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POPULATION DYNAMICS OF TWO SPECIES OF KLEPTOPARASITIC SPIDERS UNDER DIFFERENT HOST AVAILABILITIES

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ABSTRACT. Kleptoparasitic spiders are known to have a close association with host spiders, yet there have been few studies demonstrating how host availability influences the dynamics of kleptoparasites. Field surveys were conducted at five sites differing in host composition in sub-tropical areas in Japan, at about two-months intervals. *Argyrodes flavescens* and *A. bonadea* were both found more frequently on webs of two *Nephila* species than expected from the web areas they occupied among webs of all web spiders. Seasonal dynamics of *Argyrodes* changed greatly according to whether *N. clavata* was present or not, indicating the importance of *Nephila* on *Argyrodes* populations. The peak density of *A. bonadea* came earlier than that of *A. flavescens.* Because *A. flavescens* is known to limit the number of *A. bonadea* on host webs, the decrease in the density of *A. bonadea* may be due to the effect of interspecific competition by *A. flavescens.*

Keywords: Interspecific competition, parasite, Theridiidae, phenology

Spiders in the genus *Argyrodes* Simon 1864 are often called kleptoparasites that rely almost exclusively on host spiders. However, the interaction between *Argyrodes* and their hosts is complex: *Argyrodes* can be kleptoparasites, commensals, or predators to their hosts depending on the species and host conditions (e.g., Trail 1980; Tanaka 1984; Larcher & Wise 1985; Whitehouse 1986; Cangialosi 1997). These close associations lead to the inference that population dynamics of *Argyrodes* is highly dependent on host availability. Vollrath (1987) demonstrated the dynamics of two *Argyrodes* species and their host *Nephila clavipes* (Linnaeus 1767). However, there have been no studies showing how changes in host species composition influences *Argyrodes* dynamics. Ideally such a causal relationship should be evaluated by field experiments in which a particular host is removed, but population manipulation on a large scale sufficient to change host availability is impractical. Examining the variation of kleptoparasite dynamics in areas differing in host availability seems to be the only way to estimate the strength of associations between the host and kleptoparasite at the population level.

On Okinawa Island located in the southwestern part of Japan, two *Argyrodes* species, *A. flavescens* O. Pickard-Cambridge 1880 and *A. bonadea* (Karsch 1881), are commonly found on orb-webs of various spider species. Preliminary observations revealed that a large number of the two species was found on the webs of *Nephila clavata* and *N. maculata* (Fabricius 1793). These two *Nephila* species have different phenologies, the former emerging later in the season. Also, the distributions of the two species differ, *N. maculata* lives all over the island while *N. clavata* inhabits only the northern part of the island. These characteristics enable us to estimate the importance of host availability.

In this paper I examined seasonal dynamics of the two *Argyrodes* species and their potential host spiders in five sites differing in host species compositions. I hypothesize that 1) the *Nephila* species are the preferred host for *Argyrodes,* and 2) the presence or absence of *Nephila clavata* changes population dynamics of *Argyrodes* greatly.

METHODS

Field studies were conducted at four sites on Okinawa Island, Nakagusuku (NK), Nangusuku (NG), Shoshi (SH), Nakijingusuku (NJ), and at one site on Iheya Island (IH), southwestern Japan. The climate of these sites is sub-tropical, with an average temperature of 22.6 °C and an annual rainfall of 2,100 mm. Previous observations revealed that *Nephila clavata,* a major host for *Argyrodes,* lives at all sites except for NK which is located at the southern part of Okinawa Island. Iheya Island lies about 60 km away from Okinawa Island and is much smaller (about 20 km^2) than that of Okinawa Island (about 1,199 km^2). Thus I expected densities and/or species richness of host spiders to be low on that island.

