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BIONOMICS OF THE SPIDER, *CROSSOPRIZA LYONI* (ARANEAE, PHOLCIDAE), A PREDATOR OF DENGUE VECTORS IN THAILAND

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ABSTRACT. The pholcid spider, *Crossopriza lyoni* (Blackwall 1867) is a common inhabitant of homes in a rural village in Chachoengsao Province, Thailand. Studies on the spider were initiated because its microhabitat closely coincided with that of adult *Aedes aegypti* (Linnaeus 1762), mosquito vectors of dengue virus. Laboratory observations showed that females deposited eggs 4–6 days after copulation. Females held the egg sac in their mouthparts for 11–13 days, until all spiderlings (mean = 34) had left the sac. Spiderlings did not feed until they had molted, but as soon as feeding commenced they were capable of overpowering a mosquito many times their own size. Sometimes spiderlings would share a single mosquito or eat a mosquito wrapped by the mother spider. Spiderlings separated from their mother grew more rapidly than those left with the mother and reached maturity in as little as 74 days. The spiders' principal means of capturing prey was to throw silk with the aid of the hind legs. Spiders used this method to immobilize mosquitoes which were entangled in the standing web or to catch flying mosquitoes. The mosquito was not bitten until the time of feeding, up to six days after capture. Feeding occurred on only 34–48% of the days, and spiders ate about one mosquito per day. Cannibalism was a significant mortality factor, accounting for 67–84% mortality in a cage of spiderlings. An enzyme-linked immunosorbent assay (ELISA) was adapted to test spider tissue for presence of dengue virus. The ELISA was used to show that spiders did not become infected when fed dengue-infected mosquitoes. The results of the study suggested that *C. lyoni* could form an important component of integrated control of *Aedes aegypti* mosquitoes in foci of dengue transmission.

Mosquitoes have a tremendous impact on humans almost everywhere, either as significant sources of irritation or as vectors of serious disease. Dengue is the most common viral pathogen transmitted by mosquitoes. The virus, which consists of four distinct serotypes, causes a spectrum of disease ranging from mild fever to fatal shock. Since the late 1970's, occurrence of the disease has steadily expanded throughout the tropics and subtropics, to the point that there are millions of cases every year. All confirmed vectors of dengue virus are in the genus *Aedes* and the most important vector is *Ae. aegypti* (Linnaeus 1762) (Gubler 1988). This mosquito thrives in association with humans, larvae of the species developing in almost any water-filled container (Christophers 1960). In at least some geographical areas, the adult females of *Ae. aegypti* preferentially bite humans indoors (Scott et al. 1993).

Spiders can be efficient predators of adult mosquitoes both outdoors and indoors. Studies on spider predation of mosquitoes have examined whether various spider species eat mosquitoes. For example, detailed observations on the rate at which spiders ate mosquitoes located in large cages in a Polish forest indicated that species of spiders varied in their

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appetite for mosquitoes and that the rate of consumption was not constant over time (Dabrowska-Prot et al. 1966, 1968). Other observations have shown that spiders eat mosquitoes in Japanese homes (Ori 1974) and in the prairies of Nebraska (Rapp 1978). Another approach has been to test wild-caught spiders for the presence of mosquito antigen in their guts by the use of antibody-based tests. This method showed that a large proportion of spiders in Kenyan homes were eating mosquito vectors of malaria (Service 1973). In Malaysia, spiders were eating *Ae. albopictus* (Skuse 1894), mosquito vectors of dengue outdoors (Sulaiman et al. 1990a), and *Ae. aegypti* vectors indoors (Sulaiman et al. 1990b). We saw only one study in which an attempt was made to determine whether spiders had a significant impact on a mosquito population in the field (Ramoska & Sweet 1981). That study found that discarded tires colonized by spiders contained fewer mosquito larvae than those tires without spiders. Since spiders generally eat a variety of prey, their usefulness as a biocontrol agent of mosquitoes would depend on the relative abundance of mosquitoes and other prey species. Maximum effect from spiders could be expected where the microhabitat of the mosquito and the spider coincide so that a large proportion of prey are mosquitoes.

