

Population variation of web-invading spiders (Theridiidae: *Argyroides* spp.) on host webs in Guam, Mariana Islands, Micronesia

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Most *Argyroides* spiders live in the webs of other spiders as kleptoparasites, stealing food from the host and scavenging small prey from the web. We observed three species of *Argyroides* from the Micronesian island of Guam to learn (1) if *Argyroides* species differ in their use of host-species webs, (2) whether some *Argyroides* species occur more often in certain habitats, (3) whether population size of *Argyroides* is a function of web size, and (4) how the presence of congeners affects population size on a web. *Argyroides* lived most often in the large, long-lasting orb webs of *Argiope appensa* and *Cyrtophora mollucensis*, and, rarely, in the smaller, less durable orb webs of *Neoscona* spp. and *Leucauge* spp. *Argyroides argentatus* and *Argyroides* sp. A frequently co-occurred in *Argiope* webs, but *A. argentatus* was more common in beach strand and open disturbed habitats, while *Argyroides* sp. A was more common in shaded native forest. The abundances of *A. argentatus* and *Argyroides* sp. A in *Argiope* webs and the abundance of *Argyroides* sp. B in *Cyrtophora* webs were positively correlated with the areas of the webs' prey-catching surfaces. The abundance of *A. argentatus* was inversely proportional to that of *Argyroides* sp. A on *Argiope* webs and to that of *Argyroides* sp. B on *Cyrtophora* webs, suggesting interspecific avoidance.

KEYWORDS: Kleptoparasite, kleptobiotic, Micronesia, *Argyroides*, *Argiope*, *Cyrtophora*, *Neoscona*, *Leucauge*, Guam, Mariana Islands, orb web, Theridiidae, Araneidae, Tetragnathidae.

Introduction

Most members of the large, cosmopolitan genus *Argyroides* live in the webs of other spiders. Most species usually feed on small insects that have gone unnoticed by the host (Whitehouse, 1986) or on prey stolen from the host (Robinson and Olazarri, 1971). These unusual foraging strategies have earned them the name 'kleptoparasites' and have generated substantial interest in their ecology. Less attention, however, has been paid to factors that influence *Argyroides* density and species

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diversity on host webs. A single host web may support several species of *Argyrodes* (Robinson and Robinson, 1973; Vollrath, 1976; Trail, 1980; Lubin and Robinson, 1982; Sierwald and Fenzl, 1999). As well, a single species of *Argyrodes* often inhabits the webs of more than one host species (Robinson and Robinson, 1973; Vollrath, 1979; Larcher and Wise, 1985; Whitehouse, 1986; Cangialosi, 1997; Grostal and Walter, 1999; Henaut, 2000). In this study, we report observations on variation in host-web populations in species of *Argyrodes* from Guam, Mariana Islands. To investigate the factors associated with choice of host, we catalogued the hosts and web types selected by three sympatric species of tropical *Argyrodes*. Specifically, we asked: (1) do *Argyrodes* species differ in their use of host species? (2) Do some *Argyrodes* species occur more often in certain habitats? (3) Is population size of an *Argyrodes* species a function of web size? (4) Does the presence of congeners affect population size on a web?

There are three species of *Argyrodes* reported from the southern Mariana Islands, including Guam. The first, *Argyrodes argentatus* O. P. Cambridge, is a small (adult female body length *ca* 5 mm) spider with a tall, conical, silvered abdomen, and is reported from Madagascar eastward to South America (Cambridge, 1880; Exline and Levi, 1962). Two possibly undescribed *Argyrodes* endemic to Micronesia (J. E. Beatty, personal communication) also occur in the southern Mariana Islands: *Argyrodes* sp. A, a small (5 mm body length) colourful spider, and *Argyrodes* sp. B, a large (15 mm) elongate species. There are several common orb-weaving spiders on Guam which may host *Argyrodes* in their webs. *Argiope appensa* (Walkenaer) (Araneidae) (25 mm) 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 centre (Kerr, 1993). *Cyrtophora mollucensis* (Doleschall) (Araneidae) (25 mm) is a Malayo-Papuan species which extends to western Micronesia (Sabath *et al.*, 1970) and builds a non-sticky, horizontal, domed orb web with extensive barrier strands above (Lubin, 1973). Unlike *Argiope*, *Cyrtophora* is facultatively semi-social or communal, commonly living in groups of two to six adult females and many adult males and juveniles (though only solitary webs were used in this study). When living together, the spiders share vertical support strands, but each female and juvenile build their own catching spiral. Both host species are common inhabitants of edge areas such as forest gaps, forest/field ecotones and beach strand. Unidentified *Leucauge* spp. (Tetragnathidae) (10–15 mm) in the Marianas build small, delicate orb webs tilted away from vertical, usually in shaded areas. Unidentified *Neoscona* spp. (Araneidae) (10–15 mm) construct vertical orbs in sunny locations. Both *Leucauge* and *Neoscona* rebuild their webs at least once daily.

