

BEHAVIOR OF WEB-INVADING SPIDERS *ARGYRODES ARGENTATUS* (THERIDIIDAE) IN *ARGIOPE APPENSA* (ARANEIDAE) HOST WEBS IN GUAM

Alexander M. Kerr¹: Marine Laboratory, University of Guam, Mangilao GU 96923
USA

ABSTRACT. Most *Argyrodes* live in the webs of other spiders, stealing food from the host, scavenging small prey from the web or killing and eating the host. I observed the behavior of *A. argentatus* from Guam, where it is a frequent inhabitant of the large orb webs of *Argiope appensa*. I examined the proportion of time spent in different activities, whether behavior differed between the sexes and if population density of *Argyrodes* on a host web affects *Argyrodes* behavior. *Argyrodes* spent 55% of the time hanging immobile and inverted in the support strands at the webs' margin. This was significantly more time than that spent in stationary activity, forward movement at the web's margin, feeding, foraging on the sticky spiral or in aggressive interaction. Females foraged significantly more often than did males, though the sexes spent about the same amount of time feeding and in other activities. Females also engaged in more bouts of feeding and 21% of these bouts were at prey bundles prepared by the host. In contrast, males invariably foraged for small insects unnoticed by the host.

Keywords: Kleptoparasite, Mariana Islands, Micronesia, Araneae

Most members of the large, cosmopolitan genus of *Argyrodes* Simon 1864 live in the webs of other spiders. They feed on small insects that have gone unnoticed by the host (Whitehouse 1986), prey stolen from the host (Robinson & Olazarri 1971), the host itself (Trail 1980; Tanaka 1984; Larcher & Wise 1985) or host-web silk (Shinkai 1988; Tso & Severinghaus 1998). *Argyrodes* may also capture prey themselves using an abandoned host web (Larcher & Wise 1985) or use their own small web (Whitehouse 1986).

Despite a growing literature on the ecology of this interesting spider genus (e.g., Henaut 2000; Miyashita 2001, 2002) and the prospect of powerful comparative phylogenetic approaches (Agnarsson 2002; Whitehouse et al. 2002), the behavior of most species is still poorly known. One little studied species is *Argyrodes argentatus* O.P. Cambridge 1880, a small (adult female body length c. 5 mm) spider with a tall, conical, silvered abdomen that is reported from Madagascar eastward through southeast Asia to South America (Cambridge

1880; Exline & Levi 1962; photo in Koh 2000). General observations of this species have been made on host webs of *Argiope argentata* (Fabricius 1775) in Panama (Robinson & Olazarri 1971) and *Nephila maculata* (Fabricius 1793) from New Guinea (Robinson & Robinson 1973). *Argyrodes argentatus* on the island of Guam in western Micronesia is a frequent inhabitant of the large orb webs of several species. Kerr and Quenga (2003) report on population variation in different host species and habitats for Guamanian *Argyrodes*, including *A. argentatus*. The most common orb-weaving spider on Guam hosting *A. argentatus* in their webs is *Argiope appensa* (Walckenaer 1841) (Araneidae) (25 mm), which occurs from New Caledonia and across the tropical western Pacific to Hawaii (Levi 1983). It builds a nearly vertical planar orb web with sticky spiral strands, occasionally with cruciate or diagonal strips of white silk near the center (Kerr 1993). In this paper, I record further aspects of the behavior of *Argyrodes argentatus* from Guam. Specifically, I asked: (1) What is the proportion of time spent in different activities? (2) How does behavior differ between the sexes? (3) Does population density on a host web affect *Argyrodes* behavior?

¹ Current address: Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara CA 93601 USA. E-mail: alexander.kerr@aya.yale.edu