While studying dengue virus transmission in rural Thailand, we noticed populations of *Crossopriza lyoni* (Blackwall 1867) (Araneae, Pholcidae) in village homes. The spiders were commonly seen in their webs, constructed under homes and in undisturbed areas of the primitively constructed walls. *Crossopriza lyoni* generally inhabit the interiors of buildings and other protected areas in southern Asia and Japan. Most of the literature on the species is restricted to taxonomic treatments (Yaginuma 1986; Kim 1988; Koh 1989) and studies on limited aspects of its physiology and behavior (Maya et al. 1982; Karuppaswamy et al. 1984; Downes 1987). One Indian study (Nandi & Raut 1985) noted that *C. lyoni* eats *Aedes* species indoors.

We suspected that the spiders could have an influence on adult populations of the dengue vector because the microhabitat of the spiders corresponded closely to the distribution of adult *Ae. aegypti* indoors. Predation on adult mosquitoes might be particularly significant in reducing transmission of dengue by *Ae. aegypti*, since the adult population includes older females which have survived long enough to acquire the virus and incubate it to infectious levels. In order to evaluate the possible role of *C. lyoni* in the ecology of dengue transmission, we made observations on bionomics of reproduction, development, and mosquito predation of the spider. In addition, we performed experiments to determine whether the spider might harbor dengue virus following feeding on an infected mosquito.

METHODS

Spiders.—Spiders were collected in and around homes of a village (official designation was Village 6) located 100 km east of Bangkok in Hua Sam Rong District, Plaeng Yao County, Chachoengsao Province, Thailand. The spiders were captured incidentally during weekly sampling for *Aedes aegypti* (Edman et al. 1992; Scott et al. 1993). Not all spiders were retained and no attempt was made to quantify the abundance or variety of spider species. The spiders used in this study were perceived to be the most abundant kind during initial sampling.

The pholcid specimens were identified as *Crossopriza lyoni* from the habitus, presence of depressed thoracic fovea, eye pattern, distinct abdominal shape, morphology of the male left palpus, and morphology of the dissected and cleared female epigynum (Yaginuma 1986; Kim 1986; Koh 1989). Voucher specimens of *C. lyoni* are deposited in the U.S. National Museum arachnid collection. The authors are confident of the identifications, since the third author has taxonomic experience with spiders and the specimens were carefully examined. It is possible that houses in the field also contained separate but morphologically similar species, because we did not perform a thorough survey of all spiders in the area. The work reported in this paper, however, was certainly performed on the stated species, since specimens were examined from representative familial lines reared in the laboratory.

The device for sampling was a commercial vacuum cleaner fitted with a screen-backed collection carton (12 cm diameter) affixed to a 0.5 m long section of PVC pipe. The pipe with the carton at the end was applied to crevices and spaces on the interior and exterior sides of the walls of the houses. Samples were

quickly chilled over wet ice and then refrigerated at 4 °C overnight before sorting.

Spiders were maintained in the laboratory at 30 °C (a representative temperature of the interior of village homes) and equal photophase and scotophase of 15 h. The spiders were kept in clear plastic cages (13 × 8 × 6.5 cm high) with tight lids. The lids were fitted with a small hole to introduce food and a 2-cm hole covered with screen for ventilation. The screen was covered with a square of gauze, which was wetted daily.

Behavioral and developmental observations.—Observations on behavior, feeding, and development were made during nine months on 13 different cages of spiders collected January–March 1991. In addition to general observations, quantitative measurements were made on growth of spiderlings and on rate of feeding by adult female spiders.

