
Article

A group-living spider (Araneae: Pholcidae) inhabiting the bases of large buttressed trees in the tropical rain forest of Sabah, Malaysia

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Abstract

A social pholcid spider was found on the floor of a lowland tropical rain forest near the Maliau Basin, located in the southern part of Sabah, Malaysia. This species lived in groups within an irregular three-dimensional web built at the base of large buttressed trees. Webs were usually built near the ground level of enclosed spaces surrounded by two neighboring buttresses and the main trunk. A larger colony contained all developmental stages of immature spiders and multiple adults of both sexes. In larger colonies, sex ratios were significantly biased toward females, with an average sex ratio of 23.8 (% male). Spiders exhibited some communal behavior with web repair and defense. But individuals were competitively aggressive rather than cooperative in prey capture.

Web sites of this social pholcid species were restricted to the bases of large buttressed trees of more than 70 cm diameter at breast height. In their webs there were often remained many prey remnants such as the wings of termites whose mounds were also found at the base of the same large trees. Specialization to this sort of microhabitat has some implications for the ecology and evolution of social spiders, as well as conservation of tropical rain forests.

Key words: social spider, tropical rain forest, buttressed tree, *Pholcus*, Borneo

Introduction

Most spiders are solitary and even cannibalistic predators, but a small proportion has developed group-living traits. These traits are considered to arise independently many times in the Araneae, with various degrees of "sociality" exhibited among group members ranging from tolerant but competitive interactions to communal and cooperative ones. Therefore, spiders have been regarded as model animals for studying the evolution of social behavior (for recent reviews, see Endo, 1996; Aviles, 1997; Uetz and Hieber, 1997).

Group-living spiders are conventionally called "social spiders," and classified according to two criteria: (1) whether they share a single web (non-territorial) or maintain individual webs (territorial), and (2) whether the colonies last beyond one generation (permanent) or break up at some phase of life cycle of one generation

(periodical). Social species may then fall into one of the following four types: (i) non-territorial permanent social-spiders, (ii) territorial permanent social-spiders, (iii) non-territorial periodical social-spiders, and (iv) territorial periodical social-spiders (Krafft, 1982; Endo, 1996; Aviles, 1997). It is an important question to ask what ecological conditions lead to the evolution of such diverse types of social behavior.

As several researchers have pointed out, the fact that most social spiders occur in the tropics may be shed light onto this problem (Uetz, 1992; Riechert and Roeloffs, 1993; Aviles, 1997; but see Furey, 1998). Aviles (1997) summarized the environmental factors that might favor the evolution of social spiders in the tropics, as follows: (1) plentiful year-round food supply (facilitating a delayed dispersal); (2) large prey size (making cooperation profitable), (3) intense competition (facilitating the use of more open web sites); (4) intense

predation pressure (selecting for maternal care and group defense); (5) heavy rainfall (making nest-sharing profitable); (6) a lack of distinct seasons (making a generation overlap possible); (7) aseasonal or mildly seasonal environment (facilitating inter-colony selection); and (8) high diversity of spider species (offering correspondingly more opportunities for evolving toward permanent sociality). Which of these factors is relatively important in the development of social traits for each particular spider species? We can approach this question more easily if we can rigorously identify the physical structure and biological features of the habitats in which spiders have evolved particular types of sociality.

In tropical Southeast Asia an uloborid spider, *Philoponella raffrayi* has been reported to be a territorial periodical social-species (Masumoto, 1992). We discovered another type of social spider in Southeast Asia. This spider species has an outstanding characteristic that the locations of the colony webs are restricted to the base of large buttressed trees in a tropical rain forest. Such an identifiable feature may provide us opportunities for determining which environmental factors contribute the evolutionary development of sociality in spiders. In this paper, we describe some characteristics of colonies such as colony size, colony composition, and individual behavior relevant to predation and web building. We especially addressed two questions on the microhabitat of the spiders: (1) whether or not there is a relationship between tree size and colony presence; and (2) whether or not there is any association between the spider colonies and termite mounds at the base of trees, because termite nests may be important sources of prey for spiders. We discuss some ecological implications of the use of specialized microhabitats, such as the base of buttressed trees, as well as the importance of such a microhabitat in the conservation of tropical rain forests.