METHODS

Surveys.—The surveys were performed in Mangilao and Ukudu (Dededo), Guam, 6–31 August 1989 in native forest, beach strand or disturbed vegetation. Guam (13° N, 145° E; 540 km²) is a volcanic and tectonically uplifted limestone arc island in the western Pacific Ocean. Voucher specimens of *Argyrodes argentatus* (adult males and females) and its host *Argiope appensa* (adult females) are deposited at the Department of Zoology, Southern Illinois University at Carbondale and the University of Guam Herbarium. Censusing of haphazardly encountered webs was conducted during periods of no rain between 0900–2100 h, since a preliminary survey (A. Kerr pers. obs.) suggested that the spiders were most active during this time. A dim red light was used during nocturnal observations to avoid disturbing the spiders or attracting insects to the host web. The density of *Argyrodes* was measured as number of spiders per unit area of host web. The area of *Argiope* host webs, as defined by the outermost spiral strands, was computed as an ellipse based on horizontal and vertical web diameters. To determine the behavior of *Argyrodes*, I recorded for 20 *Argiope appensa* host webs the activities of each *Argyrodes* found, after which the web was no longer used. In these webs, a total of forty-eight *Argyrodes argentatus* (23 females, 21 males and 4 juveniles) were each observed repeatedly for ca. 15 s at 5-min intervals (sensu Vollrath 1976) over a period of 1.5–4 h per web for a total of 1,286 separate observations in 107.2 spider hours. These same host webs and spiders, and their recorded behaviors, were used in all analyses. Twelve webs (60%) were from beach-strand vegetation, six (30%) were from disturbed vegetation and two (10%) occurred in native forest. I categorized behavior as quiescence (immobile and inverted), foraging (moving forward on prey-catching spiral while rotating leg pair I sensu Whitehouse 1986), forward movement on other silks at the web's margin, feeding (contact between mouthparts and prey), stationary activity (grooming, modifying silk, mating), or as agonism-avoidance (rushing towards or retreating from other spiders).

Statistical analyses.—The proportion of time a spider spent performing an activity was computed as the number of observations for

that activity divided by the total number of observations on that spider. Intersexual differences in time spent in a behavior were examined with one-way anovas or Kruskal-Wallis procedures. I examined the relationship between the density of *Argyrodes argentatus* and behavior using simple linear regressions. Recently hatched spiderlings were sometimes extremely numerous on a web, but such aggregations dispersed quickly. To prevent them from inflating estimates of population density on webs, spiderlings were excluded from the analyses. To meet assumptions of parametric procedures, densities of adult *Argyrodes* were square-root or log transformed and proportions were arc-sine-square root transformed when necessary. Statistical outliers were detected using Dixon's tests (Sokal & Rohlf 1981). Tests of association with categorical variables were done with a *G* test with Williams' correction for small sample size. Then homogeneity of variances was checked with Bartlett's tests and normality confirmed with Rankit plots (Sokal & Rohlf 1981). Otherwise analogous nonparametric procedures were used.

RESULTS

General observations.—*Argyrodes argentatus* would sometimes glean small insects from the host web. These were sometimes eaten where found or wrapped and taken to the margin of the host web and eaten there. *Argyrodes* would also remove and eat spiral catching silk from a host web, sometimes removing large sections. The host *Argiope appensa* would sometimes leave wrapped small prey at the capture site. These prey bundles were sometimes removed by *Argyrodes argentatus*, who would cut them from the web and hoist them to the host web's barrier strands. At other times, *A. argentatus* would feed together on prey bundles held in the host's mouth as the host rested at the web's hub. I also observed one possible instance of predation on the host by *A. argentatus*. In this case, several *A. argentatus* were feeding at the web hub on a dead adult female *Argiope appensa* host that had been alive the previous day.

Proportion of time in activities.—Proportional time differed significantly between activities via a Kruskal-Wallis procedure ($H = 121.62$, $P < 0.001$). The 48 *Argyrodes* (fe-

