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RATE OF PREDATION BY A KLEPTOPARASITIC SPIDER, *ARGYRODES FISSIFRONS*, UPON A LARGE HOST SPIDER, *AGELENA LIMBATA*

Koichi Tanaka

Laboratory of Applied Entomology and Nematology
Faculty of Agriculture, Nagoya University
Chikusa, Nagoya 464, Japan

ABSTRACT

A kleptoparasitic spider, *Argyrodes fissifrons*, although it is much smaller, sometimes preys upon its host spider, *Agelena limbata*, during or just after molting of the host. I evaluated the impact of predation by *A. fissifrons* upon the host population in a woody field in Nagoya, Japan. *A. fissifrons* occurred on more than 75% of the host webs, but the percentage of hosts preyed upon by *A. fissifrons* was not high: 2% at the second molting, 3% at the third molting, 1% at the fourth molting, 4% at the fifth molting, 0% at the sixth molting, 8% at the seventh (final) molting. *A. fissifrons* preferentially preyed upon the host individuals whose development was delayed.

INTRODUCTION

Spiders of the genus *Argyrodes* (Theridiidae) are generally known as kleptoparasitic. They inhabit the webs of other spider species, taking small prey from the host web that have not been attacked by the host or stealing prey that have been captured by the host (Exline and Levi 1962, Vollrath 1979a, b). Some *Argyrodes*, however, have been observed to prey upon the host or other spiders (Archer 1946, Lamore 1958, Exline and Levi 1962, Kaihatsu 1977, Eberhard 1979, Trail 1980, Lubin and Robinson 1982, Wise 1982). Trail (1980) states that kleptoparasitic *Argyrodes* are usually smaller than their hosts, whereas *Argyrodes* species that are known to prey upon other spiders are the same size or larger than their hosts.

Argyrodes fissifrons O.P.-Cambridge (adult body length 6-8 mm) is usually seen to live on the webs of araneid and agelenid spiders (Yaginuma 1960, Kaihatsu 1977, Shinkai, pers. comm.). Although this spider is much smaller than its hosts, I found that it sometimes preys upon a host spider, *Agelena limbata* Thorell (adult body length 15-16 mm) during molting of the host. The rate of predation by *Argyrodes* upon the hosts has not been assessed so far. The present paper describes the impact of predation by *A. fissifrons* upon the host population, and the relationship between the host's development and the rate of predation by *A. fissifrons*.

METHODS

The present study was conducted in the woody field of Nagoya University which mainly consisted of deciduous or evergreen, broad-leaved trees. The hosts, *A. limbata*, were individually marked after the fourth instar with dots of model-aircraft paint on the tibia of the second, third and fourth pairs of legs. The host population was censused three to six days a week from April to August, 1982 (the total census days were 84). The instar and mortality of the host were recorded. When I found *A. fissifrons* feeding on a host, I noted the instar and sex of both species and, in some cases, collected them and measured their size.

To determine the load of *A. fissifrons* on the host, the number of *A. fissifrons* on host webs was counted on 17 May, 27 June and 21 July, 1982.

RESULTS

I found only *A. fissifrons* on *A. limbata* webs throughout the study period. *A. fissifrons* occurred on most host webs but their number per host web was small (Table 1). As the host developed, the number of *A. fissifrons* joining the host web increased (Table 1).

Seventeen host individuals were found to be eaten by *A. fissifrons* (Table 2). I observed *A. fissifrons* feeding on dead or paralyzed (nondead) hosts which had not shed their old exoskeletons completely (13 of 17), or which had shed the exoskeletons but new exoskeletons were not yet hardened (4 of 17). Thus, *A. fissifrons* attacked hosts during or just after molting. In 16 instances *A. fissifrons* were found to bite the leg or the dorsal abdomen of the host; in one case it bit the eye area. The size difference between both species tended to be greater when the *A. fissifrons* bit the host legs than when they bit other parts. The *A. fissifrons* observed to prey upon the host was obviously smaller than the host in every case; in the most extreme case the host, at the fifth molting, was 5.9 times (2.83 vs 0.48 mm) in carapace width and 112 times (46.09 vs 0.41 mg) in body weight as large as *A. fissifrons*. Predation by *A. fissifrons* took place at every molting except the sixth (the first molting is performed within the egg sac). *A. fissifrons* preyed upon a small proportion of host population (Table 2).