Study Site and Methods

Studies were carried out around the Agatis camp found on the mountain slope surrounding the Maliau Basin, located in the center of the southern part of Sabah on the island of Borneo. There still remain large areas covered by lowland tropical rain forest, which consist mainly of large dipterocarps such as *Shorea* spp. (Gait et al., 1998).

We initially surveyed along the Agatis trail extending from the base camp into the forest on May 26, 1999,

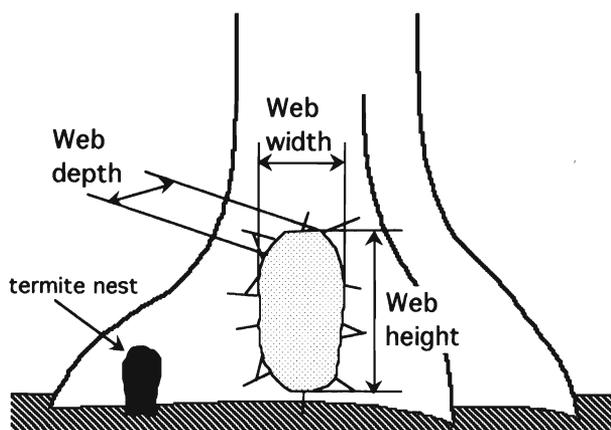


Fig. 1. Measurements of the colony web. See text for details.

and found colonies of the spider, *Pholcus*, at the base of buttressed trees along the way. After some successive observations, we found that these colonies occurred only in the spaces between buttresses, and it was then decided to investigate buttressed trees around the campsite from May 27-30, 1999. For every buttressed tree we came across during our random walks through the forest, we recorded whether the colony web was present or absent around the base of the tree, and measured the diameter of the tree at breast height (DBH). We also counted the number of termite mounds at the base of the tree because termite nests may be important sources of prey for spiders. When a colony of this species was found, we measured the web height (from lower to upper dense silk layer), width (from one side close to the buttress to the other side) and depth (from the open side to the opposite side close to the trunk) (Fig. 1). Web volume was approximated as cubic space by multiplying together the web height, width, and depth. We estimated colony size by counting the number of spiders *in situ*. Measurements are given in average \pm SD.

We could not distinguish any stage or sex of the spiders by eye, except for females with egg sacs. Therefore, we sampled whole colony members in 5 colonies in order to determine the exact composition of a single colony. It was difficult to catch all spiders at one time because they constantly would rush into the tree bark and then run about once the web was destroyed. But, they would then come back again and begin to quickly repair their web after the web was destroyed. We then collected the remainder with an additional one or two samplings. These were preserved in a 70% alcohol solution, brought back to the laboratory, and the cephalothorax width measured under a dissecting binocular microscope.

The spider described in this paper belongs to the genus *Pholcus* (T. Irie, *pers. comm*), but is still not



Fig. 2. Photographs of (A) a large buttressed tree at which a web site of social pholcid spiders was found, (B) spiders in a web, and (C) the web itself.

identified into a particular species. Specimens will be deposited at the University Museum of Malaysia, Sabah and the Museum of Nature and Human Activities, Hyogo, Japan.

Results

Webs and colonies

The *Pholcus* spiders built a communal irregular three-dimensional web in an enclosed space provided by the tree trunk and two neighboring buttresses spreading from the tree (Fig. 2). We found a total of 22 colonies in our preliminary survey and successive investigations. Measurements of each colony are shown in Table 1. On average, web size was 65 ± 30 cm in height, 43 ± 24 cm in width, and 33 ± 17 cm in depth, with an approximate volume of 0.14 ± 0.20 m³. The lower portion of the web was almost at the ground level or between 10 and 65 cm above the ground. Average colony size was 41.0 ± 50.7 , varying from 1 to 177

(Fig. 3). Eight (44%) of 18 colonies in which colony size could be determined were relatively small ones of less than 10 spiders. Only 3 large colonies containing more than 100 spiders were found, but these figures may not be exact because it was very difficult to accurately count the numbers of spiders in such large colonies under field conditions. Web volume obviously became larger with increased colony size (Fig. 4: Kendall's $\tau=0.62$, $n=13$, $P<0.01$), but larger colonies with more than 100 spiders showed a tendency to be asymptotic in web volume (Fig. 4).