Growth was observed by measurements of body length (chelicerae to posterior of abdomen) twice per week, accomplished with the aid of a drawing tube attached to a dissecting microscope. The drawing tube was positioned over a digitizing tablet (Numonics Corp., Montgomeryville, Pennsylvania) and the length recorded by placing the pointing device of the tablet over the perceived image of a spiderling. Sigma Scan software (Jandel Scientific, Inc., Corte Madera, California) was used to calibrate the tablet and to record and analyze the data. Spiderlings were from a single egg sac, but were divided one day after hatching into a group of 25 in a cage by themselves, and 24 in a cage with their mother. Data were analyzed with an independent *t*-test, comparing the difference between the mean lengths of spiderlings in the two cages each day that measurements were made. Throughout the 71 days of measurements, cages had constant access to an excess of *Anopheles dirus* Peyton and Harrison 1979 mosquitoes for food.

The number of mosquitoes eaten by female spiders was recorded for three individuals fed *An. dirus* and for two individuals fed *Ae. aegypti*. Each day, the number of mosquitoes consumed by a spider was recorded and an excess of mosquitoes added to each cage. If all mosquitoes were consumed, a greater number of mosquitoes was added the next day.

Dengue virus experiment.—An experiment was performed to determine whether dengue virus in mosquitoes eaten by spiders could subsequently infect the spiders. Male *Ae. aegypti* mosquitoes were injected in the thorax with 0.017 µl of a tissue culture suspension of dengue 2 virus (10^6 plaque-forming units (PFU)/ml) and then held at 32 °C for 10 days to allow time for the virus to amplify. In our laboratory, this procedure had been found to infect in excess of 90% of mosquitoes. Live infected mosquitoes (uninfected mosquitoes for controls) were fed to individually caged spiders which had been reared to maturity in the laboratory from eggs deposited by field-caught females. All spiders ate either three or four infected mosquitoes. After either 14 or 28 days, the spiders (one control and five virus-fed spiders for each time interval) were dissected into three pieces which were subsequently kept cold over wet ice. The pieces were: 1) poison gland, prepared by cutting a wedge from between the first and second legs on each side to the area just behind the eyes, 2) prosoma, prepared from the remainder of the prosoma, and 3) abdomen. For the 14-day samples, the poison gland was triturated in 150 µl, and the prosoma and abdomen each in 300 µl of 20% fetal bovine serum in phosphate buffered saline (FCS-PBS). For the 28-day sample, all parts were triturated in 500 µl of FCS-PBS. Each triturate was injected into five *Toxorhynchites splendens* (Wiedemann 1819) mosquitoes for amplification and detection of dengue virus (Rosen 1981). The number of poison gland triturates was limited to two virus-fed and one control spider for each time interval. The *Tx. splendens* mosquitoes were held for 12 days at 30 °C before examining them for signs of infection using indirect immunofluorescent assay of head squashes (Sithiprasasna et al. 1994). In addition, aliquots of the triturates were frozen at −70 °C until being tested using a double sandwich enzyme-linked immunosorbent assay (ELISA) designed to detect dengue virus (Sithiprasasna et al. 1994). Controls were run with the ELISA to determine the sensitivity of the method used on spider tissue, triturating each tissue in 800 µl of FCS-PBS. Five replicates of each control preparation were run, consisting of serial dilutions of dengue 2 seed (10^6 PFU/ml) diluted in either FCS-PBS, previously-frozen spider triturates, or fresh spider triturates.

RESULTS

Most spiders were collected from the interiors of homes between exposed support beams or behind furniture. Some spiders were also collected in the 1–3 m space under houses with elevated floors. The homes had wooden floors, either wooden or bamboo walls, and metal or cement composite roofs. Construction left many gaps in the walls and floors, forming holes that opened directly outdoors. *Aedes aegypti* mosquitoes were abundant indoors (Edman et al. 1992; Scott et al. 1993) because of the open nature of the houses and because of the storage of large amounts of water for household use.