I established two 50 m lines along the roadside in forests at each site, and surveyed these transects five times (four times for IH) from July 1997 to April 1998 at intervals of approximately 2–3 mo. I recorded all web spiders with body lengths larger than 4 mm living within 2 m from the transect and 2 m from the ground. I recorded the spider body length, the vertical and horizontal web diameters, any prey being consumed, and any small insects remaining in the web. At the same time I counted and recorded the body length of all *Argyrodes* found on the spider webs with calipers. Because it was difficult to know the stage of *Argyrodes* in the field, I used body length as an indicator for the stage and determined the smallest size of adults, viz., 3 mm for *A. flavescens* and 2.5 mm for *A. bonadea.*

In this study, web areas of hosts instead of density of host individuals was used for representing host availability because the body size of host spiders varies greatly depending on the species and seasons. For instance, the web of *Nephila maculata* is much larger than that of most other spiders, so that the amount of habitat and food resources available to *Argyrodes* may vary greatly.

The density of each *Argyrodes* on a particular host species (no./cm^2) was calculated as follows, $\Sigma N_i / \Sigma A_i$, where N_i is the number of *Argyrodes* on the ith web of a particular host species and A_i is the web area of the ith web. Data from the two transects were combined at each site. A binomial test was performed to ascertain whether each *Argyrodes* prefers a particular host spider species. The null hypothesis was that the total number of *Argyrodes* on webs of host species j (N_j) is determined by the proportion of the web area of that host, i.e.,

$$N_j = A_j/\sum A_j \cdot \sum N_j,$$

where A_j is the total web area of host species j and N_j is the total number of *Argyrodes* sp. on host species j. Hosts harboring at least ten *Argyrodes* or those occupying more than 30% of the total web areas of all species combined were used for the analysis. Significance level was adjusted by the sequential Bonferroni method (Sokal and Rohlf 1995) for each season.

RESULTS

Dynamics of *Argyrodes* and their host.—The kleptoparasitic spiders found in this survey were mostly *A. flavescens* and *A. bonadea.* Figure 1 shows seasonal changes in the density of the two *Argyrodes* spp. and web areas of host spiders in five study sites. In NK where *N. clavata* is absent, the dynamics of web area were mostly determined by *N. maculata.* Although the peak density of *A. flavescens* was delayed relative to that of host web area, its density decreased abruptly in November when *N. maculata* disappeared. In NG, SH and NK, however, *N. clavata* is abundant in November, and *Argyrodes* maintained high densities in November. It is noteworthy that the timing of peak density of the two *Argyrodes* species differed, with *A. bonadea* reaching the peak earlier. Another important point is that both *Argyrodes* densities declined to low levels in January and April when web areas of spiders other than *Nephila* remained at levels similar to those in November. The main species in this period were *Leucauge blanda* (L. Koch 1878), *Cyclosa confusa* Bosenberg & Strand 1906 and *Neoscona scylla* (Karsch 1879). In IH where *N. clavata* was not found on the census route, the density of *Argyrodes* showed a peak in August and then dropped sharply in November, which is similar to the situation in NK. Unlike other study sites, the density of *A. bonadea* was much higher than that of *A. flavescens.*

Percentage of adult *Argyrodes*.—The percentage of adult individuals was calculated separately for areas where both *Nephila* species were present (NG, SH, NJ) and *Nephila clavata* was absent (NK, IH). In areas where both *Nephila* species were present, seasonal change in the percentage of adults differed greatly between the two *Argyrodes* (Fig. 2). The peak occurrence of adult *A. flavescens* was found in autumn while that of *A. bonadea* was in spring and early summer. In areas where *Nephila clavata* was absent, the differ-

