2007. The Journal of Arachnology 35:143–152

INTERACTIONS BETWEEN THE SOCIAL SPIDER *ANELOSIMUS STUDIOSUS* (ARANEAE, THERIDIIDAE) AND FOREIGN SPIDERS THAT FREQUENT ITS NESTS

T. Alex Perkins, Susan E. Riechert,[1] and **Thomas C. Jones**: Department of Ecology and Evolutionary Biology, University of Tennessee, 569 Dabney Hall, Knoxville, Tennessee 37966-1610, USA. E-mail: sriecher@utk.edu

ABSTRACT. Because competition for resources generally leads to the spatial exclusion of species using similar resources, it is surprising that foreign spider species are frequently observed in or near the nests of the social spider, *Anelosimus studiosus* (Hentz 1850) (Theridiidae). In this study, we quantified the frequency of *A. studiosus*-foreign spider co-occurrence and completed experiments designed to explain the nature of the host-foreign spider species associations. Four families were numerically prominent nest associates of *A. studiosus*: Salticidae, Anyphaenidae, Araneidae and Tetragnathidae. These families and the Agelenidae (intermediate association rate) and (Philodromidae) (infrequent association rate) were subjected to further study. In choice trials, no foreign spider family discriminated nest silk or *A. studiosus*, itself, from the foliage the nest is built in. Predation events and maximum inter-individual spacing were significant outcomes of induced pair-wise interactions between host and foreign spiders for all families. Predation events were almost exclusively foreign on host. Field census results show that a close correspondence exists between the rate of loss of *A. studiosus* nests over time and the association rate of anyphaenids and agelenids at particular sites: these two families were the prominent predators on *A. studiosus* in laboratory trials. In reciprocal predation tests, juveniles suffered less predation in the presence of a mother; in the reciprocal trials, mothers also suffered less predation from foreign spiders when juveniles were present.

Keywords: Anti-predator behavior, intraguild predation, species co-occurrence

Organisms inhabit nests for many reasons, including not only the procurement of shelter from the physical environment, but also for refuge from predators, as an arena for mating and the rearing of broods, and as a site for foraging. Given the value of the nest sites themselves and energy applied to modification of them, it is not surprising that the host species encounters other species that intrude on its nests for a variety of reasons. This paper considers the extent to which foreign nest associates of a social spider species confer a benefit to the host versus a significant fitness cost.

In vertebrates such as fish and colonial nesting birds, increased protection against predators is an explanation that is frequently offered for the occurrence of mixed species nesting. There is evidence that colonial nesting among conspecifics confers similar antipredator effects in spiders (e.g., Uetz et al. 2002). However, the only known beneficial foreign nest associates to spiders are beetles and lepidopteran larvae that clean social spider nests of waste material (Robinson 1977; Furey & Riechert 1989). While many foreign spider species have been found to associate with social spider colonies, these have primarily been identified as either kleptoparasites that feed off of the webs of the host or as facultative commensals that build their own webs within the framework of the colony (reviewed in Buskirk 1981; see also Proctor 1992).

This study involves the spider *Anelosimus studiosus* (Hentz 1850) (Araneae, Theridiidae), which Brach (1977) categorized as a solitary species that offers extended maternal care of its young. Furey (1998) recently provided evidence that *A. studiosus* exhibits a mixed social strategy including solitary and communal nests at higher latitudes in the southeast US. Further documentation of the mixed strategy is presented in Jones et al. (in press). During the course of completing a lat-

[1] Corresponding author.

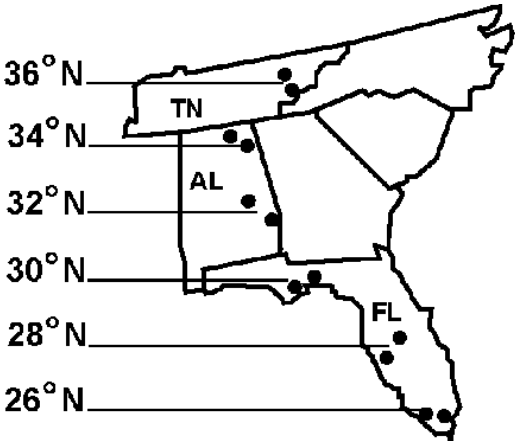

Figure 1.—Map showing latitudinal distribution of *Anelosimus studiosus* sampling locations.

itudinal study of the social structure of this species between south Florida and east Tennessee, we frequently found foreign spider species in its nests (also reported in Deyrup et al. 2004). In this paper, we quantify the frequency of co-ocurrence of *A. studiosus* and foreign spiders in its nests and examine the nature of the association between the prominent foreign spider nest associates and the host species. In particular, we consider whether the foreign spiders are attracted to *A. studiosus* nests and whether the outcome of their association with *A. studiosus* is beneficial, neutral or costly to it.