Spiders copulated readily in the laboratory. In one case, a single male (70 days old, reared in the laboratory) copulated successfully with three females during a nine day period. The first time was observed immediately after the male was introduced into the cage of a female collected in the field 50 days before. The pair remained *in copula* for 40 minutes, with the female oriented ventral side up and the male facing her posterior with both palpi inserted into her genital orifice. The male was exposed to two other females for one day each, one collected 94 days and the other 116 days previously. The third female ate the male, but apparently had copulated successfully. Fertile eggs were deposited 6, 4, and 5 days after copulation with each female, respectively.

Oviposition was not observed directly, but resulted in an egg sac held in the mouthparts of the female, as is typical of the family. Cottony flecks in the web were observed 10 times in association with oviposition (occurring up to four days before and five days after) and six times not in association with oviposition. On one occasion, six eggs fell from an egg sac to the floor of the cage and subsequently did not hatch. The number of spiderlings hatching from 12 sacs deposited by nine spiders ranged from 5–54 with a mean of 34 (±SD = 14.8) spiderlings. Eggs failed to hatch only once. In most instances, hatching was noted when spiderlings were seen in the mother's web, 11–13 days after oviposition. In one case, closer observation indicated that the spiderlings partially emerged from their eggs three days before they actually left the egg sac. The mother would hold onto the egg sac until all spiderlings had left it, even when this process took more than one day.

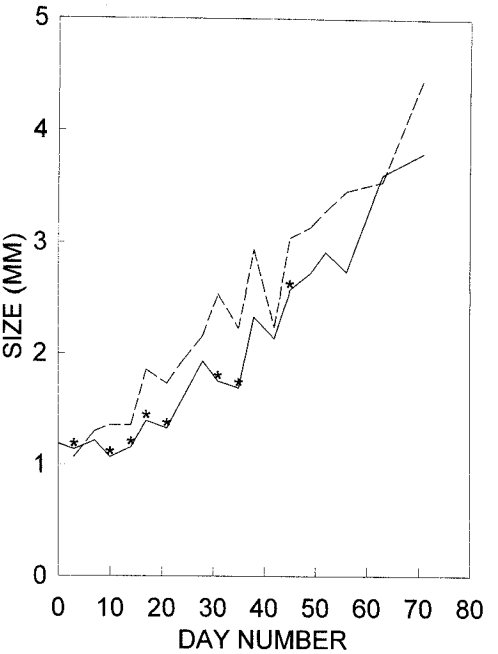

Figure 1.—Length of *Crossopriza lyoni* spiderlings emerging on Day 0 from a single egg sac, fed an excess of *Anopheles dirus* mosquitoes, and measured twice weekly. Twenty-four spiderlings remained in the cage with their mother (solid line) and 25 spiderlings were placed in a cage by themselves (dashed line). Asterisks indicate days on which there was a statistically significant ($P \leq 0.05$) difference in length.

Spiderlings were inactive for the first 2–4 (mode = 3) days after leaving the egg sac, when molting occurred. Growth continued during the entire 71 days that spiderlings were measured (Fig. 1). Those spiderlings that had been left with their mother were consistently smaller than those spiderlings in a cage without an adult spider. This size difference was observed until the end of the measurement period, at which time there was no significant difference in size. The spiderlings separated from the mother matured more rapidly and deposited their first egg sac when 74 days old, compared to 80 days for those spiders left with their mother. Mature females had a mean weight of 28.6 mg (n = 15, SD = 7.79, range: 18.2–44.6), 63% greater than the mean weight for males (17.6 mg, n = 9, SD = 3.73, range: 11.8–23.4). Although we did not hold laboratory-reared spiders long enough to get an

Table 1.—Number of mosquitoes (*Anopheles dirus* or *Aedes aegypti*) eaten by mature, female, individually-caged *Crossopriza lyoni*. Replicate spider #1 had male present 7 days; spider #4 had male present 11 days. Prey species "d" was *An. dirus*, prey species "a" was *Ae. aegypti*.