Colony composition

Table 2 shows body size distributions in cephalothorax width for 5 colonies in which all members were sampled. As this table shows, large colonies (A, B, C, and G) consisted of almost all size ranges of immatures and adults of both sexes. In comparison, a relatively small colony H consisted of small spiderlings and adult males and females. The

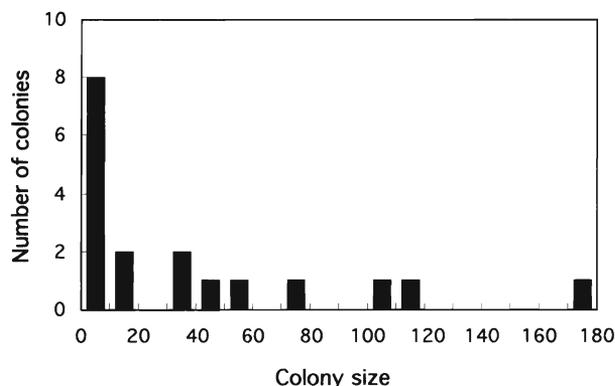


Fig. 3. Frequency distribution of colony sizes.

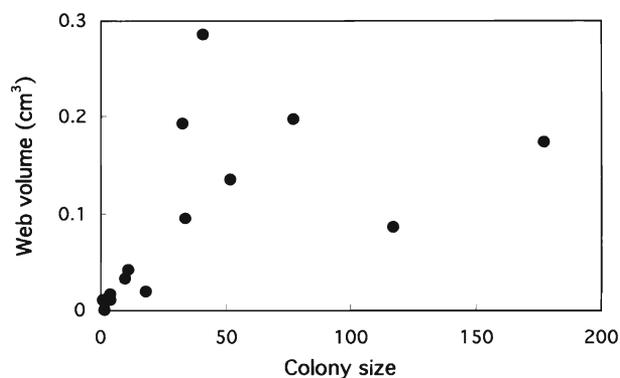


Fig. 4. Relationship between colony size and estimated web volume.

cephalothorax width of adult males and females were 1.06 ± 0.07 mm ($n=30$) and 1.13 ± 0.08 mm ($n=90$), respectively.

Sex ratios (% male) of adults in each colony varied from 5.9% (C) to 46.9% (G), for an average of 23.8%. Sex ratios in the three largest colonies were significantly biased toward females (χ^2 test, $P < 0.001$ for A, B and C, respectively), though was not significant in colonies G and H ($P > 0.5$).

Microhabitats

We found pholcid colonies in 10 of 71 buttressed

trees examined (14%). These colonies were found only on trees with a large diameter of more than 70 cm at breast height (Fig. 5). Trees with colonies were significantly larger in DBH than trees without colonies (Mann-Whitney U-test: $z=4.80$, $P < 0.001$). Moreover, 86% of colonies were found in trees larger than 100 cm in DBH.

A buttressed tree usually has 4 to 8 buttresses spreading from the main trunk in every direction. There was found only one colony web in an enclosed space supported by two neighboring buttresses, but often with more than one colony on a single tree (Fig. 6). The

Table 1. Colony and web sizes of *Pholcus* sp. and diameter at breast height (DBH) of the tree on which the colony was found.

Date of observation	Colony	No. of spiders in a colony	No. of females with egg sacs	Web				DBH (cm)
				height (cm)	width (cm)	depth (cm)	volume (cm ³)	
May 26, 1999	1	8	4	-	-	-	-	-
May 26, 1999	2	1	1	-	-	-	-	82
May 27, 1999	A	107	-	70	-	-	-	120
May 27, 1999	B	177	-	110	45	35	0.17	120
May 27, 1999	C	52	-	62	91	24	0.14	120
May 28, 1999	D	2	-	-	-	-	-	155
May 28, 1999	E	0	0	43	28	20	0.02	100
May 28, 1999	F	-	-	100	50	45	0.23	100
May 28, 1999	G	117	-	75	33	35	0.09	100
May 29, 1999	H	10	-	37	40	22	0.03	77
May 29, 1999	I	4	-	30	23	19	0.01	82
May 29, 1999	J	-	8	125	113	60	0.85	130
May 29, 1999	K	77	6	95	34	61	0.20	130
May 29, 1999	L	-	3	66	50	25	0.08	130
May 30, 1999	M	33	0	80	36	67	0.19	106
May 30, 1999	N	4	0	27	25	15	0.01	106
May 30, 1999	O	11	0	65	30	21	0.04	106
May 30, 1999	P	1	0	22	27	18	0.01	82
May 30, 1999	Q	41	1	85	62	54	0.28	115
May 30, 1999	R	34	3	65	44	33	0.09	82
May 30, 1999	S	4	0	35	23	21	0.02	82
May 30, 1999	T	18	1	34	25	22	0.02	82

Table 2. Body size distributions for 5 colonies of *Pholcus* sp.