METHODS

Frequency of nest invasion.—For every two-degree change in latitude between south Florida 26° and east Tennessee 36°, we established two independent 500 m transects along roadside or water-body edge vegetation at locations occupied by *A. studiosus* (Fig. 1). We collected 25 *A. studiosus* nests from each transect using a random draw method to determine the respective meter intervals from which to take a nest. A nest herein refers to silk bound leaves occupied by at least one *A. studiosus* individual. We collected nests coincident with the production of clutches by adult females at particular latitudes. We started the censuses in March at 26° and successively sampled higher latitudes through late spring into June. If we did not find a nest in a designated interval, we drew a new interval for that nest. If an interval had more than one nest present, we chose the most centrally placed nest within that interval. We clipped each nest from the branch of the tree or shrub it was in and bagged it for return to our field laboratory for dissection. We recorded the number and age of *A. studiosus* individuals as well as the number of foreign spiders present by family. Voucher specimens were preserved in 70% ethanol for species determination. The remaining spiders were used as test subjects in the experiments described below. The voucher specimens are deposited in the Florida State Collection of Arthropods/Division of Plant Industry, Gainesville, Florida.

We made further nest collections throughout the study as test subjects were required for the various trials. These specimens were not collected from transect intervals but rather from nests collected in surrounding areas.

Based on the results of the nest censuses, we chose a number of families for further study. These included the Salticidae (jumping spiders) and Philodromidae (crab spiders), orb weavers belonging to the families Araneidae and Tetragnathidae, the sac spider family Anyphaenidae, and the funnel-web spider family Agelenidae.

Choice trials.—We completed two sets of trials to determine whether foreign spiders are attracted to some physical characteristic of an *A. studiosus* nest: Validation and Discrimination. The Validation test was performed to verify the assumptions that spiders will sample an arena environment and that they prefer containers with foliage to empty containers in a choice situation. In this simple test, we released a foreign spider into a hole at the top of a clear plastic tube (3 cm diam., 10 cm length) that connected two choice containers (clear plastic boxes of 10 cm diam. and 10 cm height). One of these containers was empty and the other contained a cluster of silk foliage that matched the leaf clusters *A. studiosus* occupies in the field. Upon release, the spider was watched for a 10-min interval in which its behavior was recorded. At the end of the 10-min watch period period, we noted the location of the test subject within the arena system as in the Empty container, Foliage container or Connecting tube. The spider was then left within this arena system for 24 h. At this time, we again recorded its settling position as above. The containers, tubing and foliage clusters were cleaned between trials to eliminate silk and chemical cues that might influence the path a new test subject might take. Forty-two *Agelenopsis emertoni* (Chamberlin & Ivie 1942) were tested in the Validation trials.

The Discrimination test was designed to determine whether a foreign spider's association with *A. studiosus* nests reflects an attraction to the host or merely reflects selection of similar plant physiognomy to that utilized by the host. The trials were completed in a three-chamber choice arena modeled after that used to test male choice of female reproductive states in Riechert & Singer (1995). The arena was constructed as described for the Validation test with the addition of intersecting tubes in the release area that permitted movement among three chambers offering the following choices: plant physiognomy (Foliage Only container), attraction to the silk nest produced by *A. studiosus* (Empty Nest container), or attraction to the host spider species, itself, (Occupied Nest container consisting of an adult female and her young). Identical artificial leaf clusters were available in all three choice containers. The Empty Nest and Occupied Nest treatments were established in a number of containers throughout the experiment. The contents of a natural nest collected in the field (generally a female and her young) were released into a chamber on the leaf cluster positioned in it. Once a web had been established in the leaf cluster, the chamber was ready for use in a trial. The host spiders were removed following establishment of the nest for containers used in the Empty Nest treatment. As in the Validation test, the settling location of each test spider was recorded after 24 h in the arena system and the containers and connecting tubes were cleaned between trials. Thirty choice trials were completed for the family Salticidae, 35 for the Anyphaenidae, 41 for the Araneidae, 30 for the Tetragnathidae, 19 for the Agelenidae, and 33 for the Philodromidae. Each test subject was used in only one trial.

