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FACTORS INFLUENCING SPECIFICITY AND CHOICE OF HOST IN *ARGYRODES ANTIPODIANA* (THERIDIIDAE, ARANEAE)

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ABSTRACT

The spider *Argyrodes antipodiana* (O.P. Cambridge) from New Zealand is a kleptoparasite whose primary host in nature is an orb weaving spider, *Aranea pustulosa* (Walckenaer). The kleptoparasite's bias towards this host is stronger in the summer than in the winter. In the laboratory, *Argyrodes* was significantly better at obtaining food on the webs of *Aranea pustulosa*, than on the webs of *Achaearanea* sp., and *Badumna longinquus* (L. Koch). Factors that may be responsible for host preferences and for variation in efficiency on different types of webs are discussed.

INTRODUCTION

Argyrodes, a large cosmopolitan genus of theridiid spiders, is notorious for its kleptoparasitic species (Kullmann 1959; Vollrath 1979, 1979a,b; Smith Trail 1980; Rypstra 1981; Wise 1982; Larcher and Wise 1985; Whitehouse 1986). Instead of building prey-capture webs as do most theridiid spiders, *Argyrodes* roams through the periphery of other spiders' webs gleaning trapped insects from the silk, pilfering wrapped food bundles directly from the resident spider (host), and sometimes attacking and eating the host.

Vollrath (1984) suggested that *Argyrodes* can be loosely classified into two groups: Generalists and Specialists. Generalists invade a wide variety of web-types but use only a few techniques to obtain food; while specialists invade the webs of only a few species and use several techniques to obtain food. To be a specialist, *Argyrodes* often needs to respond opportunistically to the host's movements, as it frequently feeds with the host or steals food bundles the host is guarding. Thus a specialist's ability to choose the appropriate host is very important.

Argyrodes antipodiana (O.P. Cambridge) (hereafter referred to as *Argyrodes*) is a kleptoparasitic spider from New Zealand. The behavioral repertoire of this spider is that of a specialist (Whitehouse 1986). Casual field observations made during the course of this earlier study suggested that *Argyrodes* tends to be highly restricted in its host-choice.

The aims of this paper are to present more precise information on the host-choice of *Argyrodes* and to investigate possible reasons for restricted host-choice by this species.

METHODS

Field surveys of hosts of *Argyrodes*.—Two surveys, one in early winter, May (approx. average daily temperature range = 4-15°C) 1984, the other in summer, January (approx. average daily temperature range = 15-25°C) 1985, were undertaken at Te Aroha (North Island, New Zealand: 37.32°S; 175.43°E) by examining all the webs in the sample area (ca. 50 m^2), collecting any *Argyrodes* found, and recording the types of web on which they were found.

A casual survey was conducted in late winter/early spring, August (approx. average daily temperature range = 5-15°C) 1985, where the author walked over the sample area and noted the sex and maturity of the population.

Laboratory analysis.—Spiders were maintained and tested in transparent plastic cages in a laboratory with controlled light (12:12, L:D) and temperature (20°C-25°C) (for details see Jackson 1974).

Locomotion on webs: Spider webs can be divided into three categories: cribellate webs, which are sticky because they are covered by very fine strands of silk; non-cribellate sticky webs, the glue of which consists of droplets of a sticky fluid; or non-cribellate non-sticky webs which have no glue (see Foelix 1982). *Argyrodes* was placed onto the three types of webs and its locomotion observed.

Mortality on webs: Adult and sub-adult *Argyrodes* were housed upon the established webs of host species *Badumna longinquus* (L. Koch) (Amaurobiidae), *Achaearanea* sp. (Theridiidae) and *Aranea pustulosa* (Walckenaer) (Araneidae) (hereafter referred to as "*Badumna*", "*Achaearanea*", and "*Aranea*" respectively), until the *Argyrodes* were eaten, they died of natural causes, or the time period for the experiment was completed (the experiment ran for 27 days). Each host was used once only, except for one *Badumna* which was used twice. *Badumna* built cribellate sticky space webs, *Achaearanea* built non-cribellate sticky space webs, while *Aranea* built non-cribellate sticky orb webs. The spiders were fed every 1-4 days. I recorded the length of time each *Argyrodes* survived on hosts' webs, and the number of *Argyrodes* that were killed by the hosts. Survival, measured as spider-days of exposure (the number of days *Argyrodes* were exposed to the host) was compared among host species using survival rate analysis (Johnson 1979; Harris et al. in prep.).