Colony	Stage and sex	Cephalothorax width (mm)																	Total					
		0.35-	0.40-	0.45-	0.50-	0.55-	0.60-	0.65-	0.70-	0.75-	0.80-	0.85-	0.90-	0.95-	1.00-	1.05-	1.10-	1.15-		1.20-	1.25-	1.30-		
A	Immature				3	2	4	9	5	10	7	10	10	5	7	1	1							74
	Adult male													1			4	2						7
	Adult female														3	7	3	6	4	2	1			26
	Total				3	2	4	9	5	10	7	10	11	5	10	12	6	6	4	2	1			107
B	Immature	1	4	3	7	12	13	18	13	11	14	8	11	8	11	6	5	1	1					147
	Adult male												1	1	1		2							5
	Adult female												1		2	3	4	8	4	1	1	1		25
	Total	1	4	3	7	12	13	18	13	11	14	9	12	11	15	10	15	5	2	1	1	1		177
C	Immature				5	7	4	1	3	1	1	3	1	2	1	4	1	1						35
	Adult male																		1					1
	Adult female																2	1	4	6	3			16
	Total				5	7	4	1	3	1	1	3	1	2	1	4	3	2	5	6	3	0		52
G	Immature		2	8	8	17	7	9	4	8	1	8	6	1	3	1	1	1						85
	Adult male												1		3	6	5							15
	Adult female												1		1	3	5	3	4					17
	Total		2	8	8	17	7	9	4	8	1	8	8	8	1	7	10	11	4	4				117
H	Immature					2	1																	3
	Adult male															1	1							2
	Adult female																1	1	3					5
	Total					2	1									1	2	1	3					10
Total		1	6	16	25	37	26	39	23	30	25	28	33	18	37	37	35	23	16	6	2		463	

observed frequency in the number of colonies per tree was significantly different from the expected frequency in Poisson distribution (G test, $G_{adj}=11.44$, $P<0.001$). Therefore, there was a strong tendency that colony webs were clustered on larger trees. Two-thirds of colonies discovered had been built on trees with multiple colonies.

There was found no significant correlation between colony size and DBH of the tree at which the colony was found (Fig. 7: $r=0.35$, $n=16$, $P>0.05$). However, larger colonies occurred only on bigger trees in DBH.

Fifteen of 22 colonies observed (68%) were associated with termite mounds at the same tree. This association apparently resulted from the tendency that termite mounds were also found at the bases of trees

with larger DBH (Fig. 8). The DBH of trees with termite mounds was significantly larger than those of trees without termite mounds (Mann-Whitney U-test: $z=3.38$, $P<0.001$).

Predatory, web-building, and defensive behaviors

Numerous termite wings were observed as prey remnants in the web of colony L on May 29 and colonies P and Q on May 30. We have no quantitative data for prey items, but these winged termites seemed to be an important prey resource for the social pholcids.

In the present study, any cooperative behavior for prey attacking or communal feeding was not observed. On 29 May, we observed in colony J one spider capture prey and then immediately approached by two other

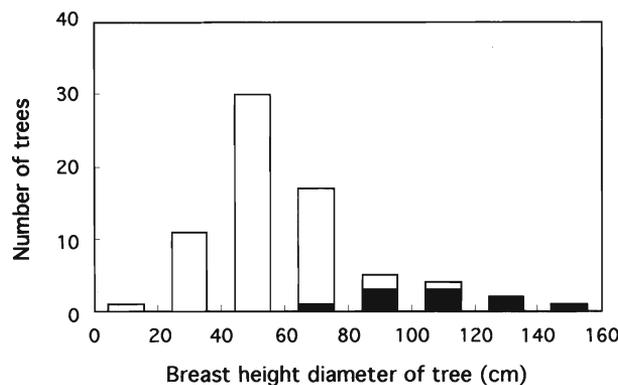


Fig. 5. Breast height diameter of trees at which colonies of social pholcid spiders were found (closed bar) and not found (open bar).