Host spider-foreign spider interactions.—Because it is difficult to observe spider-spider interactions within foliage or the confines of a nest, we tested for possible interspecific interactions by releasing a foreign spider and an adult female host simultaneously into a clear plastic box measuring 10 cm on a side and 3 cm in height. This simple arena test was used to gain some idea of whether the host and generally larger foreign spider (exception = some trials with philodromids) were indifferent to the presence of one another or exhibited avoidance as would be the case in territory defense or avoidance of predation. A square arena was used rather than a round one because spiders prefer corners for web and silk retreat construction. We left each pair of subjects in the box for a 24-h period. We then recorded: 1) whether a predation event occurred or not and if so, the direction of this event (host on foreign spider or foreign spider on host); and 2) the relative positions of the two individuals in the arena (if both survived) with reference to the box corners/sides: same corner/side, adjacent corners/sides, or opposite corners/sides. By chance, the two spiders were expected to settle 25% of the time on the same side, 25% of the time on the opposite side and 50% of the time on adjacent sides of the square arena (two times as many adjacent corner opportunities compared to other positions). Forty-five trials were completed utilizing salticids (mean ± SE length = 6.1 ± 0.5 mm) as the foreign spider, 21 with anyphaenids (8.8 ± 0.2 mm), 15 with araneids (7.1 ± 0.5 mm), 15 with tetragnathids (8.0 ± 0.5), 11 with agelenids (8.4 ± 0.05), and 25 with philodromids (4.3 ± 0.08). *Anelosimus studiosus* averaged 3.0 ± 0.1 mm in length. Most of the foreign spiders used in these trials were collected from *A. studiosus* nests and the vegetation surrounding them.

Nest status censuses.—We marked 30 nests containing a brooding female at each study site within each latitude. We also recorded nearest neighbor nests in the vicinity of each focal nest: to the bottom, to the top, and to each side in the four compass directions (N, S, E, & W). This mapping protocol permitted us to distinguish between the total loss of a female and her brood and the construction of a new nest by the female at a nearby site over time; work with marked *A. studiosus* indicates that nest moves are of very limited distances (cm, Riechert & Jones unpublished observations). We checked these focal nests once a month over a 4-mo period for nest survivorship, extinction, and relocation.

Nest defense trials.—We completed two experiments testing for potential nest defense by *A. studiosus* against predation by other spider species. In the first, we tested for juvenile survival in the presence of a predator under the two mother contexts (present vs. absent). In the second, we tested for mother survival under the two juvenile contexts (present vs. absent). As we completed each trial we recorded information on the instar of juveniles present (1^{st}–5^{th}). We completed a minimum of 50 trials of each context.

We collected single-female nests from the field for use in this experiment. We removed adult males and other individuals according to the treatment. We also removed juveniles of the desired age class in excess of five, maintaining this as a constant throughout the experiment. Each nest was then placed in a plastic container (10 cm diam. and height) and the nest composition treatment was maintained for 24-h prior to the introduction of a foreign spider.

Late instar and adult anyphaenids (mean ± SE length = 8.9 ± 1.5 mm, range = 5.7–13.1 mm) were used as the predators in this experiment, as they showed the highest incidence of predation on *A. studiosus* in the interaction trials. After its collection from the field, each anyphaenid was maintained in the laboratory for 24 h before it was released into a box containing an *A. studiosus* nest. Upon removal of the foreign spider from the nest 24 hrs later, we recorded the number of surviving *A. studiosus* by type. Each *A. studiosus* nest and anyphaenid was used in only one trial.

RESULTS

Web censuses.—On average about a quarter of the dissected *A. studiosus* nests at every site contained foreign spiders (mean ± SE proportion = 0.24 ± 0.03). Significant site and latitudinal variation existed in the frequency of foreign spider association with *A. studiosus* nests (chi-square tests, Site: χ^2 = 28.0, df = 11, $P < 0.002$; Latitude: χ^2 = 20.5, df = 5, $P < 0.001$). However, the results of a nested ANOVA (Latitude[site]) indicated that there was no significant latitudinal trend (F = 1.23, $P \approx 0.26$).

While the majority of the invaded *A. studiosus* nests had only one foreign spider, as many as five were found in a single nest. The means and standard errors presented in Table 1 for numbers of foreign spiders per invaded *A. studiosus* nest did not include spiderlings or egg sacs that were present in the case of a spider using the *A. studiosus* nest as a brooding site. When more than one foreign spider was recorded at a given *A. studiosus* nest, 70% of the time they belonged to different spider families, a highly significant deviation from a chi-square expected ratio of 50:50 same vs. unlike family (χ^2 = 30.4, df = 1, $P < 0.0001$). A nested (site within latitude) ANOVA was performed to test for geographic/habitat variation in mean number of foreign spiders per host nest; none was detected (F = 1.06, $P \approx 0.4$).