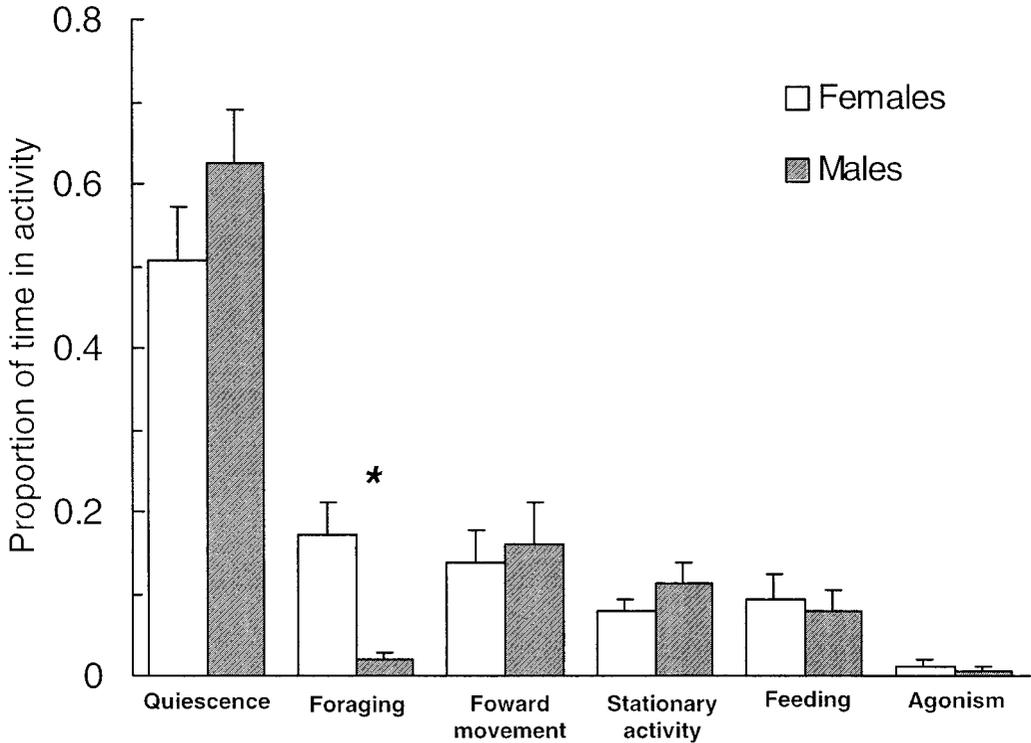


Figure 1.—Time budget of adult male and female *Argyrodes argentatus*. Males denoted by striped bars. Asterisk indicates a significant difference via a one-way anova.

males, males and juveniles combined) in the 20 host webs spent significantly more time hanging immobile and inverted in the support strands at the webs' margin than in stationary activity, forward movement at the web's margin, foraging, feeding or agonism (minimum pairwise $G = 11.02$, $P < 0.001$ adjusted for multiple comparisons). Other activities on average occupied no more than 9% of the time. Instances of agonism were least frequent, occurring 0.7% of the time.

Sex related differences.—When sexes were considered separately, there was one notable significant difference in behavior. Females foraged significantly more often than did males (females: mean proportion ± 1 SE = 0.172 ± 0.039 ; males: 0.019 ± 0.010 ; $F_{1,42} = 19.776$, $P < 0.001$) (Fig. 1). Other behaviors were not significantly different ($P > 0.05$) between the sexes: quiescence (females: 0.506 ± 0.066 ; males: 0.625 ± 0.065 ; $H = 0.798$, $P = 0.372$), stationary activities (females: 0.079 ± 0.014 ; males: 0.113 ± 0.026 ; $H = 2.19$, $P = 0.138$), movement on support strands (females: 0.138 ± 0.039 ; males: 0.160

± 0.010 ; $H = 1.57$, $P = 0.210$), or agonism (females: 0.011 ± 0.010 ; males: 0.005 ± 0.005 ; $H = 0.89$, $P = 0.344$). Of the 50 bouts of feeding (continuous feeding through multiple observations), 38 were by females and 12 were by males. Females more often fed on large prey bundles prepared by the host (21% of feeding events) than did males, who were never observed feeding on prey bundles, but rather fed on small prey (tiny dipterans and homopterans) caught on the spiral strands, but unnoticed by the host. This intersexual differences in type of prey used was not significant ($G_{adj} = 3.01$; $P = 0.0829$).

Effects of density.—The density of *A. argentatus* on host webs varied by about an order of magnitude, from a minimum of 0.027/100 cm² to 0.26/100 cm² or 1–8 individuals per web. The proportion of time that adult *A. argentatus* spent feeding on prey was weakly but significantly and inversely related with the density of this species on *Argiope* webs ($n = 44$; $P = 0.0462$; $r^2 = 0.142$; $y = -0.776x + 0.430$) (Fig. 2). I observed only six instances of agonism between *Argyrodes* individuals or

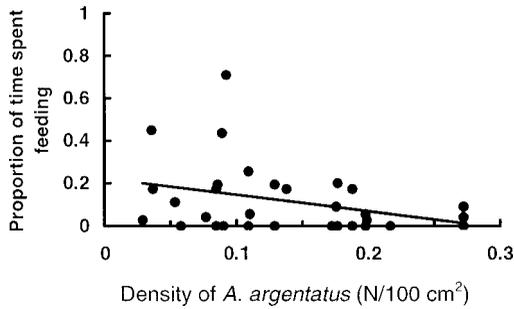


Figure 2.—Proportion of time spent feeding by adult *Argyrodes argentatus* versus its population density on host webs of *Argiope appensa*.

