Pardosa amentata* (Lycosidae)	Vlijm et al. 1963
	AL	*Pirata piraticus* (Lycosidae)	Norgaard 1951
	F	*Geolycosa godeffroyi* (Lycosidae)	Humphreys 1974
	A	*Stegodyphus lineatus* (Eresidae)	in Shear 1970
	A	*S. sarasinorum* (Eresidae)	Bradoo 1973
	FL	*Theridion saxatile* (Theridiidae)	Norgaard 1956
Catch spiderling food	AL	*Sosippus floridanus* (Lycosidae)	Brach 1976
	A	*Theridion saxatile* (Theridiidae)	Norgaard 1956
	A	*Stegodyphus sarasinorum* (Eresidae)	in Shear 1970
	L	Other eresids, theridiids	Shear 1970; Kaston 1965
Regurgitate food	L	Several eresids and theridiids	Kaston 1965; Kullmann 1972
	L	*Coelotes terrestris* (Agelenidae)	in Shear 1970
Alert young to danger, food, or water	H	*Theridion saxatile* (Theridiidae)	Norgaard 1956
	H	*Pardosa lapidicina* (Lycosidae)	Eason 1969
Release offspring from sac	L	*Peucetia viridans* (Oxyopidae)	Randall 1977
	L	*Oxyopes salticus* (Oxyopidae)	Whitcomb & Eason 1967
	L	Lycosids, pisaurids	Gertsch 1949

(Gertsch 1949; Whitcomb et al. 1966). Egg sacs that had been recently constructed when first discovered were divided into three groups in each population: (a) females were removed from egg sacs immediately after oviposition ($N = 46$) or (b) after guarding for two weeks ($N = 34$), or (c) females were not removed from their sacs ($N = 58$). The remaining 61 egg sacs were more than a week old when first discovered; although they were not assigned to experimental groups they were censused regularly and used for ant manipulations. Additional observations of unmarked spiders were made in September through December 1984 at various sites in Alachua County.

RESULTS

Source of mortality: Ants.—Three species of ants were observed on or in 13 different unguarded *Peucetia* egg sacs and on the silk surrounding one guarded egg sac: *Crematogaster* sp. (seven egg sacs), *Formica* sp. (three), and *Pseudomyrmex pallidus* (Smith) (five). Holes were chewed through the sac, and each ant carried away a single egg or first instar spiderling at each visit. Up to 10 ants were found in or on a sac, and one sac had both *Formica* and *Pseudomyrmex* removing eggs simultaneously. Seven of these unguarded sacs were completely emptied by the ants, an eighth was emptied except for a mantispid cocoon, and a ninth produced only four spiderlings. Ant damage was distinct from that caused by other predators: attachment lines were undamaged, holes were chewed rather than the silk torn, and whole eggs or spiderlings were removed rather than being damaged or only partly consumed. Based on these criteria, mortality of at least 20 additional sacs was also attributed to ants. Ants are a major threat to egg sacs both because they are so abundant in *P. viridans* habitat and because they usually destroy the entire contents of the egg sac, resulting in no surviving spiderlings.

Ants are a danger to females as well as to egg sacs. I observed one spider with an ant's head attached to her leg. On four occasions when I placed *Camponotus* and *Crematogaster* ants on unmarked egg sacs and the guarding female attacked, the ant died while clamped onto her leg or chelicera. One female removed the ant and a second autotomized her leg with the ant attached, but the other two females were not able to rid themselves of the corpse. Costs may be associated with having an ant clamped to a leg or chelicera; antlion larvae (Neuroptera) bitten on the mandibles died of starvation if they could not remove the ant (Lucas and Brockmann 1981).

Defense against ants.—A natural encounter between a guarding female and an ant was observed only once, when a female bit and killed a *Crematogaster* ant approaching her on the silk. I staged additional interactions (with females not in the three experimental groups) in order to observe the females' behavior and effectiveness. More than 135 *Solenopsis* sp. and *Crematogaster* sp. ants were collected from nests and introduced one at a time onto the silk surrounding 13 guarded egg sacs. Some ants did not elicit attacks and may not have been noticed by the females before they escaped or fell from the silk. Three distinct behavior patterns were observed: direct attack, sac moving, and sac suspension. Females attacked the first ant(s), but when I continued to supply ants the females initiated one of the other behavior patterns.