Methods

Surveys

The surveys were performed on the northern half of a small island in the southern Mariana Archipelago, western Pacific Ocean. Guam (13°N, 145°E; 540 km²) is a volcanic and tectonically uplifted limestone arc island. Vouchers of *Argyrodes* and hosts are deposited at the Department of Zoology, University of Southern Illinois at Carbondale and the University of Guam Herbarium. Censusing was conducted several times over a 7-year period: 27 July 1987, 6–31 August 1988, 18 September 1988, 6 March 1989, 20 January 1990, 6 December 1992 and 16 November 1993.

Argiope host webs were censused on all of these dates, while webs of the other three hosts (*Cyrtophora mollucensis*, *Leucauge* spp., *Neoscona* spp.) were only censused in 1987, 1992 and 1993. Web area, as defined by the outermost spiral strands, was computed as a circle via a single web-diameter measurement for solitary *Cyrtophora* and as an ellipse based on horizontal and vertical web diameters for *Argiope*. To check for possible differences in choice of habitat by *A. argentatus* and *Argyrodes* sp. A in *Argiope* webs, we also classified the vegetation at each site, according to Fosberg (1960) and Stone (1970). Forest vegetation refers to primary native limestone or ravine forest, strand to that vegetation behind sandy beaches and disturbed habitat indicates ruderal vegetation or very early successional secondary forest. To examine the relationships between densities of *Argyrodes* spp. with congeners, hosts and web area, we recorded the species and number of each spider on each occupied host web.

Statistical analyses

Habitat use and host use, defined as the presence of each *Argyrodes* species on each host species' web, were analysed using a three-way log-linear model with Williams' correction (Sokal and Rohlf, 1981). We examined the relationship between the density of *A. argentatus* and congeners or web area using simple linear regressions. We examined the differences between each host species in the density and number of each *Argyrodes* species per web with one-way Anovas. Statistical outliers were detected using Dixon's test (Sokal and Rohlf, 1981). *A posteriori* detection of differences between means was done with Tukey-Kramer tests. Recently hatched spiderlings were sometimes extremely numerous on a web, but such aggregations dispersed quickly. To prevent them from inflating counts, spiderlings were excluded from analyses of density dependence. Counts and densities of *Argyrodes* were square-root or log transformed when necessary before analyses. Homogeneity of variances were checked with Bartlett's tests and normality confirmed with Rankit plots (Sokal and Rohlf, 1981).

Results

Use of host species

In the Mariana Islands, *Argyrodes argentatus* commonly inhabited the webs of the two largest araneids, *Argiope* (48.0% of the webs examined) and *Cyrtophora* (31.7%) (table 1). *Argyrodes argentatus* was occasionally found in the webs of *Leucauge* spp. (11.1%) and *Neoscona* spp. (5.0%). *Argyrodes* sp. A was distributed

Table 1. Host webs selected by *Argyrodes* in the Mariana Islands.

Host	<i>A. argentatus</i>		<i>Argyrodes</i> sp. A		<i>Argyrodes</i> sp. B	
	Present	Absent	Present	Absent	Present	Absent
<i>Argiope appensa</i>	133	144	78	199	11	266
<i>Cyrtophora mollucensis</i>	13	28	1	40	31	10
<i>Neoscona</i> spp.	2	38	0	40	0	40
<i>Leucauge</i> spp.	4	32	3	33	0	36
\hat{G}_{adj}	49.674		34.592		107.605	
<i>P</i>	<0.001		<0.001		<0.001	

similarly among the four orb-weaving hosts with the exception that it occurred far less frequently in *Cyrtophora* webs (28.2%, 2.4%, 8.3% and 0.0%, respectively). Lastly, the larger *Argyrodes* sp. B nearly always occurred in the webs of *Cyrtophora* (75.6%), rarely in those of *Argiope* (4.0%) and never in the webs of *Leucauge* spp. or *Neoscona* spp. (table 2). An informal search for *Argyrodes* in the webs of non-orb weavers during several years of collecting spiders on Guam turned up only a single instance of co-occupancy: an adult female *A. argentatus* was once found in the web of an *Achaearanea* sp. (Theridiidae).