Host individuals that were molting after the day in which 50% of the population had already molted were significantly attacked more by *A. fissifrons* (Table 2). Thus, *A. fissifrons* preyed upon host individuals that molted late.

Table 1.—Frequency of utilization of *Agelena limbata* webs by *Argyrodes fissifrons*.

DATE	17 May	27 June	21 July
Stage of <i>A. fissifrons</i>	Immature	All	All
Instar of host (8 = adult)	4 - 5	6 - 7	7 - 8
No. of host webs observed	67	56	58
Percent of host webs parasitized	76.1	94.6	98.3
Mean \pm S. D. <i>A. fissifrons</i> per host web	1.6 \pm 1.5	2.3 \pm 2.3	2.9 \pm 1.5

Table 2.—Observed predation by *Argyrodes fissifrons* upon the host *Agelena limbata* before and after the day in which 50% of the host individuals molted. A Chi-square test (2 x 2 contingency table) was conducted with combined data from the second to seventh molting in order to test whether predation rates were the same between before and after 50% molt day ($\chi^2 = 4.91$, $p < 0.05$).

Molt No. of host	2	3	4	5	6	7	Total
Stage of <i>A. fissifrons</i>	Imm.	Imm.	Imm.	Imm.	—	Adult	
No. of hosts observed	90	131	112	99	86	73	591
Percent of hosts preyed upon by <i>A. fissifrons</i>	2	4	1	4	0	6	3
No. of hosts preyed upon:							
(a) before 50% molt day	0	2	0	1	0	1	4
(b) after 50% molt day	2	2	1	3	0	5	13

DISCUSSION

Argyrodes fissifrons occurs on more than 75% of the webs of the host spider, *Agelena limbata*, in this study area, i.e., a woody habitat. Mortality of hosts due to predation by *A. fissifrons* is 0 to 8% at each instar. These values may be underestimates, but not by much because the time span during which *A. fissifrons* is eating the host must be long, considering the size of meal. Even if *A. fissifrons* had finished eating, the dead host would remain in its web. The census was conducted intensively, every 1.8 (153/84) days on average. The rate of apparent predation may involve scavenging host already dead. I did not observe *A. fissifrons* attack and kill the host directly. Of 17 hosts eaten by *A. fissifrons* two were still living (but paralyzed), one had been about to molt two hours before I found it to be eaten by *A. fissifrons*. There were no injuries by other predators on the bodies of dead hosts. Therefore, if the hosts were not killed directly by *A. fissifrons*, they would have died from unsuccessful molts. However, I have not observed *A. limbata* die from unsuccessful molts in the field and field cage during 1981 to 1983. I consider that most of the apparent predations were indeed direct predations by *A. fissifrons*, although they might also involve scavenging. Mortality due to predation by *A. fissifrons* is low compared with total mortality for each instar, which is 30 to 50% (Tanaka, in prep.). Eight percent of predation at the final molting is not high because the mortality rate of female adults before reproduction is 47%. This suggests that predation by *A. fissifrons* is not as important as other mortality factors. There are no comparable studies that assess the influence of predation by *Argyrodes* on the host population except the experimental study by Wise (1982). He reports that *Argyrodes trigonum* (Hentz) causes a significant decline in numbers of the host spider, *Metepeira labyrinthea* Hentz. The decline results both from predation by *A. trigonum* and possibly increased emigration due to web invasion by *A. trigonum*, but the rate of decline was much higher in experimental than control populations, so the difference was probably due primarily to *A. trigonum*. *Argyrodes* that are the same size or larger than their hosts, unlike the present study, may cause significant mortality of host populations.