Ten spider families representing six different foraging strategies were found to frequent the nests of *A. studiosus* (See Table 1 for list of families and genera within families, associated foraging strategies, and the numerical representation of particular families at the respective sites). The familial association of nest invaders varied significantly among the sites (chi-square test, χ^2 = 71.0, df = 5, $P <$ 0.001). The ranking of taxon representation by site presented in Table 1 is in ascending order (most frequent [rank = 1]; least frequent [rank = 6]). Using these rankings determined for individual sites, we obtained an overall among site ranking for the foreign spider families found at *A. studiosus* nests. The Salticidae, Tetragnathidae, Araneidae, and Anyphaenidae were the most prominent nest associates overall. The Clubionidae and Agelenidae were intermediate frequency nest associates and the Philodromidae, Theridiidae, Dysderidae, and Mimetidae were infrequent nest associates. We used these results to select foreign spider families for inclusion in further studies. All of the prominent families listed above were included along with the Agelenidae, representing intermediate visitation frequency of association, and the Philodromidae representing infrequent association.

Choice trials.—In the two-choice Validation trials, 40% of the spiders were observed to visit both chambers during the course of the initial 10-min watch period and 88% ultimately settled within the container offering the foliage as opposed to the connecting tubing (7%) and Empty Container (5%).

The spider families tested in the Discrimination trials involving three chambers with varied levels of host cues differed significantly in the degree to which they settled in the choice arenas (minimally containing foliage) versus in the release location (network of tubes connecting the choice chambers) (χ^2 =

Table 1.—Nest census results by latitude and site within latitude. *Spider Taxa. Orb Webs: Araneidae (1a): *Nuctenea*, *Araniella*, *Eriophora*, *Mangora*; Tetragnathidae (1b): *Tetragnatha*; Sheet-line webs: Agelenidae (2): *Agelenopsis*; Ambush Spiders: Thomisidae (3): *Misumenops*; Diurnal Hunters: Salticidae (4): *Hyctia*, *Phidippus*; Nocturnal Hunters: Clubionidae (5a): *Clubiona*, *Trachela*, *Castianeira*; Anyphaenidae (5b): *Anyphaena*; Dysderidae (5c): *Dysdera*; Pirate Spiders: Mimetidae (6): *Mimetus*; Scattered-Line Webs: Theridiidae (7): *Argyrodes*, *Theridion*.

Latitude Site	Proportion Nests with Foreign Spiders	Mean + SE Number Foreign Spiders/Nest	Foreign Spider Taxa* #Ranked in order of decreasing abundance
26°			
Collier Seminole	0.36	1.17 + 0.11	^{1}3, ^{2}5a, ^{2}5b, ^{3}1a, ^{3}4
Miccosukee	0.35	1.35 + 0.19	^{1}1a, ^{2}4, ^{3}1b, ^{3}5a
28°			
Lake Manatee	0.33	1.28 + 0.12	^{1}1a, ^{2}1b, ^{3}4, ^{4}5a, ^{5}5b, ^{6}3, ^{6}6, ^{6}7
Lake Louisa	0.22	1.19 + 0.10	^{1}4, ^{2}1b, ^{3}5a, ^{4}1a, ^{5}5b, ^{5}6
30°			
St Marks	0.18	1.08 + 0.08	^{1}1b, ^{2}1a, ^{3}5a, ^{4}5b, ^{4}4
Bottoms Rd	0.11	1.33 + 0.21	^{1}4, ^{2}5a, ^{3}1b, ^{3}2, ^{3}5c
32°			
Lake Point	0.10	1.17 + 0.14	^{1}4, ^{2}1b, ^{2}2, ^{2}5a, ^{2}5b, ^{2}7
Wind Creek	0.33	1.47 + 0.26	^{1}1b, ^{2}1a, ^{3}2, ^{4}4, ^{4}5a
34°			
Guntersville Lake	0.21	1.10 + 0.10	^{1}1a
Lake Weiss	0.16	1.10 + 0.10	^{1}4, ^{2}1a, ^{2}2
36°			
Melton Hill	0.16	1.0 + 0.01	^{1}1a, ^{2}2, ^{3}1a, ^{3}4, ^{4}5a
Chilhowee	0.24	1.58 + 0.23	^{1}5a, ^{2}1a, ^{3}2, ^{4}1b, ^{5}4, ^{5}5b.