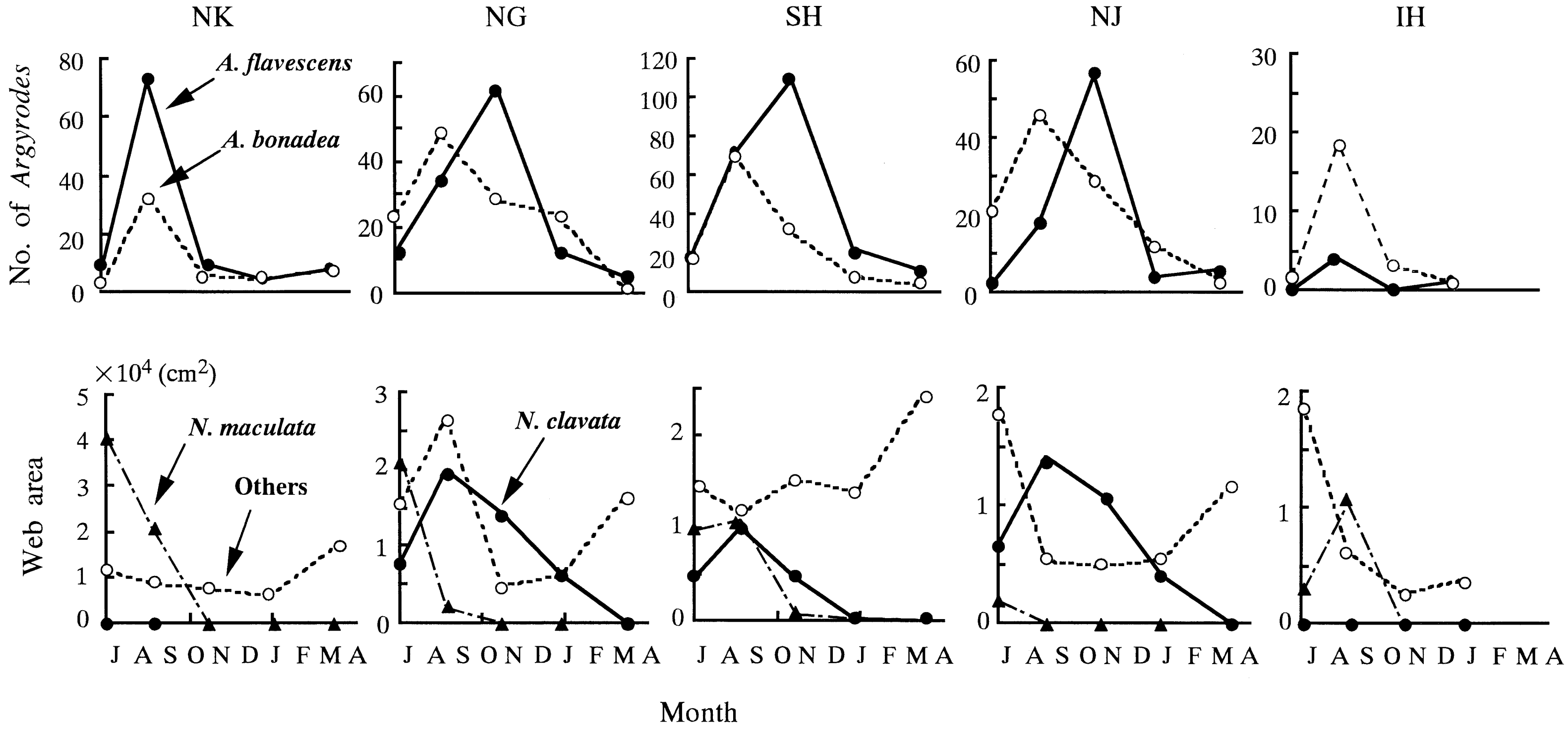

Figure 1.—Seasonal dynamics of the numbers of the two *Argyrodes* species, and web areas of the two *Nephila* species and other web spiders in 5 sites in Okinawa.

