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RESEARCH NOTE

COOPERATIVE PREY CAPTURE IN THE COMMUNAL WEB SPIDER, *PHILOPONELLA RAFFRAYI* (ARANEAE, ULOBORIDAE)

Prey capture advantage has played an important role in the evolution of communal or social spiders (Shear 1970; Rypstra 1985, 1986; Buskirk 1981; Uetz 1986, 1989). Communal web organization may improve prey capture in two ways: 1) it may improve the ability of webs to intercept prey (the "ricochet effect") (Uetz 1989), and 2) it opens the possibility of communal prey immobilization that may allow spiders to capture larger and presumably more profitable prey. Communal capture of large insect prey has been observed in a number of social web-building spiders, such as *Agelena consociata* Denis 1965 (Krafft 1969), *Anelosimus eximius* (Keyserling 1884) (Vollrath & Rohde-Arndt 1983; Christenson 1984; Pasque & Krafft 1992), *Mallos gregalis* (Simon 1909) (see Jackson 1979), and it has been demonstrated that communal spiders capture larger prey than solitary spiders (Buskirk 1981; Nentwig 1985; Uetz 1986).

Members of the genus *Philoponella* Mello-Leitão are known to construct communal webs, but most have been reported to employ only non-cooperative prey capture (see Burgess 1978; Buskirk 1981; Smith 1982; Lubin 1986). However, cooperative prey capture has been reported in a few species of *Philoponella* (see Breitwisch 1989; Binford & Rypstra 1992). To understand the diversity of cooperative prey capture and social behavior in the genus *Philoponella*, the prey capture behavior of as many species as possible should be described.

This study describes the colony composition and prey capture handling behavior of the uloborid spider *Philoponella raffrayi* (Simon 1891) and determines if the efficiency with which they capture large insects is higher when spiders hunting cooperatively than when they hunt singly.

Philoponella raffrayi is a communal web-building spider that occupies the tropical rain forest undergrowth of peninsular Malaysia (Simon 1891; Masumoto 1992). I studied this species in the Pasoh Forest Reserve in Negri Sembilan state, Malaysia. A colony of *P. raffrayi* is composed of individual orb-webs connected to one another by non-adhesive silk. All uloborids lack poison glands and must rely on wrapping to subdue prey (Lubin 1986). The average body length of this species is 6.21 mm in females and 3.15 mm in males (Masumoto 1992). The volume of colonies is variable according to the number of individuals in the colony (Table 1). The age of adult females is easily determined by their body color. Adult females are orange for at least a week after the final molt, becoming black a few weeks later.

I conducted field observations in a 2 ha research area from February–April 1992 and also in March 1993. All colonies found within this area were included in the study. To locate these colonies, I searched within the study area for 3 days before the 25 February and the 17 March study periods. All observations were made between 0800–1800 h, which corresponded to the daylight periods in this area. I recorded the number, stage of maturation and behavior of spiders in colonies on 25 February and 17 March 1992. In March 1993, I also conducted a total of 17 hours of field observations on the only colony (4♂33♀) still present in the study area. For this colony, I recorded the stage of maturation, relative body length of interacting individuals and each insect that entered the colonial web. Individuals were not marked and the relative body length between the spider and the insect prey was estimated by eye. I collected females and their egg sacs from the No. 2 colony described below. I preserved them in 70% alcohol and counted the number of eggs per egg sac and,

Table 1.—The composition of *Philoponella raffrayi* in the research area of Pasoh Forest Reserve on 25 February and 17 March 1992. Between the two dates, colonies #7 and 8 disappeared, and the new colonies #9, 10, 11, 12 appeared in the study area. The asterisk (*) or double asterisks (**) indicates the number of *Argyrodes* spp. or *Portia* spp., respectively. The single dagger (†) indicates that of 24 females, 17 had produced eggsacs by 17 March.

	25 February 1992					17 March 1992					
Colony No.	No. of adult females (A)	No. of adult males (B)	No. of juveniles (C)	Other species	Colony size (cm) (length, width, height)	No. of adult females (D)	No. of adult males (E)	No. of juveniles (F)	Other species	Colony size (cm) (length, width, height)	Survivorship (D+E+F/ A+B+C)
1	0	0	28	0	30, 30, 60	20	1	0	0	40, 40, 60	75%
2	24	1	0	1*	60, 60, 60	24†	1	0	4*	70, 60, 70	100%
3	25	7	0	0	55, 55, 32	23	1	0	1*, 1**	60, 60, 35	75%
4	0	0	35	0	20, 15, 30	0	0	25	0	40, 40, 60	71%
5	44	2	0	0	70, 40, 70	44	0	0	0	200, 150, 150	96%
6	6	0	0	0	10, 15, 15	4	0	0	0	30, 20, 20	67%
7	15	0	0	0	40, 40, 40	—	—	—	—		—
8	15	5	0	0	30, 30, 30	—	—	—	—		—
9	—	—	—	—		28	2	0	1**	80, 80, 80	—
10	—	—	—	—		4	0	0	0	40, 40, 40	—
11	—	—	—	—		3	0	0	2*	20, 20, 20	—
12	—	—	—	—		14	1	0	0	40, 50, 40	—

Table 2.—The number of prey entering the colony, captured or not captured, in a colony of *Philoponella raffrayi*. Relative prey size is the ratio of prey body length to spider body length.