Coexistence of *Argyrodes* spp.

The log number of adult pooled *Argyrodes* spp. on *Argiope* webs was weakly but significantly positively correlated with web area ($N=258$, $r^2=0.251$, $P<0.001$), but not those on solitary *Cyrtophora* webs ($N=33$, $r^2=0.037$, $P=0.278$) (figure 1). In addition, the log abundance of adult *Argyrodes argentatus* was weakly and inversely proportional to that of adult *Argyrodes* sp. A on *Argiope* webs ($N=169$, $r^2=0.271$, $P<0.001$) and to that of adult *Argyrodes* sp. B on *Cyrtophora* webs ($N=30$, $r^2=0.234$, $P=0.007$) (figure 2). Mean size of *Argiope* host webs differed depending on the number of *Argyrodes* species present ($df=3,243$; $F=22.565$; $P<0.001$) (figure 3a). *Argiope* webs without *Argyrodes* were significantly smaller than occupied webs and webs with only *A. argentatus* were smaller than those with two species (via a Tukey-Kramer test). Mean web size in our sample also increased with number of *Argyrodes* species present for *Cyrtophora* webs, but the differences were not significant ($df=3,243$; $F=1.500$; $P=0.237$) (figure 3b). In table 2, the significant two-way terms in the log-linear analysis indicate that within each habitat abundances of each species of *Argyrodes* differed more than expected by chance. The significant three-way interaction indicates that the relationship between any two variables is modified by the third variable. Therefore, the three-factor term in table 2 signifies that (1) *A. argentatus* was more abundant than *Argyrodes* sp. A; (2) *A. argentatus* commonly occurred in beach strand and disturbed vegetation, while *Argyrodes* sp. A more often lived in native forest; and (3) the degree to which each species chose a habitat differed, e.g. *Argyrodes* sp. A more often chose forests than *A. argentatus* chose disturbed vegetation (via the magnitude of the two-way terms in table 2).

Table 2. G-test summary table of *Argyrodes* presence on *Argiope* webs.

Species	Beach strand	Native forest	Disturbed	Three-way interaction
<i>Argyrodes argentatus</i>				
Present	11	31	57	$G_{\text{adj}} = 87.158$
Absent	2	112	93	
<i>Argyrodes</i> sp. A				
Present	2	63	7	$P < 0.0001$
Absent	11	33	143	
Two-way tests of independence				
G_{adj}	12.443	46.716	54.489	
P	<0.0001	<0.0001	<0.0001	