a. Direct attack. The females attacked and removed a total of 71 ants. A female did not pursue an ant on the silk or sac, but reacted to it only when it was directly in front of her or walking over her legs or body. When an ant walked on a spider's leg the spider often waved the leg (15 observations), flicking the ant off the plant, and one ant crawling on the spider's abdomen was removed by wiping with a leg. These ants fell from the plant and seemed to be unharmed. Other ants touching the spider or walking directly in front of her were grabbed in the chelicerae (55 observations) and either dropped quickly to the ground or held in a slow bite; none was eaten, but most were moribund or dead.

b. Sac moving. On three occasions when two to five ants had been introduced in succession, the spider cut the silk lines connecting the egg sac to the plant and moved it to a new plant or a new location on the original plant. I watched one female for more than an hour after introducing the ants. After the second ant was introduced the spider began to bite and break individual silk lines near the sac. New lines were spun between the sac and the new site, 10 cm lower on the same plant. Not all lines went directly between the new and old sites; others were spun to two adjacent leaves. These actions, cutting old lines and attaching new, alternated in bouts of several minutes with periods of sac guarding. During this time I continued to introduce ants. Some were attacked, while others triggered new bouts of silk cutting. Within half an hour most of the original lines attaching the sac had been severed, and the sac was suspended on new lines midway between the leaves. By the next census the sac was fastened firmly at its new site, and the attachment lines to the original site had been severed.

The method of moving the sac is different from that used by lycosids, which attach the sac to the spinnerets, or pisaurids, which attach it also to the chelicerae. In *Peucetia* the move is done entirely by sequentially attaching and detaching lines between the sac and the new and old sites; the female never actually carries the sac.

On 73 occasions guarded egg sacs were relocated to new plants or to new positions on the same plant between censuses. Although the distance moved was not always recorded, most movements were over short distances (< 0.5 m), and movements greater than 1 m were recorded seven times. Twenty-eight of the 73 sac moves (38%) occurred after females were removed for marking and measuring, and therefore indicate that the female moves her sac when disturbed.

c. Sac suspension. Seven spiders began cutting the lines after one to four ants had been placed on the sacs, but did not move the egg sac to a new location. After cutting almost all connections, so that the egg sac dangled from only one to three lines, each female climbed onto the sac and resumed guarding. This behavior is not an aborted attempt to move the egg sac, but a specific response in itself. The effect of silk-cutting is to reduce the probability that a wandering ant will encounter the sac, and to force it to approach from only one direction. This behavior also removes the female herself from the ant's search path, and therefore may lower her own risk.

Source of mortality: Sac disappearance.—The silk attachment lines of eight unguarded egg sacs gradually broke, presumably due to wind and rain. These sacs became loosened from the vegetation and then disappeared. Eight other unguarded sacs also disappeared from their plants, leaving only a few silk lines, and probably had been dislodged similarly. No such loosening and dangling of egg sacs occurred among those that were guarded. Nine guarded egg sacs disappeared simultaneously with their guarding female, but probably were relocated by the female (see b above) rather than dislodged. Alternatively they may have been removed by unidentified predators (such as birds, lizards, or mice), but I have seen no definite evidence of vertebrate predation on egg sacs.

Sac maintenance and prevention of sac dislodgement.—When a female constructs her egg sac the attachment lines are short and inconspicuous, and for several weeks the female does not noticeably alter the sac's appearance. Her spinning, however, prevents the sac from becoming dislodged. Before the spiderlings emerge the female spins more and longer lines, so that the sac is enclosed in a three-dimensional tent of silk. After the spiderlings have emerged the female may spin still more lines, radiating up to 0.3 m from the sac in several directions. The increased number of lines is not necessary to keep the sac attached, and therefore must serve an additional, still undetermined, function.

Other sources of mortality.—*Mantispa viridis* (*Neuroptera: Mantispidae*). *M. viridis* Walker is a generalist brood parasite, appearing in the egg sacs of a number of spider species in Florida (Hieber 1984). Four unguarded, four partially-guarded, and 10 guarded egg sacs contained mantispid cocoons. Fifteen of the broods were completely destroyed by the mantispid, but three had at least one spiderling emerge in addition to the parasite. Five additional sacs, not assigned to the experimental treatments, also produced mantispids.

Mantispid parasitism rates did not differ among the three experimental groups (Fink 1986); however, the proportion of sacs parasitized did vary among sites. At the three sites, 12 of 38 sacs (32%), 5 of 72 sacs (7%), and 6 of 89 sacs (7%) were parasitized (Chi-square = 18.36, df = 2, $p < 0.001$).