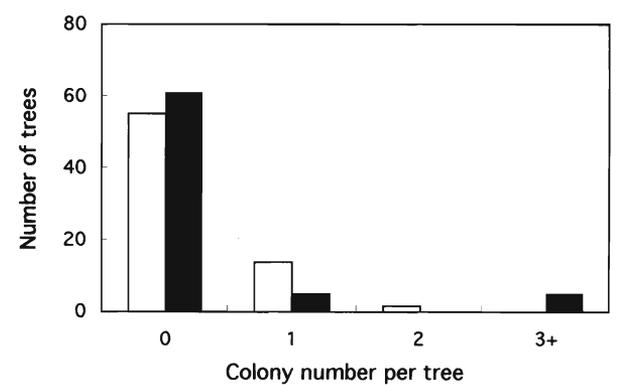


Fig. 6. Observed frequency of colony numbers per tree (closed bar) and expected Poisson frequency (open bar).

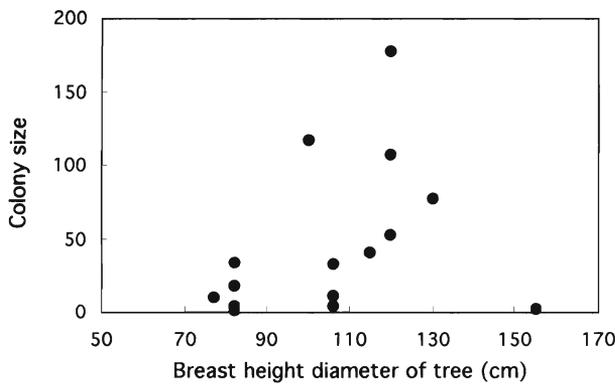


Fig. 7. Relationship between breast height diameter of tree and colony size.

nearby spiders. The owner soon carried the prey to a location in the web apart from them, and then began feeding on it after wrapping it. The two other spiders resumed their original places after a short time. In the same colony, we observed an ant dropping into the upper portion of the web. Several spiders successively attacked the insect until it eventually escaped from the bottom of the web. There was no cooperation between spiders attempting to attack. In colony M, we also observed an interaction between individuals for prey on May 30. Some individuals disputed one prey, and eventually a single spider won it. These observations were anecdotal, but at least indicated no evidence that spiders within a colony cooperatively attacked prey in the web or communally fed upon one prey.

When we destroyed the webs to sample whole colony members, a number of spiders in some colonies fled away to surrounding tree trunks. These spiders did not disperse, but immediately returned to actively repair the web together.

We did not observe any natural enemy attacking the spiders. However, it was often observed that many individuals vigorously vibrated the web all together whenever we approached the colony. This behavior lasted for several minutes and then they became motionless.

Discussion

The group-living *Pholcus* in this study has the following characteristics. First, numerous spiders were living in a single large colony web. Second, large colonies contained full ranges in size classes of spiders, including multiple adults of both sexes. Such a colony composition suggests that it may have persisted for a considerably long period of time.

In the family Pholcidae, varying degrees of social

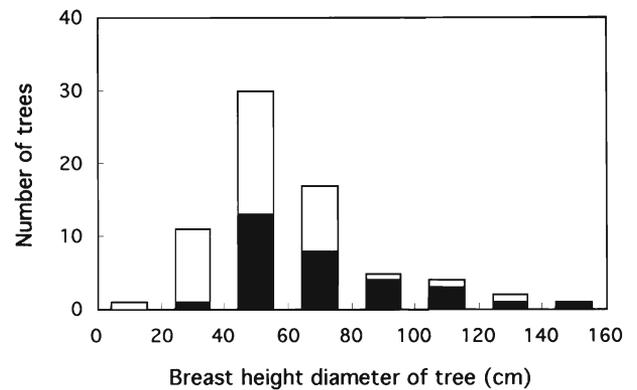


Fig. 8. Breast height diameter of trees at which termite mounds were found (closed bar) and not found (open bar).

behavior are known thus far. Aggregations of several individuals are found in interconnected webs for *Physocyclus dugesi* (Burgess, 1978), *Hoplopholcus asiaeminoris*, and *H. longipes* (Brignoli's observation referred in Eberhard and Briceno, 1983). Eberhard and Briceno (1983) describe cohabitations of males with mature females' webs for *Blechnoscelis* sp. and *Modisoma* spp. Another interesting example comes from *Holocnemus plucheii* introduced to North America from the Mediterranean region (Jakob, 1991). In this species small spiderlings facultatively live in groups by invading the webs of larger spiders. Jakob (1991) discusses that the main benefit of group living in this spider is likely to be the reduction in web-building cost when spiderlings take advantage of webs built by large conspecifics. In addition, some pholcids such as *Pholcus phalangioides*, *P. ancoralis*, and *Psilochorus sphaeroides* are also known to invade the webs of other species (Jackson and Rowe, 1987). Based upon these observations that pholcid spiders frequently enter into the webs of other spiders, Jakob (1991) proposed the possibility of a 'parasitic route' to sociality.

