

Influence of spatial heterogeneity and prey density on predatory behaviour of the tropical spiders *Cyrtophora cicatrosa* (Stoliczka) and *Marpissa calcutaensis* (Tikader) (Araneae, Araneidae)

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Abstract. Tropical spiders *C. cicatrosa* and *M. calcutaensis* were allowed to predate individually in different terraria at different prey densities. Both the species were satiated within 5 hr of predation in all the volumes. Prey density exerted significant influence on the predatory behaviour of both the species. The predation increased with increasing prey density, but the volume of terraria exerted only marginal influence. The functional response curve of *C. cicatrosa* and *M. calcutaensis* was neither linear nor sigmoid, but was curvilinear representing type II response of Holling's model.

Keywords. Predatory behaviour; prey density; *Cyrtophora cicatrosa*; *Marpissa calcutaensis*.

1. Introduction

Spiders are known to achieve phenomenal densities in natural situations and consume astronomical quantities of insects; but these alone are not sufficient to demonstrate a significant role for them in the regulation of insect population. Rather they must be shown, by field observation or experimentation, to destroy prey in a density-dependent fashion (Greenstone 1978). They may be important to the balance of nature, but considerable quantitative evidence is lacking. Although a few publications are available on temperate spiders (Kajak 1965; Dabrowska-Prot *et al* 1966; 1968; Kajak *et al* 1968; Sandness and McMurtry 1970; Hardman and Turnbull 1974), the present study was undertaken to investigate the influence of spatial heterogeneity and prey density on the predatory behaviour of tropical spiders *Cyrtophora cicatrosa* and *Marpissa calcutaensis*.

2. Material and methods

C. cicatrosa, an orb-weaving spider with much evolved spinnerts, generally longer legs with specialised claws and silk glands (Palanichamy 1980) and *M. calcutaensis*, a hunting spider which does not spin its webs with small spinnerts, strong and stout legs, were collected from nearby fences of *Euphorbia antiquorum* at Palni (10°23'N 77°31' E). They were acclimated to laboratory conditions (30±1°C; RH 60-80%) and fed on mosquito, *Culex fatigans* for seven days. *C. cicatrosa* and *M. calcutaensis* feed mainly on dipterans, hymenopterans, hemipterans and orthopterans in

the field. *C. fatigans* which could be easily cultured in the laboratory were used as prey organisms in this work. Adult females were used and food was deprived to them for 24 hr before the experiments began. *Culex fatigans* served as prey, were cultured from the larval stages in the laboratory and only the adults which emerged during the day were used for feeding and experimental spiders (Palanichamy 1980).

Thirty individuals of each species were divided into six sets, each comprising five individuals. They were reared individually in transparent terraria of different volumes such as 25, 50, 100, 200 and 1000 mm³ and supplied with five adult *C. fatigans* per terrarium; the corresponding prey density was 0.2, 0.1, 0.05, 0.025, 0.01 and 0.005 fly/mm³, respectively. Similarly five series of experiments were conducted on prey density using 10, 20, 50, 100 and 200 *C. fatigans*/terrarium. The animals were released into the terraria containing a known number of test prey and the number of prey captured was replaced as and when they were captured to maintain a constant prey density.

Those mosquitoes which were chewed into food balls were counted as 'killed', chewed remains of prey were counted as 'consumed' and prey dying from other causes noted as 'dead'. Dead ones and spider silk were removed daily with a camel hair brush.

3. Results

3.1 Satiation

An animal is said to be satiated when it no longer accepts the offered prey after a period of active predation and feeding. The time from the start of feeding to voluntary cessation is the satiation time (Brett 1971). Satiation time was about 5 hr in the tested spiders irrespective of the volume of terraria. The number of