Female *P. viridans* do not abandon sacs that contain mantispid larvae or cocoons, or moldy spider eggs, and the behavior of females guarding such sacs was not distinguishable from that of females guarding healthy egg sacs. Females on parasitized sacs guarded for the same length of time (Fink 1984a), spun extra silk lines around the sacs, and bit at the sac to open the seam. Once the seam was open the white cottony mantispid cocoon was visible, as on several occasions was the bright green mantispid within the cocoon. Both cocoon and mantispid are visually quite distinct from a group of globular orange spiderlings. Female green lynx spiders fail to discriminate parasitized sacs not only when the mantispid is invisible within the sac, but also when it is quite obvious to a human observer.

Conspecifics. Peucetia viridans are major predators of immature and mature conspecifics (Turner 1979; personal observation); I found that mature females act as egg sac predators as well. A marked non-parous female was found on another spider's egg sac, which had a hole with a dampened, dark edge unlike the holes made by ants. The partially-digested sac owner was dead on the ground. The non-parous female consumed all of the spiderlings within the sac, and then bit at the sac itself. I observed two other pre-oviposition females adjacent to similarly-damaged egg sacs, but did not see the predation event. The holes in the three egg sacs were distinct from those made by other predators. In each case, the attacking female had not yet constructed her own sac. After a female has oviposited, she is likely to guard another female's egg sac if she encounters it, rather than to eat the eggs (personal observation).

Other predators. In contrast to ants, many arthropods that attack egg sacs and spiderlings cause only partial brood destruction. Five additional species of spiders were observed feeding at or associated with unguarded *Peucetia* egg sacs. *Phidippus pulcherrimus* Keyserling (Salticidae) ate unguarded spiderlings on four occasions, but never consumed an entire brood. *Metaphidippus galathea* (Walckenaer) (Salticidae, two occasions), *Chiracanthium inclusum* (Hentz) (Clubionidae, five), and *Sergiolus bicolor* Banks (Gnaphosidae, four) were found in or on egg sacs but were never seen eating eggs or spiderlings. The clubionid and gnaphosid spiders may have chosen previously-emptied egg sacs as retreat sites.

Unidentified pentatomid bugs (Hemiptera: Pentatomidae) were found on five unguarded egg sacs; at least one had its proboscis piercing the sac and apparently was feeding on eggs. Predaceous larvae of a cantharid beetle (*Chauliognathus* sp.) were found in five unguarded sacs, but were not responsible for their complete mortality. Beetle larvae did consume spider eggs when placed together in a container overnight. A 3 cm long caterpillar (Noctuidae: *Heliothis virescens* (F.)) was found with its head within an unguarded sac. When placed in a container with an undamaged egg sac, it chewed a hole in the side but did not eat any of the sac contents.

Failure to hatch.—Eleven sacs that failed to hatch contained moldy or dried eggs or spiderlings. These unhatched sacs were distributed evenly among the three experimental groups.

Venom spitting.—On at least 15 occasions in 1983 and numerous occasions in 1984, sac-guarding spiders spat venom at me during censuses. This behavior is described in detail elsewhere (Fink 1984b). The intended object of this spitting in natural encounters is unknown; the spiders were never observed spitting at ants or conspecifics.

Interactions between mother and spiderlings.—I found no evidence of a female spider providing any direct care to her emerged spiderlings. Whitcomb et al. (1966) and Randall (1977) have found that the female green lynx spider usually opens the egg sac to allow the spiderlings to emerge, but that spiderlings can emerge unaided. Although I saw at least seven females eating in the presence of their emerged spiderlings, spiderlings did not share the meal, as was reported by Whitcomb et al. (1966). Only two spiderlings were observed feeding while still on the silk surrounding their egg sac; both were eating tiny insects which they probably had captured themselves.

DISCUSSION

This paper has identified several behavior patterns of guarding females. To demonstrate that guarding is adaptive, however, it is necessary to show that females reduce sac mortality and that their overall reproductive success is higher because of their guarding. A companion paper (Fink 1986) proves that the presence of a female significantly increases the survival of her brood. Only 9% of the unguarded egg sacs produced spiderlings, compared with 69% of the guarded sacs. Guarded egg sacs have significantly lower mortality from ants and disappearance but not from mantispids or hatching failure. In addition I showed that under north Florida conditions females have a higher lifetime reproductive success if they guard their first egg sac than if they abandon it and construct a second egg sac.