How does the *Pholcus* spider form a colony? Our study period was too short to determine the particular method(s) of colony formation of this species. Further studies are needed on both colony formation and long-term dynamics. It may also be a key problem in helping to understand the social evolution of pholcid spiders.

Non-territorial permanent social-spiders usually engage in cooperative prey capture and feeding (Buskirk, 1981; Riechert and Roeloffs, 1993; Aviles, 1997). However, we did not observe any cooperative behavior in prey attacking and prey consumption. Since our observations are fragmental, we need further studies to conclude that it has not evolved cooperative behavior in prey capture and feeding. We did confirm that many spiders concurrently performed web-building and

defensive behaviors. Whenever webs were destroyed due to rainfall or wind, other pholcid spiders immediately repair their webs (Eberhard and Briceno, 1983; Jakob, 1991). In this social *Pholcus*, many spiders were also actively engaged in web-building behavior just after the web was destroyed. Group web building may enable spiders to repair their web rapidly as well as lower the webbing cost per individual spider (Jakob, 1991).

It is well known that some species of non-territorial permanent social-spiders, such as *Agelena consociata*, *A. republicana* (Agelenidae), *Aebutina binotata* (Dictynidae), *Tapinillus* sp. (Oxiopidae) *Achaearanea disparata*, *Anelosimus domingo*, *A. eximius*, and *Theridion nigroannulatum* (Theridiidae), occur on forest floors or edges of tropical mountain forests at altitudes of several hundred meters (Aviles, 1997). However, it has been rarely documented that their web sites were constrained to a particular physical structure. Our study showed that the social *Pholcus* colonies were closely associated to buttressed trees, especially large ones. This association was very strong in our study site, although in other places the colony web of this species has been found at the entrance of a cave near Poring, in the northern part of Sabah (T. Irie, *pers. comm*). Whether at the base of large buttressed trees or at a cave entrance, this species seems to build its web in highly specialized microhabitats that can offer a location protected from rain and wind. This finding may be important in understanding the ecological context to enhance evolution of sociality in arachnids. Those microhabitats are very scattered on forest floors because large mature buttressed trees are few in number, even if the buttressed trees are relatively abundant in lowland tropical rain forests (Richards, 1996). For animals with limited mobility specialized to such microhabitats, it would be relatively easy to move to a neighboring space within a tree, but must be highly difficult to move between trees. Moreover, the microhabitats available to this pholcid are supposed to be saturated because large trees had become nearly entirely occupied (Figs. 4 and 5). Therefore, it seems to be difficult for the spiders to find vacant spaces and establish new colonies. Such a feature may influence on the process of colony foundation, as well as the degree of inbreeding (Riechert and Roeloffs, 1993). Further detailed studies on ecological consequences of highly specialized microhabitat use will promise a better understanding of group-living in the *Pholcus* spiders.

Termites are probably one of the most important prey

for the social *Pholcus*, though we have no quantitative data to support that. At least three species of mound-building termites are recorded in the lower montane forest of the Maliau Basin, which is located at a higher altitude than our study site, and termite abundance is likely to increase at lower altitudes (Jones et al., 1998). Although the spatial association between termite mounds and spider colonies might apparently arise from a coincidence of the preferences of both for larger trees, this would not deny the importance of termites as a food resource. It is necessary to note that the availability of termites may vary temporally and spatially. Insects available for spiders are winged alates that are reproductive, and do not always emerge from their mounds in all seasons. Such variability in prey availability could be relevant to the development of group-living colonies (Caraco et al., 1995).