Comparison of the capture efficiency of Argyrodes *on the webs of three host species*: Host species *Aranea*, *Achaearanea*, and *Badumna* of a similar size (ca. 7 mm) were collected and housed in cages suitable for their web-type. The hosts were given ca. 10 days to establish a web before a subadult (i.e., a spider one molt before maturity) or adult *Argyrodes* (body length: ca. 3 mm) was introduced to the cage. At 1-4 day intervals a test was started by dropping 10-20 *Drosophila melanogaster* (Meigen) (fruit flies) onto the host's web, then 30 min later dropping another 10 fruit flies onto the web (a variable time scale was used to avoid host satiation as satiated hosts are less likely to construct webs). I recorded whether or not *Argyrodes* obtained food during a 2 h test period. If the host's web did not retain five or more flies, the results were discarded as at this level of prey availability I deemed it too difficult for *Argyrodes* to obtain food. Each test was assumed to be independent of each other as the *Argyrodes* were responding to new conditions. For instance, the time between tests had enabled the host to reconstruct its web and the distribution of restrained flies on the web varied greatly between tests.

RESULTS

Hosts of *Argyrodes* in nature.—Only juvenile *Argyrodes* were discovered during winter. Of the 133 found, 59% were associated with araneid webs (Table 1). Besides being on or near the araneid orbs which are the food capture webs of the host, many *Argyrodes* were found in the eggsac webs of *Aranea crassa* (Walck.) while the maternal spider was standing on the eggsac. Eggsac webs are non-sticky arrays of silk (ca. 5x5x9 cm) which surround the eggsac. Up to 15 juvenile *Argyrodes* (body length: 1.0-2.5 mm) were found motionless in a single eggsac web.

Of 95 *Argyrodes* (11 males, 12 females, and 72 juveniles) found during summer, 85% were associated with *Aranea* webs (Table 2). All adults were found on orb webs.

The casual survey (n = ca. 50 spiders) conducted to reveal population structure of *Argyrodes* in early spring revealed the presence of three adults (2 males, 1 female), numerous sub-adult males (ca. 20), and juveniles (ca. 30).

Locomotion on webs.—*Argyrodes* stuck to the cribellate webs of *Badumna*. After landing on the web, *Argyrodes* "froze", then carefully tried to remove any legs stuck to the silk. If successful, the spider proceded to clean the freed leg by moving the tarsi through its chelicerae. Often, however, *Argyrodes* had great difficulty in freeing legs and remained motionless on the web, for several minutes at a time, in a posture not normally associated with resting. If the spider was unable to free itself completely after ca. 10 min, I removed it manually and returned it to its own web. In contrast, *Argyrodes* was seen to walk through large glue droplets on non-cribellate sticky webs of *Aranea* without any apparent difficulty. *Argyrodes* also had no evident difficulty moving on the non-cribellate sticky webs of *Achaearanea*.

Mortality on webs.—*Argyrodes* varied greatly in its ability to survive on the host's web. Of the 6 *Argyrodes* placed on webs of *Badumna*, 5 were killed in 42 spider-days; of the 5 *Argyrodes* placed on webs of *Achaearanea*, 3 were killed in 51 spider-days; and 6 *Argyrodes* placed on webs of *Aranea*, none were killed in 81 spider-days although one died of natural causes (that is, it was found dead rather than eaten). *Argyrodes* survived significantly better on webs of *Aranea* compared with webs of *Badumna* ($Z = 2.10$, $P < 0.05$), and survival on webs of *Achaearanea* was intermediate to, and not significantly different from survival on webs of either of the other species (*Aranea* versus *Achaearanea*: $Z = 1.68$ $P < 0.1$; *Achaearanea* versus *Badumna*: $Z = 0.85$, $P < 0.1$).

Capture efficiencies.—*Argyrodes* varied significantly in its ability to capture food on the three types of host webs, being successful in capturing food in webs of *Aranea* in 81% of the trials ($n = 22$), successful in 44% of the trials on webs of *Achaearanea* ($n = 18$), and successful in only 6% of the trials on webs of *Badumna* ($n = 17$) ($P < 0.001$, $\chi^2 = 21.42$, 2 *df*).

Foraging behavior.—*Argyrodes* obtained food by either feeding with the host, stealing the host's food bundles, or capturing *Drosophila* caught on the host's web. For all these methods of food capture, *Argyrodes* proceded through the following six steps: (1) *Argyrodes* stands in its cryptic posture, not responding to food; (2) *Argyrodes* stands in its alert posture; (3) *Argyrodes* moves on web but not apparently towards a food item; (4) *Argyrodes* moves towards a food item; (5) *Argyrodes* touches the food; (6) *Argyrodes* feeds. The "cryptic" and "alert"

Table 1.—Webs occupied during winter by juvenile *Argyrodes* ($n = 133$) expressed as percentages of the total number of *Argyrodes* found.