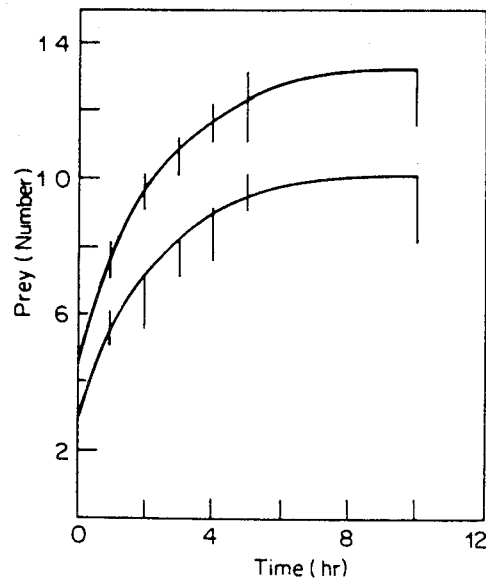


Figure 1. Predation of *C. cicutrosa* and *M. calcutaensis* at 500 mm³ terrarium at the density of 20 flies/terrarium as a function of time.

C. fatigans predated as a function of successive periods of *C. cicatrosa* and *M. calcutaensis* when allowed to predate in the terrarium volume of 500 mm³ is shown in figure 1. About 50% of the prey were predated within the first 1 hr and the predation decreased during subsequent 1 hr intervals.

Table 1. Mosquito predation by *C. cicatrosa* and *M. calcutaensis* in relation to prey density at different terraria volume.

Volume of Terraria (mm ³)	Prey density (No.)	<i>C. cicatrosa</i>		<i>M. calcutaensis</i>	
		Prey killed (No.)	Prey consumed (No.)	Prey killed (No.)	Prey consumed (No.)
25	5	3.2 ± 0.2	2.3 ± 0.2	3.5 ± 0.3	3.3 ± 0.2
	10	6.2 ± 0.4	4.8 ± 0.3	7.8 ± 0.5	4.9 ± 0.4
	20	9.1 ± 0.5	6.6 ± 0.4	9.7 ± 0.8	6.6 ± 0.5
	50	14.2 ± 0.9	9.6 ± 0.7	15.2 ± 1.1	10.1 ± 0.7
	100	18.0 ± 1.3	11.9 ± 0.9	18.6 ± 1.4	12.6 ± 1.1
	200	—	—	—	—
50	5	4.2 ± 0.4	2.6 ± 0.2	4.0 ± 0.3	3.9 ± 0.3
	10	6.7 ± 0.5	5.1 ± 0.3	8.1 ± 0.5	5.4 ± 0.4
	20	9.3 ± 0.7	6.9 ± 0.4	10.1 ± 0.7	6.9 ± 0.7
	50	14.7 ± 1.2	9.7 ± 0.7	15.6 ± 1.2	10.5 ± 0.9
	100	18.4 ± 1.4	12.4 ± 1.0	19.0 ± 1.4	12.7 ± 1.1
	200	—	—	—	—
100	5	4.6 ± 0.3	2.9 ± 0.2	4.8 ± 0.4	4.0 ± 0.3
	10	7.1 ± 0.5	5.6 ± 0.4	8.5 ± 0.6	5.6 ± 0.5
	20	10.1 ± 0.7	7.1 ± 0.5	10.7 ± 0.8	7.2 ± 0.6
	50	14.9 ± 1.0	10.9 ± 0.7	16.0 ± 1.4	10.9 ± 1.0
	100	18.9 ± 1.2	10.5 ± 0.8	19.6 ± 1.6	13.2 ± 1.1
	200	19.4 ± 1.4	12.8 ± 0.9	19.9 ± 1.5	13.4 ± 1.2
200	5	4.8 ± 0.3	3.1 ± 0.2	5.0 ± 0.4	4.1 ± 0.2
	10	7.5 ± 0.5	5.8 ± 0.3	8.9 ± 0.7	5.9 ± 0.4
	20	10.5 ± 0.6	7.6 ± 0.4	11.3 ± 0.9	7.6 ± 0.6
	50	15.4 ± 0.9	10.5 ± 0.6	16.4 ± 1.2	11.0 ± 0.8
	100	19.2 ± 1.1	12.8 ± 0.9	19.7 ± 1.4	13.4 ± 1.0
	200	19.7 ± 1.3	13.1 ± 1.0	20.4 ± 1.4	13.7 ± 1.1
500	5	5.0 ± 0.3	3.3 ± 0.2	5.0 ± 0.3	4.3 ± 0.3
	10	7.7 ± 0.5	6.1 ± 0.4	9.2 ± 0.5	6.4 ± 0.3
	20	10.9 ± 0.7	8.3 ± 0.6	11.5 ± 0.8	8.0 ± 0.4
	50	15.7 ± 1.2	10.9 ± 1.0	16.7 ± 1.1	11.2 ± 0.8
	100	19.7 ± 1.4	13.1 ± 1.0	20.0 ± 1.3	13.7 ± 0.9
	200	20.1 ± 1.6	13.8 ± 1.4	21.0 ± 1.6	14.1 ± 1.2
1000	5	5.0 ± 0.4	3.9 ± 0.3	5.0 ± 0.4	4.7 ± 0.4
	10	8.1 ± 0.5	6.3 ± 0.4	9.7 ± 0.7	6.9 ± 0.5
	20	11.0 ± 0.8	8.7 ± 0.6	11.9 ± 0.8	8.4 ± 0.5
	50	16.1 ± 1.1	11.5 ± 0.7	17.1 ± 1.2	11.5 ± 0.9
	100	19.7 ± 1.2	13.4 ± 0.9	20.4 ± 1.4	13.9 ± 1.0
	200	20.3 ± 1.4	14.1 ± 1.1	21.6 ± 1.7	14.9 ± 1.2