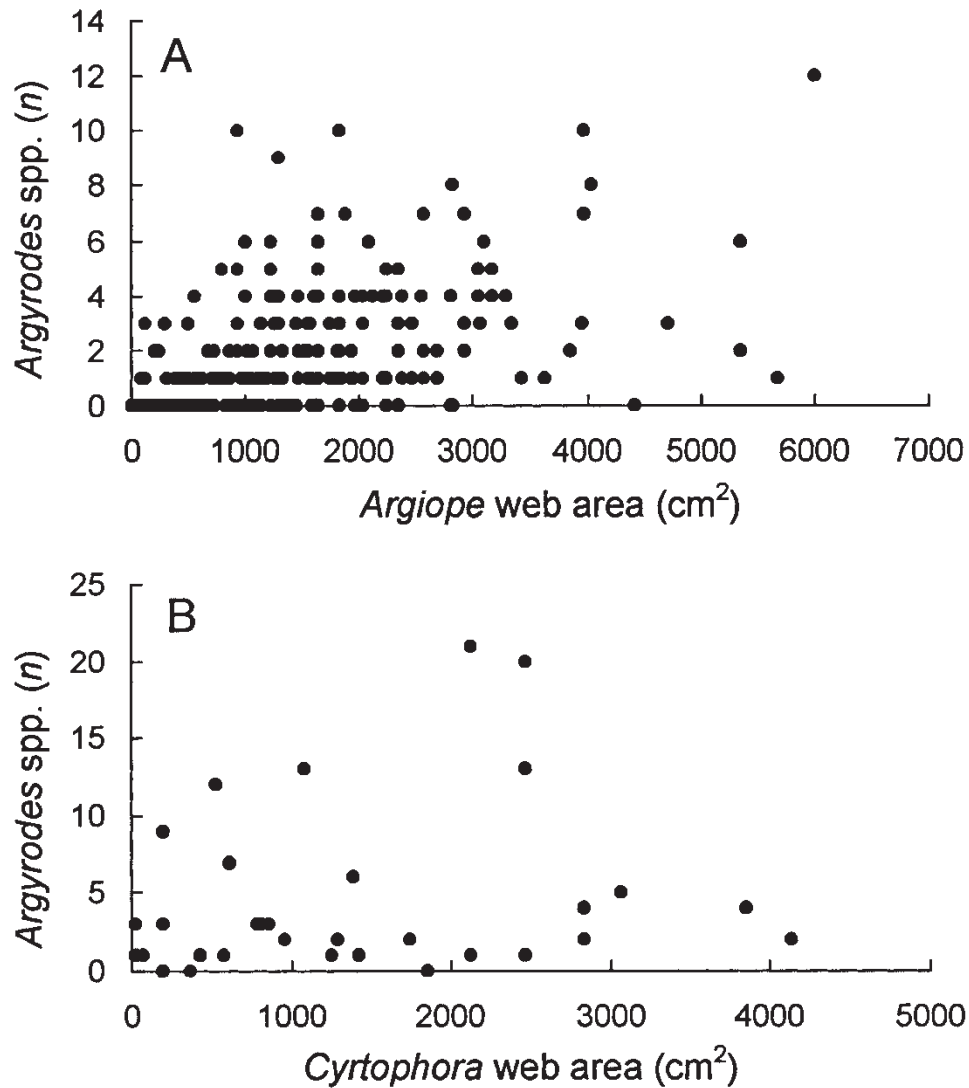


FIG. 1. Abundance of adult *Argyrodes* spp. on host webs: (a) *Argiope* webs ($N=258$, $r^2=0.251$, $P<0.0001$); (b) *Cyrtophora* webs ($N=33$, $r^2=0.038$, $P<0.2276$).

Discussion

Argyrodes reported from the literature often select hosts having large or long-lasting webs (Exline and Levi, 1962; Vollrath, 1979; Trail, 1980; Lubin and Robinson, 1982; Whitehouse, 1986; Cangialosi, 1991, 1997; Grostal, 1999; Guarisco, 1999; Sierwald and Fenzl, 1999; Tso and Severinghaus, 2000). In this study, *Argyrodes* also often selected hosts known to build large, long-lasting webs. However, the species differed in which host web they most commonly inhabited. *Argyrodes argentatus* occurred most often in the persistent webs of *Argiope* and *Cyrtophora*. *Argyrodes* sp. A occurred primarily in *Argiope* webs (table 1). Conversely, *Argyrodes* sp. B occurred almost exclusively in those of *Cyrtophora* (table 1). All three species occurred only rarely or not at all in the smaller, less durable webs of *Neoscona* spp.