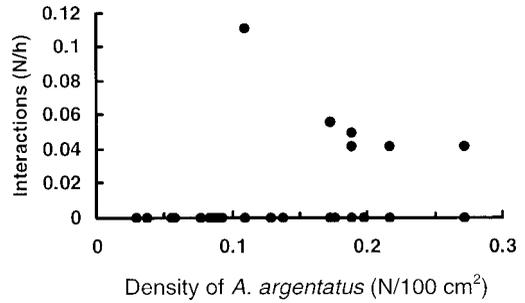


Figure 3.—The rate of agonism and avoidance of hosts and other *Argyrodes* versus adult *Argyrodes argentatus* population density on host webs of *Argiope appensa*.

between *Argyrodes* and their host. In three of these encounters, the aggression resulted in one of the pair of *Argyrodes* leaving the web. Pooled intra-*Argyrodes* and *Argyrodes*-host agonism was not significantly correlated with *Argyrodes* density ($r^2 = 0.005$; $n = 44$; $P > 0.05$) (Fig. 3). Other behaviors were also not significantly correlated with the density of adult *A. argentatus*: quiescence ($r^2 = 0.009$), stationary activities ($r^2 = 0.051$), movement on support strands ($r^2 = 0.051$), or foraging ($r^2 = -0.021$).

DISCUSSION

Of the *Argyrodes* species that take food in the webs of larger spiders, sometimes foraging is for small prey unnoticed by the host (Whitehouse 1986; Pasquet et al. 1997), while at other times *Argyrodes* concentrates on sharing large prey captured by the host (Vollrath 1979; Whitehouse 1997). There may also be species-specific differences in the use of these strategies (Tso & Severinghaus 2000). Intersexual differences in foraging mode have also been noted. Cangialosi (1990) found that male *Argyrodes ululans* O.P. Cambridge 1880 in webs of *Anelosimus eximius* (Keyserling 1884) spend more time foraging than do females. This is apparently because females wait until alerted by the hosts to steal freshly captured prey, while males more often search for previously caught prey for which it presumably spends more time in locating. Conversely, in this study, female *A. argentatus* spent more time foraging than males. I also did not find an intersexual difference in proportional feeding times (Fig. 1) (contra Cangialosi 1990). However, females engaged in over three times as many bouts of feeding as

did males (38 versus 12, respectively). Hence feeding in females is spent in more, but shorter feedings. This difference might occur if some of the feeding events by females were shorter because of higher food quality. Females spent 21% of feeding events at large prey bundles, while males were never observed doing so. One possibility that might account for these differences between the sexes is if females possess a larger energy and nutrient budget, such as needed for egg development and egg-sac construction (Toft 1999).

Food availability can affect a spider's growth rate, adult size, fecundity (Miyashita 1990, 1991) and web-site tenacity (Caraco & Gillespie 1986; but see Smallwood 1993), as well as influence the degree of intra- and interspecific competition (Spiller 1984). *Argyrodes antipodianus* are known to aggressively compete for food (Whitehouse 1997), suggesting that food is a limiting resource. In this study, the time adult *Argyrodes argentatus* spent feeding was inversely proportional to their density on host webs (Fig. 2). One possible explanation for this pattern is that as *Argyrodes* density increases, so does competition for food because of increased intraspecific agonism among *Argyrodes* and aggression by hosts which limits access to food. However, aggressive interactions were very few and uncorrelated with *Argyrodes* density (Fig. 3). Another possibility is that time spent feeding is positively correlated with an unmeasured variable, such as food quality, which itself negatively correlates with *Argyrodes* density. Webs may be densely populated with *Argyrodes* because of better food

that requires less time to consume. For example, feeding bouts (defined as a putatively continuous term of feeding through consecutive observations made five minutes apart) are shorter when feeding with the host on large predigested prey bundles. This has also been observed by Whitehouse (1997) in another species, *A. antipodanus* O.P. Cambridge, 1880.

There is growing interest in the evolution of behavior in *Argyrodes* (Whitehouse et al. 2002). Several researchers are generating a phylogeny of the genus to use, for example, in ancestral state analyses of the correlated evolution of kleptoparasitism and araneophagy. The success of this promising approach will depend not only on the quality of the phylogenetic estimates, but also in large measure on natural history information from a behaviorally diverse suite of *Argyrodes*. Robinson and Olazarri (1971) listed several observations on the behavior of *A. argentatus* in *Argiope argentatus* host webs from Panama. Most of the behaviors of Panamanian *Argyrodes* appeared to parallel those of populations in *Argiope appensa* host webs from Guam in the western Pacific. Guamanian populations also gleaned insects from the host web, stole host food bundles, fed with the host and appeared to occasionally attack, kill and feed on the host. However, I did not find, as reported for Panamanian populations, that *Argyrodes* removed host-wrapped prey bundles from the host web. Despite this possible difference, there is apparently little intraspecific variation in these behaviors within the nearly pantropical species *A. argentatus*.

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