Korean J Biol Sci 3: 167-172, 1999

Life History of a Colonial Spider *Philoponella prominens* (Araneae: Uloboridae) in Korea

Tae Soon Park, Jun Namkung[1], and Jae Chun Choe*

Department of Biology, College of Natural Sciences, Seoul National University, Seoul 151-742, Korea;
[1]Ohkum-dong 164, Uchang Apt. 2-805, Seoul 138-739, Korea

Key Words:
Colonial spider
Commensal spider
Life history
Philoponella prominens
Social spider
Web-building cost

We report for the first time the life history of a 'social' spider, *Philoponella prominens,* living in a temperate region. *Philoponella prominens* hibernated as immatures or subadults for 7-8 months in 1995 and 1996 from September-October to April-May in central Korea. When they emerged from their winter hibernation, a majority began their lives as commensals in the webs of other species. As the mating season approached, however, commensal spiders switched to become colonial or solitary. The mating season began in early June and lasted until early August. Newly-hatched spiderlings began to appear in the field in late June. They formed a colony by building their webs connected to the mother's by using part of the mother's web as supporting substrates. As the season progressed, however, some of the colonial spiderlings became commensal or solitary individuals. Our field observations suggest that *Philoponella prominens* form colonies or commensal associations to reduce the web-building cost.

The evolution of sociality in animals has been investigated most extensively in insects (Wilson, 1971; Choe and Crespi, 1997). In recent years, however, group-living spiders have also been actively studied and many new findings have shed light on social evolution in general (reviewed by Avilés, 1997 and Uetz and Hieber, 1997). Most spiders are solitary predators that are aggressive, territorial, and even cannibalistic. According to a recent review by Uetz and Hieber (1997), however, approximately 50 species exhibit varying degrees of social behavior beyond simple subsociality. 'Colonial' spiders physically connect their webs together, but individual webs are independently built and occupied (Burgess and Witt, 1976; Uetz and Burgess, 1979; Burgess and Uetz, 1982; Uetz and Hieber, 1997). 'Social' spiders, on the other hand, not only live together in complex web-nests, but also cooperate in web building, prey capture and feeding, and sometimes brood care (Shear, 1970; Burgess, 1978; Buskirk, 1981; Burgess and Uetz, 1982; Uetz and Hieber, 1997).

Although the term 'social' has been widely used in the literature of group-living, it is a rather vague term in the whole scheme of social systems. If we follow the terminology of Crespi and Choe (1997a), social spiders can be classified as being 'colonial' if they share breeding sites, 'communal' if they cooperate in brood care, or possibly 'cooperatively breeding' if indeed they exhibit alloparental care. 'Eusocial' spiders must show a division of labor involving a trade-off between reproduction and helping, which is a required condition for eusociality (Wilson, 1971; Michener, 1974; Crespi and Yanega, 1995, Crespi and Choe, 1997a). It is still not clear if any species of spiders can be classified as eusocial (Crespi and Choe, 1997b), despite the possibility in *Anelosimus eximius* suggested by Vollrath (1986) and Rypstra (1993). Association in which one species reaps some benefits while the other, the host species, is essentially unaffected is considered commensal (Rypstra and Binford 1995). Mutualistic associations occur when both species gain benefits from the association (Elgar, 1994).

Species of the genus *Philoponella* show a wide range of social behavior (Opell, 1979; Smith, 1982, 1983; Uetz and Hieber, 1997). Both solitary and colonial individuals have been found in *P. arizonica* (Buskirk, 1981), *P. fasciata* (Smith, 1982), *P. oweni* (Smith, 1982, 1983), *P. semiplumosa* (Lahmann and Eberhard, 1979; Spiller, 1992), *P. tingena* (Struhsaker, 1969), and *P. vittata* (Smith, 1982). *Philoponella republicana* is either highly colonial (Simon, 1891; Struhsaker, 1969; Lubin, 1980; Smith, 1985; Binford and Rypstra, 1992) or commensal to species of *Achaearaneae*, *Nephila*, or *Scytodes* (Struhsaker, 1969; Opell, 1979), and to *A. eximius* (Rypstra and Binford, 1995). Earlier, Simon (1891) reported *P. servulus* to be commensal to a species of *Cyrtophora* in Venezuela. *Philoponella ferokus* is commensal to *Stegodyphus sarasinorum* in India (Bradoo, 1979, 1986, 1989), *P. tingena* to species of *Achaearaneae*, *Nephila*, or *Scytodes* in Colombia and Panama (Opell, 1979), and *P. vicina* to *Tengella radiata* in Costa Rica (Fincke, 1981). Recently, Elgar (1994) re-

---

* To whom correspondence should be addressed.
Tel: 82-2-880-8158, Fax: 82-2-882-7195
E-mail: jcchoe@snu.ac.kr

ported a mutualistic association of *P. undulata* with *Psechrus argentatus* in Papua New Guinea.

Philoponella prominens, originally described by Bösenberg and Strand (1906), is distributed throughout East Asia including Japan and Korea (Paik, 1978; Yoshida, 1980, 1991; Platnick, 1989). According to Paik (1978), the spider lives widely throughout Japan and Korea. As a member of the Uloboridae, this non-poisonous spider typically builds an orb-web consisting of sticky spirals made of cribellate silk (Eberhard, 1972). To date 'social' spiders have been found and studied only in tropical and subtropical regions of the world (Opell, 1979; Riechert, 1984; Avilés, 1997; Uetz and Hieber, 1997). The following account is the first report on the life history and social behavior of a colonial spider, *Philoponella prominens*, naturally occurring in a temperate region.