Host	Description of host's web	Condition of host's web	Position of *Argyrodes*' web	Percentage of *Argyrodes* found
Argyrodes pustulosa (Araneidae)	Non-cribellate sticky orb	Maintained & used by host	Attached to host's web	47.4%
Aranea crassa (Araneidae)	Eggcase lattice	Maintained & used by host	Attached to host's web	12%
Leucauge dromedaria (Araneidae)	Non-cribellate horizontal orb surrounded by a maze of threads	Maintained & used by host	Attached to host's web	0.8%
Cyclosa trilobata (Araneidae)	Non-cribellate vertical orb with stabilimentum	Maintained & used by host	Attached to host's web	0.8%
Argyrodes antipodiana (Theridiidae)			In isolation	7.5%
			Isolated but behind old, unidentified silk	6.0%
				(13.5%)
Achaearanea sp. (Theridiidae)	Non-cribellate sticky space web	Maintained & used by host	Attached to host's web	6.0%
Cambridgea sp. (Agelenidae)	Non-cribellate non-sticky large sheet web (<100 cm^2)	Maintained & used by host	Attached to host's web	6.6%
Stiphidion sp. (Agelenidae)	Non-cribellate non-sticky small sheet web (<10 cm^2)	Maintained & used by host	Attached to host's web	1.5%
Pholcus sp. (Pholcidae)	Non-cribellate non-sticky space web	Maintained & used by host	Attached to host's web	0.8%
Badumna longinquus (Amaurobiidae)	Cribellate space web	Maintained & used by host	Attached to host's web	0.8%
		Maintained & used by host	Isolated but behind host's web	6.0%
		In disrepair & abandoned by host	Attached to host's web	3.8%
				(10.6%)

postures are described elsewhere (Whitehouse 1986). The closest step towards feeding reached by the *Argyrodes* during the observation period was recorded.

In nearly all the tests on webs of *Aranea, Argyrodes* reached step 6 (Fig. 1). *Argyrodes* on the webs of *Achaearanea* either stopped at step 3 or continued until it obtained food (step 6); it rarely failed to obtain food once it had located it (Fig. 1). *Argyrodes* often made several attempts to obtain food on the webs of both *Achaearanea* and *Aranea* before succeeding. *Argyrodes* on the web of *Badumna* rarely passed step 3.

Table 2.—Webs occupied during summer by *Argyrodes* (n = 95: 23 adults, 72 juveniles) expressed as percentages of the total number of *Argyrodes* found. Adults were only found on *Aranea pustulosa* webs.

Host	Description of host's web	Condition of host's web	Position of *Argyrodes*' web	Percentage of *Argyrodes* found	
Aranea pustulosa (Araneidae)	Non-cribellate sticky orb	Maintained & used by host	Attached to host's web	82.1%	
		In disrepair & abandoned by host	Attached to host's web	3.2%	
					(85.3%)
Aranea crassa (Araneidae)	Eggcase lattice	Maintained & used by host	Attached to host's web		12%
Cambridgea sp. (Agelenidae)	Non-cribellate non-sticky large sheet web (<100 cm^2)	Maintained & used by host	Attached to host's web		3.2%
Stiphidion sp. (Stiphidiinae)	Non-cribellate non-sticky large sheet web (<10 cm^2)	Maintained & used by host	Attached to host's web		1.0%
Argyrodes antipodiana (Theridiidae)			In isolation	5.3%	
			Isolated but behind old, unidentified silk	4.2%	
					(9.5%)
Unidentified	Unidentified	In disrepair & abandoned by host	No web present		1.0%

DISCUSSION

Field surveys of hosts of *Argyrodes*.—*Argyrodes* were found to mainly kleptoparasitize the webs of a single host species, *Aranea*. This characteristic supports the conclusion gained from its wide range of foraging behaviors (Whitehouse 1986) that *Argyrodes antipodiana* is a specialist kleptoparasite.

The field surveys also reveal that the population structure of *Argyrodes* appears to be seasonal. *Argyrodes* overwinter as juveniles, mature in spring, and reproduce in summer. More work is needed to determine if one generation survives for the whole year or if there are two generations, a short one which survives only through summer and a longer one which overwinters.