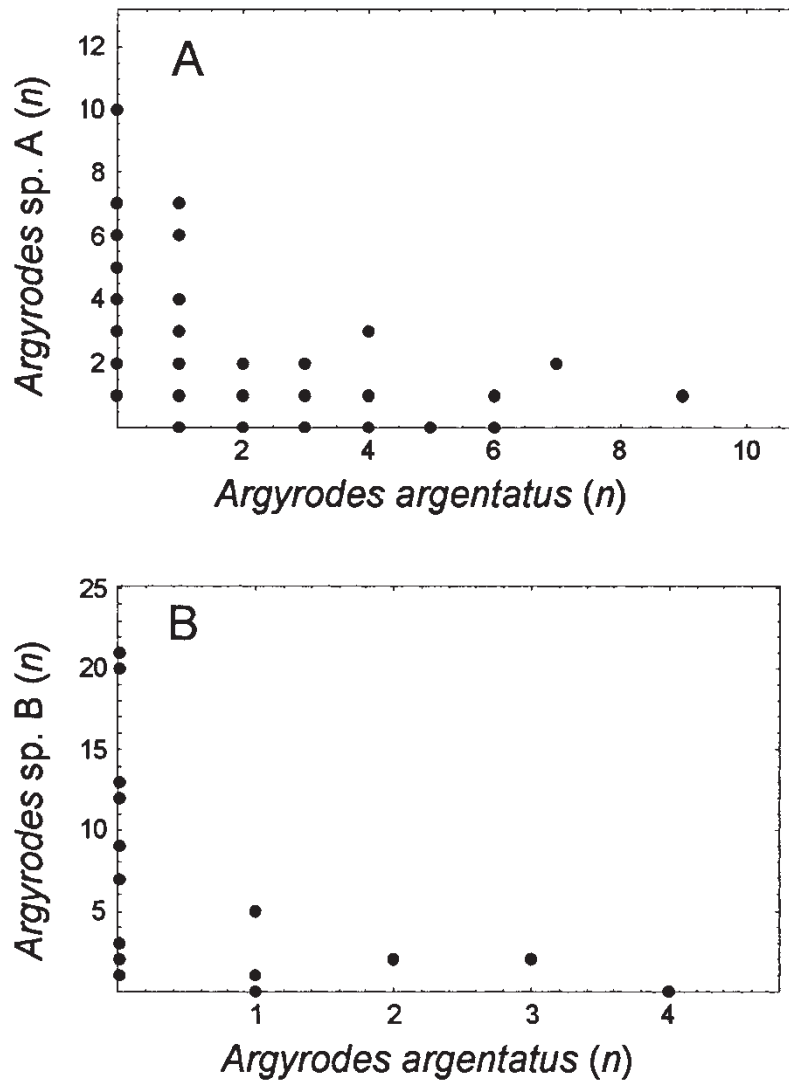


FIG. 2. Abundance of adult *Argyrodes argentatus* versus the most common co-occurring congeners in (a) *Argiope* webs ($N=169$, $r^2=0.271$, $P<0.0001$) and (b) *Cyrtophora* webs ($N=30$, $r=0.234$, $P<0.0067$).

and *Leucauge* spp. One possibility accounting for these differences is that web use depends on evolved responses of the potential hosts. Wise (1982) and Tanaka (1984) speculate that spiders building energetically more expensive, persistent webs tolerate *Argyrodes* when the cost of abandoning a web exceeds that of invasion. Others (Levi, 1978; Shear, 1986) conjecture that the circadian removal of webs by derived non-host species could have evolved to prevent kleptoparasitism by *Argyrodes*. Alternatively, host use is primarily a result of kleptoparasites specializing on different host webs. *Argyrodes* sp. B is a large species (to 15 mm body length), which may give it the advantages that go with increased size (e.g. increased fecundity, competitive superiority), but make it too heavy to forage on all but the sturdy webs of