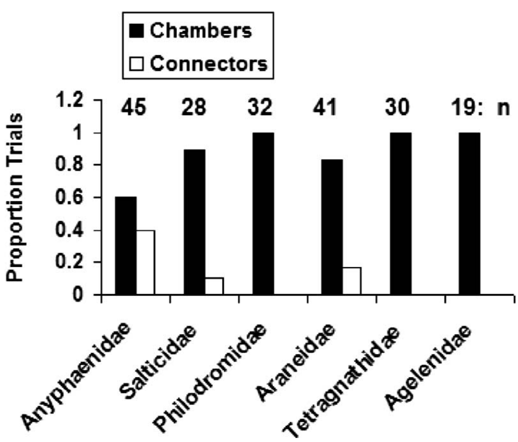

Figure 2.—Comparison of spider settling patterns by family in Discrimination choice trials: Chambers vs. in central tube area that radiated out to three chambers (Connectors). Number of trials indicated above bar for each family.

43.3, $df = 5$, $P < 0.0001$). The Anyphaenidae were the major contributors to this significant difference: 40% of them settled in the release area as opposed to in the chambers (Fig. 2). No significant differences were exhibited among the families in the particular chambers they settled in (Foliage Only, foliage with Empty Nest present, and foliage with Occupied Nest) (chi-square test for heterogeneity, $\chi^2 = 15.9$, $df = 10$, $P \approx 0.15$) (Fig. 3).

Host spider-foreign spider interactions.—Thirty nine percent of the interaction trials involved a predation event. The results of an R by C chi-square test suggest that predation events were not evenly distributed among the spider families paired with *A. studiosus* ($\chi^2 = 15.5$, $df = 5$, $P < 0.01$). Inspection of the individual cells of the chi-square test contributing most to this significant test result identified the agelenid and anyphaenid trials; greater frequencies of predation events were observed than expected for these cells. The tetragnathids, and to a lesser extent the

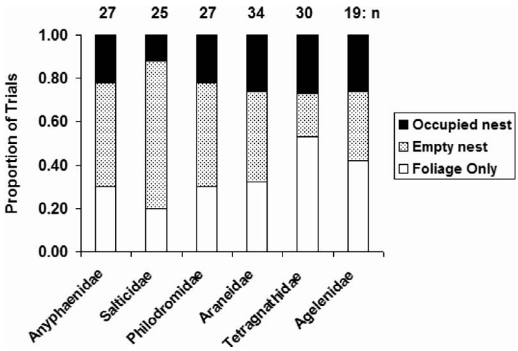

Figure 3.—Choices made among three chamber types by foreign spiders that frequent the nests of *A. studiosus*. All chambers had foliage present. Number of trials at top of bars. Chi-square test analysis of frequency distribution among families was non-significant.

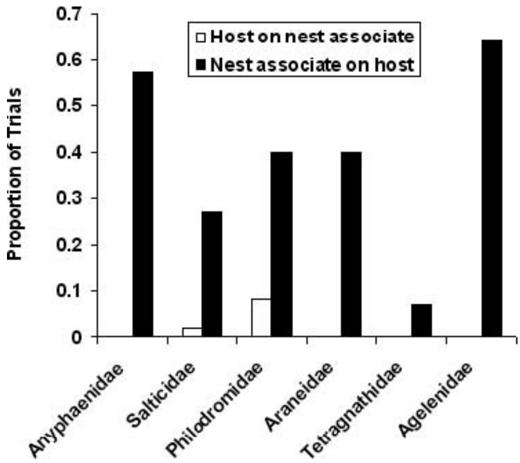

Figure 4.—Frequency of predation observed in host spider-foreign spider interaction trials.

salticids, also contributed to the significant chi-square test result. These latter families exhibited a lower frequency of predation events than expected. The majority of the predation events were in the direction of foreign spider on the host, *A. studiosus* (Fig. 4). The host predated only on spiders from two families: Philodromidae and Salticidae.

With the exception of the trials involving tetragnathids, the settling patterns of surviving foreign spiders and *A. studiosus* in the square arena significantly differed from the random expectation of 25% same side, 50% adjacent side and 25% opposite side (Table 2). The high frequency of location at opposite ends of the arena contributed the most to the significant results in all but the araneid trials. In the case of this orb weaver, the exceptionally low number of close distances was the major contributing cell to the significant test result (Table 2).

Nest status censuses.—No focal nest relocations were detected. Comparison of the proportion of nests lost in the temporal censuses to the overall frequency of foreign spider associates recorded for the respective localities suggests that no significant relationship exists between foreign spider association with *A. studiosus* nests and nest extinctions ($R^2 = 0.06$; $F = 0.90$, $P \approx 0.36$). However, in restricting the comparison to the two spider families that exhibited high predation rates on *A. studiosus* in the interaction trials, (Anyphaenidae and Agelenidae; [Fig. 4]), we found a significant correlation to exist between the frequency of nest association by spiders and nest extinction rate ($R^2 = 0.77$; ANOVA, $F = 31.2$, $P < 0.0002$; [Fig. 5]).