Each value represents the mean (±S.D) of 5 individuals.

Table 2. Mosquito predation by *C. cicutrosa* and *M. calcutaensis*; rate of predation as a function of prey density and volume of terraria.

Density of prey (No.)	Volume of Terraria (mm ³)					
	25	50	100	200	500	1000
<i>C. cicutrosa</i>						
5	0.18	0.24	0.27	0.28	0.29	0.29
10	0.36	0.39	0.41	0.44	0.43	0.47
20	0.55	0.54	0.59	0.61	0.64	0.65
50	0.83	0.86	0.87	0.90	0.92	0.94
100	1.05	1.08	1.11	1.12	1.14	1.15
200	—	—	1.14	1.15	1.18	1.19
<i>M. calcutaensis</i>						
5	0.20	0.27	0.28	0.29	0.29	0.29
10	0.45	0.47	0.50	0.52	0.54	0.57
20	0.57	0.59	0.63	0.66	0.68	0.70
50	0.89	0.91	0.94	0.96	0.98	1.00
100	1.09	1.10	1.44	1.15	1.17	1.20
200	—	—	1.17	1.20	1.23	1.27

3.2 Predation as a function of spatial heterogeneity

The volume of terraria exerted only marginal influence on the predatory behaviour of *C. cicutrosa* and *M. calcutaensis*. For instance, *C. cicutrosa* killed 6.2 and 8.1 flies at a density of 10 flies/terrarium in 25 and 1000 mm³, respectively (table 1). Corresponding values for *M. calcutaensis* were 7.8 and 9.7 flies.

The number of prey successfully captured can also be considered as the rate of successful attack (predation) which can be calculated considering the exposure time of the predation and the number of prey captured. The rate of predation for the predator-prey interactions, *i.e.* *C. cicutrosa* vs *C. fatigans* and *M. calcutaensis* vs *C. fatigans* were 0.36 and 0.45 at the terrarium volume of 25 mm³ increased to 0.47 and 0.57 at the terrarium volume of 1000 mm³. The same trend persisted at the tested densities of 10, 20, 50, 100 and 200 flies/terrarium also (table 2). Terrarium size has no influence on the rate of successful attack.

3.3 Predation as a function of prey density

The number of prey killed as a function of prey density can be expressed in terms of prey risk, *i.e.* the number of prey killed per unit time per unit density. The prey risk increased with increasing prey density. *C. cicutrosa* and *M. calcutaensis* have increased prey capture with increasing density of prey up to 100 prey per terrarium and subsequently levelled off (table 1). Rate of attack increased with increasing prey density irrespective of the predator (figure 2).