Finally we will mention conservation problems. This social pholcid species, as described above, seems to be highly restricted to large buttressed trees in tropical rain forests. At the present time, this species is known to be only from Sabah. Tropical rain forests are still under strong logging pressure, and larger trees with commercial value are now especially selected in forests near the reserve where the present study was conducted. It is not difficult to imagine that such logging endangers this spider species. The base of a large buttressed tree harbors diverse fauna and provides an important microhabitat for the social *Pholcus* and other arthropods, including web-building spiders, termites, ants, solitary and social wasps and bees to construct their webs and nests. How important this kind of microhabitat is for sustaining biological community in the lowland tropical rain forest is certain to be a challenging problem in the near future.

Acknowledgements

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References

Aviles, L. (1993) Interdemic selection and the sex ratio:

- a social spider perspective. *Amer. Natur.*, **142**: 320-345.
- Aviles, L.** (1997) Causes and consequences of cooperation and permanent-sociality in spiders. In J. C. Choe and B. J. Crepsi, eds., *The Evolution of Social Behavior in Insects and Arachnids*. Cambridge Univ. Press, Cambridge, pp.476-498.
- Burgess, J. W.** (1978) Social behavior in group-living spider species. *Symp. Zool. Soc. Lond.*, **42**: 69-78.
- Buskirk, R.** (1981) Sociality in the Arachnida. In H. R. Hermann, ed., *Social Insects, Vol. II*. Academic Press, London, pp.282-367.
- Caraco, T., Uetz, G. W., Gillespie, R. G. and Gildeau, L. A.** (1995) Resource consumption variance within and among individuals: on coloniality in spiders. *Ecology*, **76**: 196-205.
- Eberhard, W. G. and Briceno, R. D.** (1983) Chivary in pholcid spiders. *Behav. Ecol. Sociobiol.*, **13**: 189-195.
- Endo, T.** (1996) Coloniality and sociality in arachnid. In Y. Saito, ed., *Evolutionary Ecology of Parent-offspring Relationship: Social Lives in Arthropods*. Hokkaido Univ. Press, Sapporo, pp.37-57. (In Japanese)
- Furey, R. E.** (1998) Two cooperatively social populations of the teridiid spider *Anelosimus studiosus* in a temperate region. *Anim. Behav.*, **55**: 727-735.
- Gait, B., Awang, R. and Urit, L. M.** (1998) Checklist of commercial timber and rattans in the Maliau Basin. In M. Maryati, W. Sinun, A. Anton, M. Noh Daliman and A. Ahmad, eds., *Maliau Basin Scientific Expedition*. Universiti Malaysia Sabah, Kota Kinabalu, pp.63-72.
- Jackson, R. R. and Rowe, R. J.** (1987) Web-invasion and araneophagy by New Zealand and Australian pholcid spiders. *New Zeal. J. Zool.*, **14**: 139-140.
- Jakob, E. M.** (1991) Costs and benefits of group living for pholcid spiderlings; losing food, saving silk. *Anim. Behav.*, **41**: 711-722.
- Jones, D. T., Tan, J. and Bakhtiar, E. Y.** (1998) The termite (Insecta: Isoptera) of the Maliau Basin, Sabah. In M. Maryati, W. Sinun, A. Anton, M. Noh Daliman and A. Ahmad, eds., *Maliau Basin Scientific Expedition*. Universiti Malaysia Sabah, Kota Kinabalu, pp.95-112.
- Krafft, B.** (1982) Eco-ethology and evolution of social spiders. In P. Jaisson, ed., *Social Insects in the Tropics*. Universite Paris-Nord. Paris, pp.7-84.
- Masumoto, T.** (1992) The composition of a colony of *Philoponalla raffrayi* (Uroboridae) in Peninsular Malaysia. *Acta Arachnol.*, **41**: 1-4.
- Richards, P. W.** (1996) *The Tropical Rain Forest, an Ecological Study, 2nd. ed.* 598p., Cambridge Univ. Press, Cambridge.
- Riechert, S. E. and Roeloffs, R. M.** (1983) Evidence for and consequences of inbreeding in the cooperative spiders. In N. Thornhill, ed., *The Natural History of Inbreeding and Outbreeding*. The Univ. Chicago Press, Chicago, pp.283-303.
- Uetz, G. W.** (1992) Foraging strategies of spiders. *Trends Ecol. Evol.*, **7**: 155-159.
- Uetz, G. W. and Hieber, C. S.** (1997) Colonial web-building spiders: balancing the costs and benefits of group-living. In J. C. Choe and B. J. Crepsi, eds., *The Evolution of Social Behavior in Insects and Arachnids*. Cambridge Univ. Press, Cambridge, pp.458-475.

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