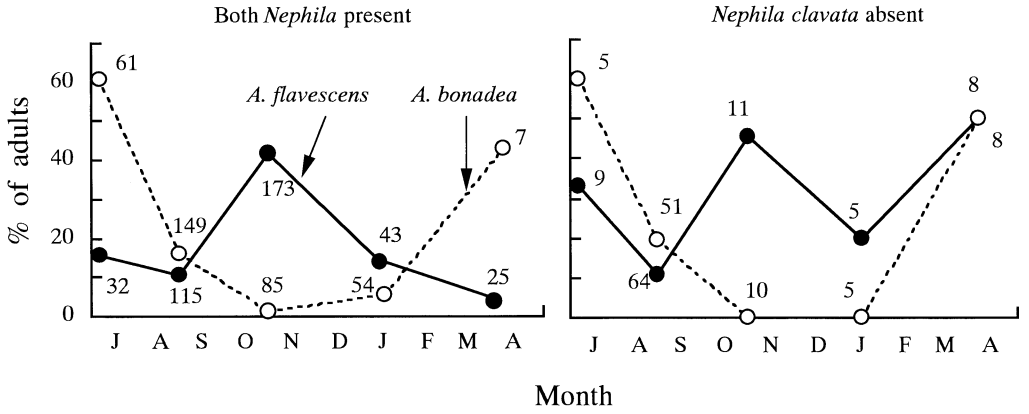

Figure 2.—Percentage of adult *Argyrodes* in areas with and without *Nephila clavata.* Numerals in the figure represent sample size.

ence was less conspicuous due to the high percentage of adult *A. flavescens* in spring. *Argyrodes bonadea* showed a similar seasonal pattern in the two types of areas.

Host preference of *Argyrodes*.—A total of 18 species of web spiders was recorded including all sites and seasons (Table 1). Twelve species were found to be hosts for *A. flavescens,* and 14 were hosts for *A. bonadea.*

The results of the binomial tests (Table 2) revealed that *A. flavescens* had a strong tendency to prefer *Nephila clavata* in August and November, although no preference was found in July when *Nephila clavata* was still small in body size. *Nephila maculata* was preferred in July probably because *Nephila* was already large. Besides the two *Nephila* species, only *Argiope minuta* was preferred significantly. *Leucauge blanda* and *Cyclosa confusa* had significantly fewer *A. flavescens* on their webs than expected from their web areas.

Argyrodes bonadea also preferred *N. clavata* in August and November, but the preference for *N. maculata* was obscure. Unlike *A. flavescens, Cyrtophora moluccensis,* which builds large, horizontal and tightly-meshed webs, was a preferred host for *A. bonadea. Leucauge blanda* had fewer *A. bonadea* than expected from its web area.

Prey density on host webs.—Figure 3 shows seasonal changes in prey density on *Nephila* webs. In all areas, prey density on host webs increased in November and then decreased markedly in January. The main prey in November were small plant hoppers in all study sites.

DISCUSSION

The dynamics of the two *Argyrodes* species were largely affected by the phenologies of *Nephila* species. This is clearly illustrated by the following findings: 1) where there is no *N. clavata* (NK and IH), densities of *Argyrodes* declined rapidly in November when *N. maculata* had disappeared; but where both *Nephila* species were present, the density increased in November for *A. flavescens* and decreased slightly for *A. bonadea*; 2) preference for *Nephila* webs was prominent, especially by *A. flavescens.* The first finding is particularly good evidence for the importance of *Nephila* on *Argyrodes* dynamics because this can be viewed as a ‘‘natural experiment’’ in which one major host was ‘‘removed’’. Grostal & Walter (1999) revealed a similar result showing that *Nephila* spp. were the preferred hosts for *A. antipodianus.* The reason why *Nephila* webs are suitable for *Argyrodes* may be that these webs have a barrier web on both sides of the capture web, providing a space for living. The significance of barrier webbing for *Argyrodes* has already been argued by several researchers (Whitehouse 1986 & 1997; Cangialosi 1997). Comparing the two *Nephila* species, *N. clavata* has a more elaborate barrier web and *N. maculata* sometimes lacks a barrier web (unpub. obs.). This may explain why *N. clavata* was preferred more frequently

Table 1.—Host spiders for the two *Argyrodes* species found in the census route in each study site (all seasons pooled). (+) = *Argyrodes* found, (−) = *Argyrodes* not found, blank = host not found.