Evidently *Argyrodes* was more restricted to webs of *Aranea* during the summer than during winter. This may be linked to the seasonal variation in population structure. Adult *Argyrodes*, which only exploited *Aranea*, were abundant in summer, scarce in spring, and absent in winter. The feeding and mortality experiments showed that *Argyrodes* was significantly better at obtaining food and surviving on the webs of *Aranea* than on any other webs. Thus adults which must reproduce within a short period of time (probably ca. one month) in summer, are apparently limited to the webs of *Aranea* from which they can obtain food. Juvenile *Argyrodes* are able to survive for a long time in the laboratory (three months) without feeding (unpubl. data). While they are overwintering they need a web for shelter only, and so would not be restricted to the webs of *Aranea*. In

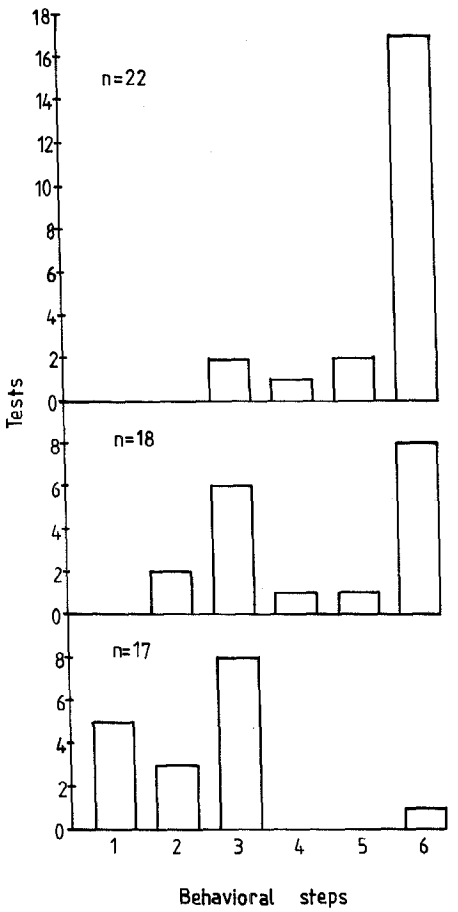

Fig. 1.—Distribution of the final behavioral step (as defined in foraging behavior section of results) that *Argyrodes* reached during a feeding bout: a, *Argyrodes* on the webs of *Aranea*; b, *Argyrodes* on the webs of *Achaearanea*; c, *Argyrodes* on the webs of *Badumna*.

spring, when they need food to grow and mature, they apparently move to the webs of *Aranea*.

Steps towards obtaining food.—The sequence of behaviors leading towards food acquisition was arrested for many spiders at step 3 (Fig. 1). In particular, nearly all spiders on the webs of *Badumna* and half on the webs of *Achaearanea* stopped at this point. Spiders that proceded past step 3 (moving on the web) usually persevered and continued to approach food items until they managed to obtain one. This observation suggests that *Argyrodes* may be better at obtaining food on webs of *Aranea* because it is unable to interpret vibrations on the webs of *Badumna* and, to some extent, *Achaearanea*. That is, *Argyrodes* appears capable of sensing vibrations upon the webs of *Badumna* and *Achaearanea* (in that it responds to the vibrations by moving), but is apparently unable to determine the direction from which the vibrations are coming. A complicating factor on the web of *Badumna*, however, is that *Argyrodes* is unable to walk on these webs. Nevertheless, *Argyrodes* uses its own web as a scaffolding to approach food on a hosts' web (Whitehouse 1986) and so could conceivably use this to approach food on the web of *Badumna* and thus avoid, to a large extent, walking on the web of this host.

Host preference.—The ability of *Argyrodes* to inhabit the webs of *Badumna* (cribellate, sticky, space web), *Achaearanea* (non-cribellate, sticky vertical orb

web) was examined by looking at three parameters: the abilities to move, survive, and feed on the host's web. *Argyrodes* was able to walk on webs of both *Aranea* and *Achaearanea*, but they became ensnared by the cribellate glue on webs of *Badumna*. In both ability to survive and feed, *Argyrodes* performed best on webs of *Aranea*, worst on webs of *Badumna*, and intermediately on webs of *Achaearanea*. Thus these parameters are probably major factors limiting adult *Argyrodes* to the webs of *Aranea* in the field. It is interesting, however, that other non-cribellate sticky orb webs, such as those of *Cyclosa trilobata* (Urqu.) which, common along with *Aranea* in the habitat of *Argyrodes antipodiana*, were not exploited. Thus not all orb webs and their residents fulfill the criteria upon which *Argyrodes antipodiana* bases its choice of hosts.

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