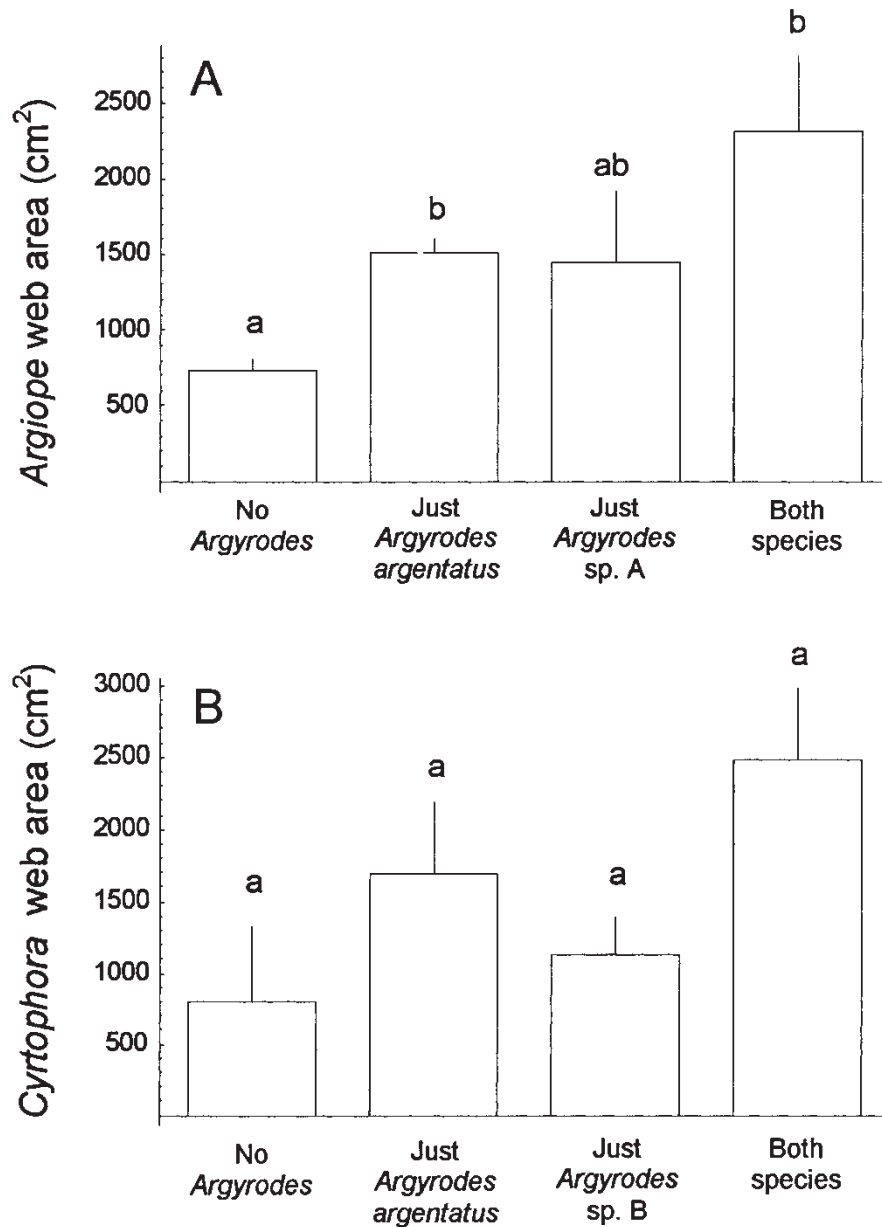


FIG. 3. Size of webs with zero, one or two species of *Argyrodes*: (a) *Argiophe* webs ($N=169$); (b) *Cyrtophora* webs ($N=33$). Letters above bars indicate significantly different means via a Tukey-Kramer test. Vertical error lines above bars are standard errors.

Cyrtophora. The few *Argyrodes* sp. B which did occur on the relatively spare webs of *Argiophe* were small, were always observed quiescent in the barrier strands and never foraging on the prey-catching surface.

Host-web size likely places an upper limit on the number of *Argyrodes* that can inhabit a web. Grostal and Walter (1999) observed that the mean size of *A. antipodanus* O. P. Cambridge populations increased with increasing host-web size and

posited that there existed an upper limit on *Argyrodes* numbers for a given web area. We also found a weak positive association between Guamanian kleptoparasite numbers and web area for *Argiope* webs, though not for *Cyrtophora* webs (figure 1). Additional factors potentially explaining the large residual variation in *Argyrodes* numbers on *Argiope* web size include variable net immigration rates, food resources and site tenacity of host spiders (Smallwood, 1993). Henaut and Lachaud (1999) and Henaut (2000) found that *Argyrodes globosus* (Keyserling) in Mexico sometimes preferred webs that were smaller or larger on average than unoccupied webs. We also found that *Argiope* host webs with *Argyrodes* spp. are larger than webs lacking the kleptoparasites, a result unrelated to survey dates or habitat (via Kruskal-Wallis tests; results not shown). Henaut (2000) suggest that selection for host webs is sometimes based on optimal size and involves trade-offs between factors such as food capture, web access and host agonism.