	Host species																	
Site	*Nm*	*Nc*	*Av*	*Ar*	*Cm*	*Cu*	*Gm*	*Lb*	*Ns*	*Nsu*	*Nt*	*Er*	*Cc*	*Cm*	*Aa*	*Am*	*Te*	*Ac*
Argyrodes flavescens																		
NK	+		+				+	+	+	+			+	−				−
NG	+	+	+	−	−	−	−	+	+	+		−	+					
SH	+	+	−		−		+	+	+	−	+		+	−	+	+		
NJ	−	+	−		+		+	+	−	−			+	−		+	−	
IH	+				−		−	−	−	−			+		−	−		−
Argyrodes bonadea																		
NK	+		+				+	+	−	+			+	+				−
NG	+	+	+	−	+	+	−	−	+	−		−	+					
SH	+	+	−		−		+	+	+	−	+		+	+	+	+		
NJ	+	+	+		+		+	+	+	+			−	+		+	−	
IH	+				−		−	+	+	−			+		−	−		−

Nm = *Nephila maculata*, *Ar* = *Araneus* sp., *Gm* = *Gasteracantha mammosa*, *Nsu* = *Neoscona subpullata*, *Cc* = *Cyclosa confusa*, *Am* = *Argiope minuta*, *Nc* = *Nephila clavata*, *Cm* = *Cyrtophora moluccensis*, *Lb* = *Leucauge blanda*, *Nt* = *Neoscona theisi*, *Cm* = *Cyclosa mulmeinensis*, *Te* = *Tetragnatha* sp., *Av* = *Araneus ventricosus*, *Cu* = *Cyrtophora unicolor*, *Nc* = *Neoscona scylla*, *Er* = *Eriophora yanbaruensis*, *Aa* = *Argiope aemula*, and *Ac* = *Achaearanea* sp.

Table 2.—Results of binomial test to assess whether each *Argyrodes* species prefers a particular host spider. The null hypothesis is that an *Argyrodes* chooses a host spider in proportion to its web area. Positive signs mean preference (+++ = $p < 0.001$, ++ = $p < 0.01$, + = $p < 0.05$), negative signs mean avoidance (−−− = $p < 0.001$, −− = $p < 0.01$, − = $p < 0.05$).
Abbreviations for species name are the same as in Table 1.

Argyrodes flavescens

		Host species							
Site	Month	*Nm*	*Nc*	*Av*	*Cm*	*Lb*	*Ns*	*Cc*	*Am*
NK	Aug	+++			ns			−	
NG	Jul	ns	ns				ns		
	Aug		+++	−−−					
	Nov		++	ns				ns	
SH	Jul	+++	ns			ns			ns
	Aug	ns	+++						ns
	Nov	ns	+++			−−−			++
NJ	Jul								
	Aug		ns					ns	+
	Nov		+++			−			
IH	Aug								

Argyrodes bonadea

		Host species							
Site	Month	*Nm*	*Nc*	*Av*	*Cm*	*Lb*	*Ns*	*Cc*	*Am*
NK	Aug	++				−		ns	
NG	Jul	ns	ns				ns		
	Aug	ns	+++	−−	ns				
	Nov		+	ns				ns	
SH	Jul	ns	ns			ns			
	Aug	−−−	++			−			+
	Nov	ns	ns			ns		ns	ns
NJ	Jul		ns	ns	+				
	Aug		+++		+				ns
	Nov		+			ns			
IH	Aug	ns						ns	

than *N. maculata* by the two *Argyrodes*. Other studies have shown that *Argyrodes* spiders often live in *Nephila* webs (e.g., Elgar 1993) but only a few of them have demonstrated the seasonal dynamics of *Nephila-Argyrodes* systems. Vollrath (1987) showed that the dynamics of *A. elevatus* and *A. caudatus* were closely related to the number of *N. clavipes* in Panama, yet no evidence was provided showing that alternative host spiders were not responsible for this pattern. The present study clearly demonstrates the importance of *Nephila* as hosts for *Argyrodes* both from the ‘‘natural experiment’’ and preference analysis.