Although maternal care by *Peucetia viridans* decreases mortality from several sources, I propose that ants were, and continue to be, the major selective factor favoring egg sac guarding. The general importance of ants in the evolution of spider parental behavior has not been assessed. Foelix (1982) and Turnbull (1973) did not include ants in their discussions of spider egg sac predators, and Bristowe (1941) assumed that they were incapable of penetrating the silk sacs. These authors, however, emphasized temperate zone spiders.

Ant predation is more severe in the tropics, and ants can be major selective agents in the evolution of tropical animal adaptations. Jeanne (1975), for example, argues that ant predation has been a major factor in the evolution of social wasp nest architecture. *Peucetia viridans* is a member of a primarily tropical family (Brady 1964), and its range extends through Central America. Some features of its maternal care—in particular severing silk and suspending the sac from a few lines—may be specialized anti-ant adaptations. Additional experiments are necessary before it can be determined if lynx spiders recognize ants as a particular class of danger, and if silk cutting is a specific response.

The fact that a large proportion of unguarded egg sacs were dislodged may be an effect rather than a cause of maternal care. If a female were not going to guard her sac, presumably selection would result in more secure attachment lines. Because the female's presence is selected for by predation, there may be reduced selection for careful attachment behavior. In addition, having fewer attachment lines allows females to move their egg sacs more quickly when disturbed. Although this scenario may be correct, it is also possible that sac dislodgement could not be prevented. During late fall in north Florida the majority of herbaceous plants in *P. viridans* habitats die back, and a plant which provides a secure substrate for a new egg sac in early October may be prostrate before the spiderlings disperse in mid-November. Christenson et al. (1979; Christenson and Wenzl 1980) found that dislodgement was a major cause of mortality of the egg sacs of *Nephila clavipes* L. in Louisiana, and that it was higher in areas with herbaceous vegetation than in woody areas. Remaining with her egg sac, a green lynx spider can prevent it from falling to the ground by fastening new attachment lines or moving to a safer location.

Some spiders are capable of determining the status of their egg sac contents; thus *Cyrtophora moluccensis* Doleschall females discriminate against parasitized egg sacs (Lubin 1974), and *Agelena consociata* Denis against empty and dead sacs (Krafft 1981). Given that high parasitism rates by *Mantispa viridis* occur (up to 32% of the egg sacs in a particular site), why does *P. viridans* not develop anti-mantispid behavior, or abandon parasitized egg sacs? At least three factors may explain the absence of such behavior in *P. viridans*. (1) At two of three field sites spiderlings emerged from some parasitized sacs. If the probability of successfully producing a second egg sac is lower than the probability that one or a few spiderlings will emerge from a parasitized egg sac, there will be little selection for sac abandonment. This is certainly true for females in north Florida and further north (Fink 1986); however, in south Florida females do produce second sacs successfully (personal observation). (2) Mantispids are active throughout the entire *P. viridans* reproductive season; if a female abandons a sac in a field with a high parasitism rate, then the probability that a second sac would be parasitized is equally high. (3) The mantispid larva, which is approximately 1 mm long when it approaches the egg sac (McKeown and Mincham 1948), initially may be small enough to avoid the female's notice. If a female had a physical rather than a chemical mechanism for checking the status of her egg sac, she might not perceive a mantispid for weeks. Because the weight gain of a female abandoning her egg sac after two weeks of guarding is significantly lower than if she had abandoned immediately, the probability of constructing a second egg sac after perceiving a mantispid in the first would be slight (Fink 1986).

Rovner (1980) has suggested that the Oxyopidae are more closely related to a web-spinning ancestor than to other cursorial families, and Griswold (1983) has described a web-building oxyopid. To my knowledge the green lynx spider's method of moving the egg sac is unlike that of any other hunting spider. Its great reliance on silk lines and the fact that the sac is not carried in its chelicerae or on its spinnerets may be more evidence pointing to a web-building ancestry for the family.

ACKNOWLEDGMENTS

I thank H. J. Brockmann and Giselle Mora-Mora for comments on this manuscript. Scientists from the Florida State Collection of Arthropods, Gainesville, Florida identified specimens: G. B. Edwards, Jr. (spiders), J. C. Nickerson (ants), J. B. Heppner (immatures), and L. Stange (mantispids). The Florida Fish and Game Commission and the Venable and Crevasse families of Archer, Florida kindly gave me access to field sites. The graduate ethology course, fall 1984, helped collect the data on spider responses to ants. This research was supported by a National Science Foundation predoctoral fellowship and by the Department of Zoology, University of Florida.

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Manuscript received December 1985, revised December 1986.