Interspecific avoidance has been reported among co-occurring species of *Argyrodes*. Most recently, Miyashita (2001) showed that immigration of *A. bonadea* (Karsch) increased when *A. flavascens* O. P. Cambridge was removed from host webs. In Panama, Vollrath (1976) found that *A. elevatus* Taczanowski and *A. caudatus* Taczanowski were more often found on webs in different habitats and, when they did co-inhabit a web, would forage at different times of day. On Guam, both *Argyrodes argentatus* and *Argyrodes* sp. A primarily occurred in *Argiope* webs, but often on webs from different habitats. As well, *Argyrodes argentatus* occurred mostly in beach strand and disturbed vegetation (table 2). *Argyrodes* sp. A, though, usually inhabited host webs in the shaded understorey of native forest. Moreover, the abundance of adult *Argyrodes argentatus* was inversely proportional to that of adult *Argyrodes* sp. A and B (figure 2). Finally, we also noticed that the number of species of *Argyrodes* on a web was an increasing function of mean web size. *Argyrodes argentatus* inhabited smaller *Argiope* host webs than when co-occurring with *Argyrodes* sp. A (figure 3a). One possibility is that *Argyrodes* tolerate conspecifics more than other species, allowing higher monospecific populations. This is unlikely, however, since *Argiope* host webs are smaller in the preferred habitat of *Argyrodes argentatus*, beach strand and disturbed vegetation, than in native forest. The mean size of a random sample of webs from disturbed habitats ($N=65$) was significantly less than that from native forest ($N=62$) (Kruskal-Wallis $H=10.04$, $P=0.0015$). When *Argyrodes argentatus* did co-occur with *Argyrodes* A on host webs it was more often in forest, the preferred habitat of *Argyrodes* A. This also explains why the size of webs hosting only the latter species did not differ from those supporting two species (figure 3a), since in both cases most webs were from the forest.

While the observations presented here are largely consistent with the idea that interspecific competition structures assemblages of *Argyrodes* on host webs in Guam, other factors may be involved, such as resource segregation or different physiological tolerances of habitats, and confirmation from manipulative experiments is still required. Experiments have generally failed to uncover interspecific competition among cursorial and web-building spiders (review in Wise, 1994). One of the strongest cases, though, for interspecific competition among spiders involves *Argyrodes* which reduces the prey taken by *Argiope* and *Nephila* hosts (Vollrath, 1979; Rypstra, 1981). The host spiders react by shortening their prey-catching times and by relocating their webs. As well, there is density-dependent immigration by *Argyrodes* on to host webs (Miyashita, 2001). This indicates that, in addition to competing with hosts, *Argyrodes* competes with congeners and that this interspecific competition probably helps limit the size of *Argyrodes* populations on host webs.

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References

- CAMBRIDGE, O. P., 1880, On some new and little-known spiders of the genus *Argyrodes*, *Proceedings of the Zoological Society, London*, **1880**, 320–342.
- CANGIALOSI, K. R., 1991, Attack strategies of a spider kleptoparasite: effects of prey availability and host colony size, *Animal Behavior*, **41**, 639–647.
- CANGIALOSI, K. R., 1997, Foraging versatility and the influence of host availability in *Argyrodes trigonum* (Araneae, Theridiidae), *Journal of Arachnology*, **25**, 182–193.
- EXLINE, H. and LEVI, H. W., 1962, American spiders of the genus *Argyrodes* (Araneae, Theridiidae), *Bulletin of the Museum of Comparative Zoology*, **127**, 75–202.
- FOSBERG, F. R., 1960, The vegetation of Micronesia: general descriptions, the vegetation of the Mariana Islands, and a detailed consideration of the vegetation of Guam, *Bulletin of the American Museum of Natural History*, **119**, 3–75.
- GROSTAL, P., 1999, Five species of kleptobiotic *Argyrodes* Simon (Theridiidae: Araneae) from eastern Australia: descriptions and ecology with special reference to southeast Queensland, *Memoirs of the Queensland Museum*, **43**, 621–638.
- GROSTAL, P. and WALTER, D. E., 1999, Host specificity and distribution of the kleptobiotic spider *Argyrodes antipodianus* (Araneae, Theridiidae) on orb webs in Queensland, Australia, *Journal of Arachnology*, **27**, 522–530.
- GUARISCO, H., 1999, Distributional status and natural history observations of the genus *Argyrodes* (Araneae: Theridiidae) in Kansas, *Transactions of the Kansas Academy of Science*, **102**(3/4), 138–141.
- HENAUT, Y., 2000, Host selection by a kleptoparasitic spider, *Journal of Natural History*, **34**, 747–753.
- HENAUT, Y. and LACHAUD, J.-P., 1999, Cleptoparasitic spiders: host selection by its web, *Annales de la Societe Entomologique de France*, **35**(Suppl.), 148–153.
- KERR, A. M., 1993, Low frequency of stabilimenta in orb webs of *Argiope appensa* (Araneae: Araneidae) from Guam: an indirect effect of an introduced avian predator?, *Pacific Science*, **47**, 328–337.
- LARCHER, S. F. and WISE, D. H., 1985, Experimental studies of the interactions between a web-invading spider and two host species, *Journal of Arachnology*, **13**, 43–59.
- LEVI, H. W., 1978, Orb-weaving spiders and their webs, *American Scientist*, **66**, 734–742.
- LEVI, H. W., 1983, The orb-weaver genera *Argiope*, *Gea*, and *Neogea* from the Pacific region (Araneae: Araneidae: Argiopinae), *Bulletin of the Museum of Comparative Zoology*, **150**, 247–338.
- LUBIN, Y. D., 1973, Web structure and function: the non adhesive orb web of *Cyrtophora mollucensis* (Doleschall) (Araneae: Araneidae), *Forma et Functio*, **6**, 337–358.
- LUBIN, Y. D. and ROBINSON, M. H., 1982, Dispersal by swarming in a social spider, *Science*, **216**, 319–321.
- MIYASHITA, T., 2001, Competition for a limited space in kleptoparasitic *Argyrodes* spiders revealed by field experiments, *Population Ecology*, **43**, 97–103.
- ROBINSON, M. H. and OLAZARRI, J., 1971, Units of behavior and complex sequences in the predatory behavior of *Argiope argentata* (Fabricius) (Araneae: Araneidae), *Smithsonian Contributions to Zoology*, **65**, 1–36.
- ROBINSON, M. H. and ROBINSON, B., 1973, Ecology and behavior of the giant wood spider *Nephila maculata* (Fabricius) in New Guinea, *Smithsonian Contributions to Zoology*, **149**, 1–76.
- RYPSTRA, A. L., 1981, The effect of kleptoparasitism on prey consumption and web relocation in a Peruvian population of the spider *Nephila clavipes*, *Oikos*, **37**, 179–182.