Nest defense trials.—No significant differences were observed in the frequencies of nests suffering predation relative to the instar of the juveniles present (range tested: instars 1-5) (chi-square test, $\chi^2 = 7.6$, $df = 4$, $P \approx 0.11$). Instar was thus pooled in the subsequent analyses under the category juvenile. In experiment 1, juveniles in nests with their mothers present suffered significantly less predation than they did in nests from which mothers were removed (chi-square test, $\chi^2 = 8.68$, $df = 1$, $P < 0.003$; [Fig. 6]). In experiment 2, the mothers suffered significantly less mortality from predators when they had juveniles present compared to when they did not

Table 2.—Foreign spider-host spider relative position (%) in square chamber at end of interaction trials. *Chi-square test results significant at 0.05 after Bonferroni correction. Cells contributing greatest value to test results in bold type.

Associate Family	Same side/corner	Adjacent side/corner	Opposite side/corner
Expected %	*25*	*50*	*25*
Salticidae*	11.6	25.6	**62.8**
Tetragnathidae	14.3	57.1	29.6
Araneidae*	**6.7**	40.0	53.3
Anyphaenidae*	4.8	23.8	**71.4**
Agelenidae*	0	9.1	**90.1**
Philodromidae*	4.0	24.0	**72.0**

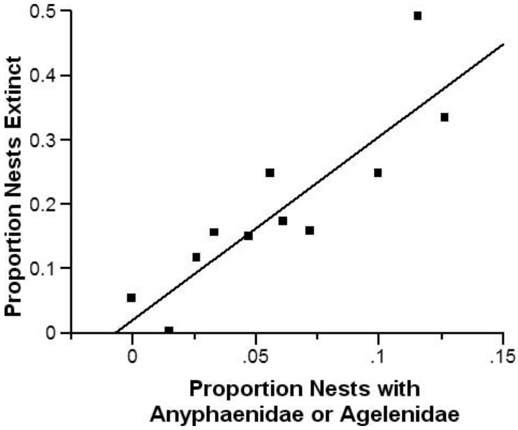

Figure 5.—Relationship between rates of nests lost in temporal nest censuses at 12 localities (two replicates at latitudes: 26°, 28°, 30°, 32°, 34°, & 36°) and rates of nest association by Agelenidae and Anyphaenidae in initial nest census at these sites ($R^2 = 0.77$).

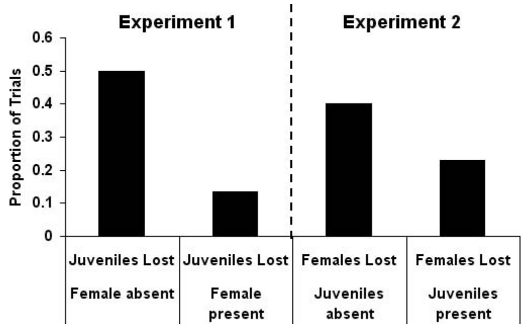

Figure 6.—Predation results for anti-predator trials: relationship between class present/absent and incidence of predation on other class.

have young (chi-square test, $\chi^2 = 5.44$, $df = 1$, $P < 0.02$; [Fig. 6]). Finally an ANOVA comparing the mean number of juveniles lost in nests with the mother present ($n = 11$, mean $\pm$ SE = 1.73 $\pm$ 0.24) and those with no mother ($n = 26$, 1.77 $\pm$ 0.17) identified no significant differences between the two treatments ($F = 0.017$, NS): the presence of mothers appears to totally prevent predation from occurring as opposed to merely limiting the number of young lost.

DISCUSSION

Foreign spiders frequenting *A. studiosus* nests.—Censuses of *A. studiosus* populations across a broad portion of its latitudinal range indicate that foreign spiders commonly associate with *A. studiosus* nests. Salticids, anyphaenids, araneids, and tetragnathids were the numerically prominent nest associates across the latitudinal range studied, but agelenids and clubionids were also quite common. Although usually only one foreign spider was found in a host nest, when two or more individuals were present, they usually were not conspecifics, but rather belonged to families with dissimilar foraging strategies. One possible explanation for this observation is that nest associates of different familial affiliations might exploit different resources offered by the host nest compared to spiders that share a closer taxonomic affiliation. Another possibility is that because spiders have been shown to maintain energy-based territories throughout their lives and may even engage in territorial cannibalism (Riechert 1978, 1982; Marshall 1995; Moya-Laraño et al. 1996, 2002), spatial exclusion would be exhibited towards conspecifics.