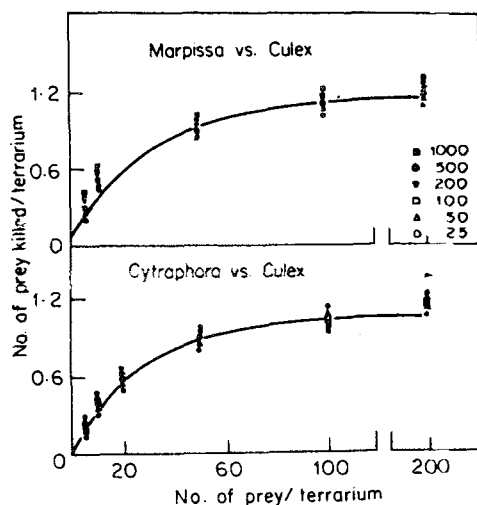


Figure 2. Rate of predation (*M. calcutaensis* vs *C. fatigans* and *C. cicatrosa* vs *C. fatigans*) as a function of prey density.

4. Discussion

There are several reports on the satiation time of fish (*e.g.* Brett 1971) and insects (*e.g.* Pandian *et al* 1978). But there is paucity of information about the satiation time of spiders. The present work showed that *C. cicatrosa* and *M. calcutaensis* required 5 hr for satiation which is much longer when compared to the fish *Onchorhynchus nerka* that satiated by 1 hr (Brett 1971); the dragonfly nymph *Mesogomphus lineatus* that took only 40 min (Pandian *et al* 1978). The greater lapse in the satiation time of spiders may be due to their mode of feeding. They cannot ingest the prey as such, as in other predators, but the process involves (i) handling the prey, (ii) dissolving prey tissues externally with digestive enzymes introduced into wounds made by the fangs, (iii) ingestion of semidigested broth and (iv) discarding of the remains (Palanichamy 1980). Hence, they require a longer time for satiation when compared to that of other predators which ingest the prey outright.

Majority of studies on the predatory behaviour have been made with predators and prey kept in relatively simple containers (Chant and Turnbull 1966; Dabrowaka-Prot *et al* 1966; 1968; Kajak 1965; Kajak *et al* 1968; Sandness and McMurtry 1970). However the predatory behaviour in response to prey density may be altered in a spatially complex environment (Griffiths 1969; Huffaker *et al* 1963; Levins 1966; MacArthur and Pianka 1966). But in the present investigation, the volume of different terraria exerted marginal influence on the predatory behaviour of the spiders *C. cicatrosa* and *M. calcutaensis*.

It is known for a variety of predators that a predator attacks a greater number of prey as the prey density increases. Solomon (1949) has called this as functional response which is of three types (Holling 1963). Type I is a linear rise in the consumption of prey to a plateau characteristic of filter feeder. Type II curve is a negative accelerated rise to a plateau and is representative of most invertebrates

and some fish. The type III functional response is a sigmoid curve rising to a plateau which is characteristic of vertebrates. Spiders do respond functionally to prey availability. In spite of their functional response, there is species difference in the predatory behaviour *i.e.*, the jumping spider *M. calcutaensis* killed more number of prey when compared to that of weaving spider *C. cicatrosa* (figure 1). Hunting spiders may be able to change their rate of attack than do the web building spiders which are filter feeders and generally less mobile than the hunting spiders (Pointing 1966; Palanichamy 1980).

The functional response is said to be non-regulating in some species of spiders (Kiritani *et al* 1972). In wolf spider *Pardosa vancouveri*, type III response is seen (Hardmann and Turnbull 1974). In the present investigation the functional response of both the species of spiders *C. cicatrosa* and *M. calcutaensis* is curvilinear representing the typical invertebrate type of functional response *i.e.*, Type II response of Holling (1965). Nonlinearity may be due to the following reasons: Though the time available to the predator for hunting prey decreases as the rate of prey capture increases, an individual predator cannot consume food above a satiation rate of prey exploitation, at which point the functional response levels off.

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