	Replicate spider					
	1	2	3	4	5	Mean
Prey species	d	d	d	a	a	
No. of days	67	67	67	66	66	
Spider weight (mg)	37	45	23	42	25	34.4
Mean eaten per day	1.6	0.81	1.4	0.89	0.73	1.1
SD eaten per day	1.3	0.87	1.4	1.1	0.85	1.2
Max. eaten per day	4	4	6	4	3	4.2
% days not eating	40	42	34	47	48	42.2

accurate estimate of longevity, we observed that wild-caught mature females lived as long as 120 days in the laboratory, implying longevity of at least 194 days.

Mature spiders captured mosquitoes which landed on their webs or which flew nearby. Hungry spiders actively pursued prey within their cages, generally capturing the mosquito within seconds of its introduction. The spider threw silk over the mosquito, the spider guiding the silk with its hind legs. The prey was then wrapped loosely in silk by manipulating the silk with abdomen and hind legs, but without rotating the prey. The first time a spider bit its prey was at the time of consumption, sometimes delayed as long as six days after capture. The quantity of mosquitoes consumed (Table 1) varied among individual spiders, but generally approached one mosquito per day, regardless of mosquito species. Feeding was discontinuous, with spiders fasting 34–48% of the days. Spiders with egg sacs continued to feed at approximately the same rate, setting aside the egg sac temporarily in order to consume the prey. Feces appeared as dark, tarry spots on the floor of the cage.

Spiderlings began feeding 2–4 days after their first molt, at which time they could overpower a mosquito which was 4.0 mm long (i.e., approximately 4× the length of the spider). Up to three spiderlings at once sometimes fed on a single, wrapped mosquito. Spiderlings sometimes fed on a mosquito wrapped by their mother or caught in their mother's web. Three different cohorts of spiderlings ate between 0.178–0.523 mosquitoes per spiderling per day during the first 11–17 days after beginning to eat. Cannibalism was common among the spiderlings, especially following introduction of mosquitoes when activity was at its greatest. Although probably an artifact of the confined conditions within a cage, cannibalism caused 67–84% mortality in four separate cohorts which were maintained until maturity.

Toxorhynchites splendens were not infected by triturates from spiders which had fed on dengue-infected mosquitoes. Also, none of the spider triturates were positive for virus in the ELISA. The ELISA was sufficiently sensitive to detect a dilution of 1:160 (6.25×10^3 PFU/ml) of the virus seed in any of the fresh or frozen spider tissue triturates (Table 2).

DISCUSSION

Our laboratory observations on *C. lyoni* help fill in some of the gaps in bionomic knowledge of this species. Females deposited eggs shortly after copulation. The male was capable of mating successfully at least three times over a nine-day period, suggesting that a small number of males could keep a large group of females inseminated. Despite previous reports (Downs 1987), we saw no evidence of the female eating any of her own eggs, possibly because most eggs were fertile. Prey-capturing techniques were described in detail by Nandi & Raut (1985), including manipulation of silk and prey with the hind legs and biting only at the time of feeding. In addition, they noted that the spiders actively removed carcasses of prey from the web.

One of the interesting aspects of the spiders' behavior was the interaction of the spiderlings with their mother and with each other. The mother spider could evidently sense the presence of spiderlings in the egg sac, since the sac was retained until all spiderlings had

Table 2.—ELISA sensitivity to dengue 2 virus (seed from tissue culture, 10^6 PFU/ml) in *Crossopriza lyoni* tissue triturates.