Relative prey size (prey/spider)		Single	Cooperative
<0.1	Success	30	1
	Fail	1	0
	Efficiency (%)	97	100
0.1–0.5	Success	32	2
	Fail	4	0
	Efficiency (%)	89	100
0.5–1.0	Success	1	4
	Fail	11	0
	Efficiency (%)	8	100
1.0<	Success	0	0
	Fail	6	0
	Efficiency (%)	0	—

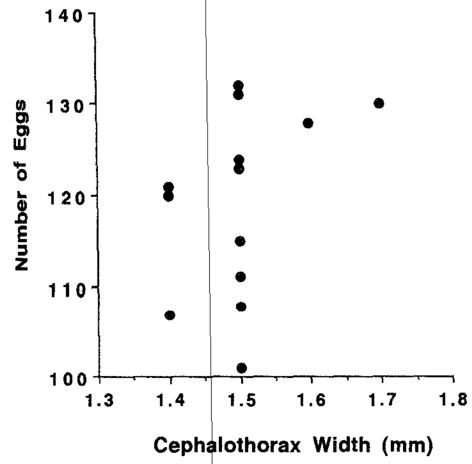

Figure 1.—The correlation between the cephalothorax width of females and the number of eggs deposited. Spearman's rank correlation: $Rs = 0.523$, $n = 15$. $P = 0.046$.

under a binocular microscope, measured to the nearest 0.1 mm the width of females' cephalothorax. Two of them were deposited as voucher specimens in the collection of the Department of Zoology, National Science Museum, Tokyo (NMST-Ar 3514, 3525). Capture efficiency is defined as the ratio of the number of insects captured compared to the number of insects entering the webs.

I observed eight colonies in February and ten colonies in March 1992 (Table 1). Each colony consisted of members of a similar developmental stage, apparently representing only variation in size of the same instar. Between 25 February–17 March (3 weeks), six of the eight colonies remained at the same web site, but two colonies disappeared from the study area and four colonies newly appeared. In March 1992, females of No. 2 colony produced twig-like egg sacs, hung them from the hub and began guarding the eggs. The mean number of eggs per egg sac was 118 ±9.96 ($\bar{x}$ ±SD, $n = 15$). This value was correlated with the cephalothorax width of its mother (Spearman's rank correlation; $Rs = 0.523$, $n = 15$, $P = 0.046$; Fig. 1). However, 8 of 13 females measured had a cephalothorax width of 1.5 mm but produced 101–132 eggs. Factors that may have contributed to the difference would be energy gain during the adult stage. Oviposition occurred between March–April in 1992, and the juveniles remained in the same colony where they had hatched. Developmental stages of females were synchronous within the same colony, but not synchronous among different colonies. Furthermore, the number of spiders in the same colony never increased, and no fusion of colonies was observed. During April, no colonies remained at the same web site and three colonies, each containing more than 100 juvenile *P. raffrayi*, appeared at different web sites. All adult females disappeared from the juvenile web colony, and I could detect no parent-offspring interaction except for egg sac guarding. Furthermore, *Argyrodes* and *Portia* were found in the colonies.

During the observation, I recorded 92 insects of four orders entering webs; Diptera (75), Hymenoptera (15), Coleoptera (1), Lepidoptera (1 larva). Of these insects, the spiders captured 66 Diptera, two Hymenoptera, one Coleoptera and one larva of Lepidoptera. Wrapping was dominantly conducted by individual females. However, when prey was trapped in the periphery of an individual orb web, 7 out of 70 prey items (10%) were wrapped by two cooperating females. They first subdued prey by throwing silk on it from a distance and began to more tightly wrap prey cooperatively as they rotated it. The prey capture efficiency of a single females was 89–97% when prey size was less than the half the body length of the spider, but this decreased to only 8% when the relative prey size was between 0.5–1, and no prey was captured when the prey length was greater than spider body length. However, cooperative prey capture by two females resulted in 31% prey capture efficiency when the relative prey size was between 0.5–1 spider length, which was higher than that by a single female (Fisher's exact probability = 0.0027; Table 2). Even in cases where two females caught prey cooperatively, only one female fed on the prey item. In six out of seven cases, females that were larger by 10% of body length and more matured females fed alone on the captured prey. The effect of web ownership on the advantage in taking over a prey could not determined because I could not discriminate the owner from the intruder.

Communal uloborid spiders, such as *Philoponella oweni* Chamberlin 1924 were thought to lack any cooperative prey capture behavior (Buskirk 1981). However, cooperative prey capture has since been reported in a species of *Philoponella* in the Cameroon (Breitwisch 1989), and for *P. republicana* Simon 1891 (see Binford & Rypstra 1992). The prey capture by *P. raffrayi* is similar to that of *P. republicana,* except that no more than two individuals were observed to share in this behavior. These results indicate that there may several types of cooperative prey capture in the genus *Philoponella.*

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