We were most interested here in considering why foreign spiders were found associated with *A. studiosus* nests, as this might provide insight into whether their presence had costs or benefits to the host. The Anyphaenidae was the only spider family that significantly settled in the tubes that interconnected the choice chambers to one another as opposed to actually settling in the foliage or nests of *A. studiosus* (Fig. 2). The curvatures of the tubes provide an ideal location for the construction of the silk sac retreat members of this family build. The anyphaenids are a major problem to the gas grill industry, because they have an affinity for the burning tubes of these grills and block air flow through them causing explosions (Riechert, personal communication).

While the other foreign spider families chose to settle primarily in the chambers, they did not distinguish among chambers that offered a foliage cluster alone, one with a recently produced nest in the foliage cluster that lacked the host, and one that contained a foliage cluster with an occupied nest. The simplest explanation for this result is that foreign spiders simply chance upon *A. studiosus* nests and associate with them at particular sites because of generally high densities of the host and foreign species at the sites. Another alternative is that all of the choices we presented each test subject (foliage, silk web, host spider) could cue the presence of *A. studiosus*. Riechert (1985) showed that when selecting web-sites in a laboratory experimental setup, the desert spider *Agelenopsis aperta* (Gertsch 1934) more often chose sites that were desirable in one respect and less than ideal in another, as opposed to choosing sites that were optimal with regard to both categories (temperature and prey in that case). This was despite the fact that the combined sites were equally as accessible as the suboptimal locations. One explanation Riechert offered for this result is that in multiple-goal contexts individuals will settle for choices that appear to be suboptimal because the optimum changes with increased search time (after Williams & Nichols 1984). Thus, accepting a suitable yet less than ideal opportunity is safer than risking either future unavailability of better resources (e.g., better nest sites are taken by conspecifics) or vulnerability associated with not making a choice at all (e.g., being eaten by a predator while searching for a nest site away from cover). Another possibility was that, in the desert environment, prey and temperature might be correlated: cuing on one or the other of these alternatives would have provided the same optimal result in nature.

Because the foreign spider test subjects we used in our choice trials were placed in a multiple-goal context, their indecision may not necessarily indicate a lack of preference for the alternatives we presented. Foliage clusters could cue the presence of *A. studiosus*. To test for correlated cues, we would need to complete additional choice tests in which the choice was among foliage and non-foliage containers with and without nests and host spiders. From the experiment we completed here, we can conclude only that the foreign spider taxa tested were not repelled by the presence of *A. studiosus* nests or spiders. Li & Jackson (1996), however, did find evidence of a spider web's repelling effect on other spiders. They completed two-chamber choice experiments on the araneophagic spider, *Portia fimbriata* Doleschal 1859 (Araneae, Salticidae), which preferred to attack spider lures in chambers lacking webs compared to those presented on webs

Documenting costs vs. benefits.—The interaction trial results provided evidence that most interactions that might occur between *A. studiosus* and the spiders that associate with its nests would be negative ones that incur a cost to the host. The Tetragnathidae were the only family tested that showed random positioning relative to *A. studiosus* in the arena to which pairs of spiders were released (i.e., 25% same corner, 50% adjacent corners, and 25% opposite corners). For the other families tested, the paired spiders settled significantly more often at opposite corners of the arena indicating repulsion or avoidance of one another. There was also a high incidence of predation by the foreign spiders on *A. studiosus* during the course of these trials. The anyphaenids and agelenids exhibited the majority of the predation events on *A. studiosus* in the experiment, despite the fact that most of the taxa that associated with *A. studiosus* nests were larger in size than this small theridiid. *Anelosimus* predated on only a couple of philodromids that were close in size to it and only on one larger spider, a salticid, during the course of the interaction trials.

The interaction trial results provided an upper limit estimate of the potential costs of foreign spider nest associates to *A. studiosus*. As there was no nest present in the trial, encounter between the foreign spider and *A. studiosus* was highly probable and escape from predation improbable. Nevertheless, results from the censusing of active nests over time at the 12 field sites support the findings of the interaction trials. The frequencies of the range of foreign spider taxa in host nests did not correlate with the rate of loss of nests at particular sites. However the rate of co-occurrence of *A. studiosus* with anyphaenids and agelenids (the two families that preyed significantly on the host in the interaction trials) was positively correlated ($R^2 = 77\%$) with the rate of *A. studiosus* nest extinction. Wise & Chen (1999), in a removal experiment, identified a similar example of intraguild predation in a forest floor arthropod community. Predation by two spider families, Ctenidae and Gnaphosidae, significantly depressed the population numbers of two *Schizocosa* species *S. ocreata* (Hentz 1844) and *S. stridulans* (Stratton 1984). Further study indicated that the noted araneophagic effects were complex and varied both spatially and temporally (Lensing & Wise 2004). An individual-based model of the *A. studiosus* system is under development that will address the population consequences of araneophagy to *A. studiosus*.