Diluent source	Virus dilution	*n*	Mean optical density (O.D.)		
			Poison gland	Prosoma	Abdomen
Virus seed	1:2	5	0.550	0.347	0.447
	1:8	5	0.301	0.193	0.298
	1:16	5	0.224	0.164	0.207
	1:32	5	0.179	0.128	0.154
Fresh spider	1:5	5	0.305	0.287	0.313
	1:40	5	0.126	0.106	0.091
	1:80	5	0.093	0.088	0.080
	1:160	5	0.099	0.079	0.066
Frozen spider	1:5	5	0.291	0.350	0.312
	1:40	5	0.115	0.108	0.096
	1:80	5	0.098	0.087	0.079
	1:160	5	0.080	0.082	0.068
Cutoff value		2	0.080	0.052	0.058
Infected *Toxorhynchites*			0.182	0.164	0.186

left it. The mother's hunting activity sometimes benefitted the spiderlings when they ate mosquitoes captured and wrapped by their mother or mosquitoes trapped in the mother's web. Despite the apparent advantages near their mother, spiderlings kept by themselves grew and matured significantly faster than those kept with their mother, probably because they conserved energy which would have been spent following disturbance by the mother and because they were not competing with the mother for food. Among themselves, the spiderlings interacted in at least two ways. First, several spiderlings sometimes fed simultaneously on the same mosquito. Second, the spiderlings ate each other, especially when excited by the introduction of prey. Such cannibalism was a significant mortality factor in the confined conditions of a cage, though it was not observed in the field.

We thought there was a possibility that spiders could harbor dengue virus, since spiders in village homes undoubtedly eat infected *Ae. aegypti*. Our laboratory experiment failed to demonstrate the presence of virus in spiders which had fed on dengue-infected mosquitoes. Triturates of the spiders were negative for virus when injected into *Toxorhynchites* and when triturates were tested directly with an ELISA capable of detecting low titers of virus in spider tissues.

Judging from observations of spiders feeding on mosquitoes in the laboratory, spiders could have a significant impact on the population of *Ae. aegypti* in a home. Our estimate of consumption was about one mosquito per mature female spider per day, but under other conditions this rate might be much higher. By feeding recently killed mosquitoes to *C. lyoni* occurring naturally in a house, Nandi & Raut (1985) observed that a single spider ate 12—20 mosquitoes per day for 2–3 consecutive days. Although we did not survey for other prey, small flies and spiders could have formed a part of the diet of *C. lyoni* in the field, diluting its effect on mosquitoes. It is significant, however, that juvenile and mature spiders were efficient at capturing mosquitoes and frequented the dark corners and walls of homes, corresponding to the locations favored by *Ae. aegypti* (Sheppard et al. 1969; Kusakabe & Ikeshoji 1990). Although we did not determine the number of spiders in village homes, all available microhabitats were usually occupied. The potential significance of this predator raises the possibility that insecticidal application directed at *Ae. aegypti* adults indoors might actually exacerbate the dengue problem in rural Thailand. Indoor insecticidal fogging might eliminate both mosquitoes and spiders from inside a home, but the mosquitoes could quickly recolonize the house from existing larval sources. On the other hand, the spider population would re-

cover much more slowly because a greater proportion of the total population would have been exposed to insecticide and the spider's reproductive rate is far lower than that of the mosquito (Christophers 1960).

Crossopriza lyoni could prove valuable as an intentionally managed biocontrol agent for reduction of *Ae. aegypti* populations and dengue transmission. There is precedence for the use of spiders to control a public health pest indoors, an example being the successful reduction of fly populations and subsequent transmission of gastrointestinal pathogens (Nyffeler & Benz 1987). Introduction of *C. lyoni* into homes without spiders could result in a constant population, self-regulated by cannibalism and availability of appropriate microhabitats. Because spiders eat a variety of prey, they would tend to maintain their presence even when mosquitoes were scarce. As a result, spiders would be present to blunt sudden mosquito population outbreaks (Riechert 1974). Such outbreaks can occur when rains fill many containers at once, hatching mosquito eggs in all of them simultaneously. Where the spiders occur naturally, efforts could be made to avoid killing spiders during housecleaning or insecticidal application. The presence of dengue where the spiders now occur shows that spiders alone do not stop transmission; however, management of spider populations might provide the additional control of adult mosquitoes needed to block dengue transmission following reduction of larval populations by other, non-insecticidal means (e.g., Kittayapong & Strickman 1993).

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