A. fissifrons preys upon the host at the time of molting. Probably it is the only time when *A. fissifrons*, which is far smaller than the host, can prey upon the host if the host is not injured. An *A. fissifrons* attacking a non-molting, vigorous host will be counter-attacked and may be killed. Therefore, *A. fissifrons* has to detect when the host is molting. Vollrath (1979a, b) indicates that *Argyrodes* monitors the prey capture activities of

the host spider through vibrations of web threads and adjusts its prey stealing behavior accordingly. But whether such a mechanism is also functional in attacking the host is not clear because the molting behavior consists of quite motionless activities compared with the prey capture behavior. I observed that *A. fissifrons* sometimes moved close to a non-molting, motionless host. This behavior may serve to inspect the host's activities and, therefore, to determine when the host molts.

A. fissifrons kills spiders, other than *A. limbata*, which are not molting. I observed that subadult and female adult *A. fissifrons* preyed upon a female of *Theridion japonicum* Boes. et Str., adults of *Linyphia* sp., egg sacs and adults of *Uloborus varians* Boes. et Str., and egg sacs and males of conspecifics. The *A. fissifrons* were the same size or larger than these victims, thus *A. fissifrons* seems not to be a kleptoparasite but a predator of them. Size ratios of *Argyrodes* to the hosts may determine whether *Argyrodes* function as predators or prey-stealers or both.

Although *A. fissifrons* occurred on most host webs, only a part of the host population was preyed upon. There is a question of how *A. fissifrons* decides to feed on the host. To feed on the host involves cost and benefit. The cost is that *A. fissifrons* must search for another host web. This involves energy expenditures of locomotory activities, predation risk and possible failure to find another host web. The benefit is the gain of a great amount of food because of the large body mass of the host. The balance between cost and benefit may influence the decision to feed on the host. This hypothesis predicts that *A. fissifrons* will prey upon those host individuals which have a low foraging success (therefore, the kleptoparasite also has a low foraging success), where benefit will increase by gaining a great amount of food. On the other hand, if *A. fissifrons* steals sufficient prey, it will be more advantageous to *A. fissifrons* to allow the host to live and to forage and steal prey (whereby it will obtain food from the same host web in the future as well), than if it kills and eats the host and searches for another host web. The fact that *A. fissifrons* preyed upon the host individuals whose development was delayed would support this hypothesis. However, this is not the only hypothesis. An alternative hypothesis, suggested by Vollrath (pers. comm.), is that *A. fissifrons* kills the host accidentally. Vollrath (1984) observed that *Argyrodes elevatus* Taczanowski, when searching for prey, accidentally bit the leg of its host spider, *Nephila clavipes* (L.), and the host responded by shaking the leg. He suggests that if the host freshly molts, the host will make no response and will be killed and eaten by *A. elevatus*. Indeed, he has seen that a freshly molted host had been killed by *A. elevatus* (Vollrath, pers. comm.). Wise (pers. comm.) suggests another hypothesis; slower developing hosts are smaller and hence more susceptible to attack. It is needed for further discussion to observe the behaviors of *Argyrodes* in detail and to assess the costs and benefits of killing the host.

On the other hand, the host was not seen to prey upon *A. fissifrons*. Observations suggest that the host is not aware of *A. fissifrons* on its own web. *Argyrodes* are safe probably because they move slowly and "carefully" on the host webs (Barth 1982:77). A tropical orb-weaver, *Nephila clavipes*, avoids *Argyrodes* kleptoparasitism by abandoning the web with many kleptoparasites and relocating the web in a new site (Rypstra 1981). *A. limbata* does not seem to adopt such tactics and shows a high tenacity to its web site, the rate of web relocation is 0 to 8% in each instar in this study area (Tanaka, pers. obs.). This may be because relocation of the web is too expensive. Thus, anti-*Argyrodes* behaviors of *A. limbata* may be associated with its energetics.

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