Another interesting point in the population dynamics of the two *Argyrodes* is that the peak density of *A. bonadea* was earlier than that of *A. flavescens*. This difference may be due to interspecific competition between the two *Argyrodes* species. Miyashita (2001) demonstrated that experimental removal of *A. flavescens* increased number of *A. bonadea* within only 2 d, and the number of individuals removed was positively correlated with the rate of increase in *A. bonadea*. Although this experiment indicated interspecific competition on a small spatial scale, this effect is likely to extend up to regional scales. There is additional circumstantial evidence supporting the likelihood of interspecific competition. In a temperate area where only *A. bonadea* was present, Yasuda (pers. comm.) found that this species is most abundant in mid-October which is the late adult period of *N. clavata*

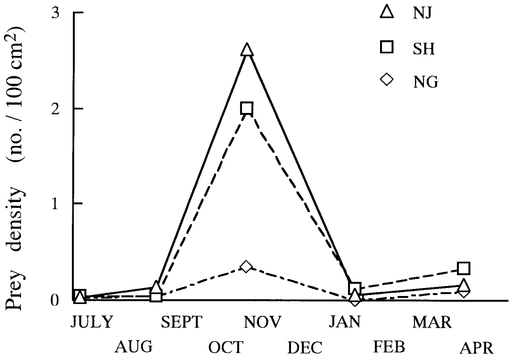

Figure 3.—Seasonal change in prey density (no./ web area) on host spider webs. The 3 sites shown here have both of the two *Nephila* species.

and 2 mo behind the peak of the web area. On Okinawa, however, *A. bonadea* showed a peak in late August and the density decreased in November, the beginning of the adult period in Okinawa. This means that *A. bonadea* living in regions without *A. flavescens* showed host-parasite dynamics similar to *A. flavescens.* Accordingly, interspecific competition by *A. flavescens* may have shifted the dynamics of *A. bonadea* to earlier seasons. An alternative explanation is that the life cycle of *A. bonadea* in sub-tropical Okinawa is different from that of the temperate area, which is unrelated to competitive interactions with *A. flavescens.* It would be difficult to test whether there is a causal relationship between the dynamics of the two *Argyrodes* species because large scale experimental manipulation is necessary.

Host composition appears to have a minor impact on the age structure of *Argyrodes,* especially for *A. bonadea* (Fig. 2). The increase in the proportion of adults in spring in areas without *N. clavata* might have been an artifact due to the small sample size (N = 8). Adults of *A. flavescens* were found throughout the year but the peak was in autumn when prey on host webs were most abundant. If the increase in prey availability had already been initiated in October, this can explain the higher proportion of adults in November, because spiderlings of *A. flavescens* can reach maturity and produce egg sacs in a month (unpub. obs.). Contrarily, adults of *A. bonadea* were rarely found in autumn, suggesting *A. bonadea* does not accerelate its developmental rate by consuming prey abundant on host webs but adjusts its life cycle by retarding its development. It appears that *A. flavescens* has a more opportunistic life cycle strategy than *A. bonadea.*

From winter to spring when the main hosts were absent, *Argyrodes* spiders were found to live on the webs of smaller orb-weavers such as *Leucauge blanda, Cyclosa confusa* and *Gasteracantha mammosa,* which were not preferred in the presence of *Nephila.* Whitehouse (1988) found that the host range of *A. antipodiana* in winter was larger than that in growing and reproductive seasons, probably because overwintering individuals need webs for shelter only. However, the situation of *Argyrodes* in the present study is quite different because I often observed *Argyrodes* ingesting silk of host webs as well as stealing prey (unpub. obs.). The difference is mainly due to climate conditions: the present study was made in the sub-tropics whereas the study by Whitehouse was in a temperate region. Although it seems unlikely that sub-tropical *Argyrodes* can obtain sufficient food in winter, they may be able to survive the harsh period by living on unfavorable hosts. Grostal & Walter (1999) found no *A. antipodianus* on webs of *Leucauge* sp. and *Gasteracantha* sp. in Australia but the season they studied was the period when the main host *Nephila* was present. It seems necessary to clarify the role of non-preferred host for the maintenance of *Argyrodes* populations.

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