- SABATH, M. D., SABATH, L. E. and MOORE, A. M., 1970, Web, reproduction and commensals of the semisocial spider *Cyrtophora mollucensis* (Araneae: Araneidae) on Guam, Mariana Islands, *Micronesica*, **10**, 51–56.
- SHEAR, W. A., 1986, The evolution of web-building behavior in spiders: a third generation of hypotheses, in W. A. Shear (ed.) *Spiders: Webs, Behavior, and Evolution* (Palo Alto, CA: Stanford University Press), pp. 364–402.
- SIERWALD, P. and FENZL, T., 1999, *Argyrodes* in webs of the Floridian red widow spider (Araneae: Theridiidae), *Florida Entomologist*, **82**, 359–361.
- SMALLWOOD, P. D., 1993, Web-site tenure in the long-jawed spider: is it risk-sensitive foraging, or conspecific interactions?, *Ecology*, **74**, 1826–1835.
- SOKAL, R. R. and ROHLF, F. J., 1981, *Biometry* (San Francisco: Freeman and Co.), 859 pp.
- STONE, B. C., 1970, The Flora of Guam, *Micronesica*, **6**, 1–657.
- TANAKA, K., 1984, Rate of predation by a kleptoparasitic spider, *Argyrodes fissifrons*, upon a large host spider, *Agelena limbata*, *Journal of Arachnology*, **12**, 363–367.
- TRAIL, D. S., 1980, Predation by *Argyrodes* (Theridiidae) on solitary and communal spiders, *Psyche*, **87**, 349–355.
- TSO, I.-M. and SEVERINGHAUS, L. L., 2000, *Argyrodes fissifrons* inhabiting webs of *Cyrtophora* hosts: prey size distribution and population characteristics, *Zoological Studies*, **39**, 236–242.
- VOLLRATH, F., 1976, Konkurrenzvermeidung bei tropischen kleptoparasitischen Haubennetzspinnen der Gattung *Argyrodes* (Arachnida: Araneae: Theridiidae), *Entomologica Germanica*, **3**, 104–108.
- VOLLRATH, F., 1979, Behaviour of the kleptoparasitic spider *Argyrodes elevatus* (Araneae, Theridiidae), *Animal Behavior*, **27**, 515–521.
- WHITEHOUSE, M. A., 1986, The foraging behaviours of *Argyrodes antipodiana* (Theridiidae), a kleptoparasitic spider from New Zealand, *New Zealand Journal of Zoology*, **13**, 151–168.
- WISE, D. H., 1982, Predation by a commensal spider, *Argyrodes trigonum*, upon its host: an experimental study, *Journal of Arachnology*, **10**, 111–116.
- WISE, D. H., 1994, *Spiders in Ecological Webs* (Cambridge: Cambridge University Press), 328 pp.