This modeling effort will have to include the significant levels of reciprocal protection from predation offered by mothers and juveniles, irrespective of age. Whether this implies the existence of an active defense mechanism remains uncertain. It appears more probable that the protection afforded by juveniles to the mother and the mother to juveniles is related to the quantity of silk present. From other work (Jones et al. 2007) we know that there is a significant correlation between the number of juveniles in a nest and nest volume. The silk network may well deter predators from locating the host spiders. Think of the silk in a nest as forming a maze; a predator might be millimeters away from its prey but on a different side of a silk wall. Many web-building spiders have structures called barrier webs attached to the capture web that function in this way and also alert the web owner to the presence of a potential predator. Inspection of the anti-predator trial data failed to support an alternative explanation for reciprocal protection—the idea that young are spared from predation in the presence of the mother and vice versa because the predator feeds on the type of individual we targeted as potential defender in the experiment. Under this latter scenario, for instance, juveniles might offer the mother protection from predation because the predator sates itself by feeding on them. We found no evidence for this type of benefit.

While the common spider inhabitants of social spider nests are kleptoparasites and facultative commensals (Buskirk 1981), this is not the case for *A. studiosus*. The nests and capture webs of this species are quite small compared to many social spider colonies. Most nests are single mother nests with the average number of females present in multiple female nests being three (Furey 1998; Jones et al. 2007). The nest structure, itself, does not provide space for commensals, which use the support strands as attachment points for their own webs. Rather, the spiders that associate with *A. studiosus* nests appear to be attracted to the foliage cluster the nests are built in and interactions between them and *A. studiosus* are either neutral or costly to the host species. We found no evidence for a particular foraging strategy (e.g., hunting, ambush, orb web) as having a common effect on *A. studiosus*. For instance, the two orb-weaving families that frequented the nests of *A. studiosus* behaved differently to the host; the araneids were antagonistic, while the tetragnathids were indifferent to it. Other comparisons of this type could not be quantified because typically only one family within a foraging strategy was prominently represented in the nests of *A. studiosus*. As argued above for the lack of multiple conspecifics in the same host nest, within-guild competition for resources should be higher than between-guild competition.

The results of this study indicate that we can add anyphaenids (genus *Anyphaena*) and agelenids (genus *Agelenopsis*) to the salticids (Jackson 2000) and pholcids (Jackson & Rowe 1987) that engage in araneophagy in social spider nests. Although the salticids were the most common nest associates of *A. studiosus* in the nest censuses, the genera, *Hyctia* and *Phidippus*, comprising the Salticidae in this system did not appear to be prominent predators on the host. Rather they may have utilized the nests as brooding sites; if a brood was present with a foreign spider in the collected nests, it usually belonged to a salticid. Perhaps the identification of an agelenid as being an araneophage is just as surprising as the failure of salticids to exhibit significant levels of araneophagy on *A. studiosus*. However, while members of the genus *Agelenopsis* occupy sheet webs with attached funnels, they are known to patrol the vegetation in the vicinity of the web and also predate on other spider taxa when encountered (Riechert 1991). There is evidence that the Anyphaenidae may be the foreign spider taxon that presents the most important consequences to the demographics of *A. studiosus* populations throughout its range. While the agelenids were prominent nest associates at some latitudes, anyphaenids were present at all latitudes and are even the common foreign spider found associated with *A. studiosus* nests in Uruguay (Viera et al. unpublished results). Foreign spider association with *A. studiosus* nests generally presents a potential fitness cost to *A. studiosus* and the anyphaenids clearly figure prominently in generating this cost.

ACKNOWLEDGMENTS

We wish to thank the Miccosukee Indian Tribe of Florida and the State Parks of Alabama, Florida, and Tennessee for permission to work on their lands. We also thank J. Appodaca, S. Dalrymple, S. Duncan, and T.W. Perkins for help with data collection. This research was supported by the Office of the Chancellor and the Department of Ecology and Evolutionary Biology at the University of Tennessee and by grant # 0235311 from the Animal Behavior Program of the National Science Foundation.

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Manuscript received 14 July 2006, revised 14 February 2007.