Materials and Methods

The study population of *Philoponella prominens* was located in Seoul National University Arboretum in Anyang, Korea (37° 36′ N, 126° 92′ E). The study was conducted at a site near the entrance of the arboretum, which was covered predominantly by oak trees (*Quercus* spp.) with patchily distributed undergrowth of herbs and shrubs. The total area of the study site was approximately 80,000 m^2.

Observations were made from mid-April to early October in 1995 and 1996. In order to assess the population dynamics and seasonal changes in the life history patterns of *P. prominens*, 5 quadrats (5 × 5 m) were set up in mid-April, 1996, where the spiders were found to be generally abundant during preliminary observations in 1995. One quadrat was set up first near the center of the study site and then each of the other four was set up at approximately 50 m distance in each of the four cardinal directions.

The clutch size was assessed by counting the number of newly-hatched spiderlings. The number of these first-instar spiderlings could not be determined until they became approximately 10-days old and readily visible through the meshwork of webs. The sex of *P. prominens* could only be determined based on the shape of the pedipalp when the spiderlings reached the second-instar stage.

Results

Life cycle and population dynamics

Philoponella prominens overwintered as immatures or subadults. They began to emerge from winter hibernation in late April (Fig. 1). The mean body length of these overwintered individuals measured on 1 May 1996 was 2.88 ± 1.18 mm (mean ± SD, n=98). Once emerged, they started to molt and grow, and the adults began to appear in late May. Then the mating season ensued from early June (Fig. 1) and egg cases started to appear in the field from 5 June. They continued to reproduce until early August (Fig. 1) and their offspring began to hatch out in late June.

The newly-hatched spiderlings remained in the mother's somewhat irregular web for a while. When the mother built a regular orb-web, however, the spiderlings used part of the mother's web as supporting substrates and built their own orb-webs consisting mainly of radial lines without a hub and silky spirals. As the spiderlings grew in size, their webs also became larger.

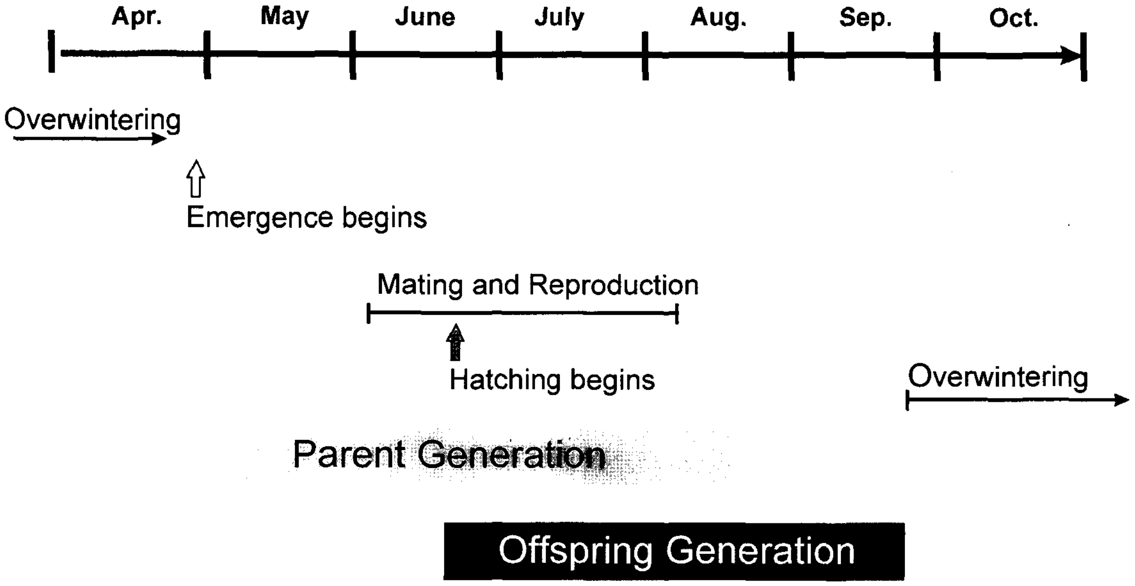

Fig. 1. A generalized life history pattern of *Philoponella prominens* at the study site.

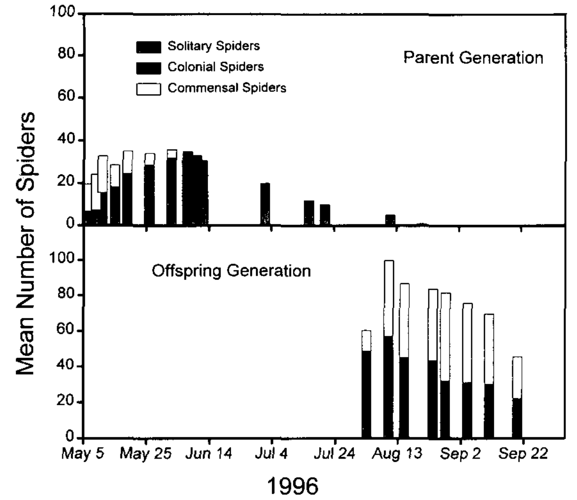

Fig. 2. Population dynamics and seasonal changes in the life history of *Philoponella prominens* in 1996.

The population size of the new generation reached its maximum around 10 August (Fig. 2). The mean body length of these spiderlings, mostly the second and third instars, measured on 10 August was 2.50±0.56 mm (n=325). The spiderlings began disappearing in mid-September for overwintering (Fig. 2) and the last individual was observed at the study site on 10 October in 1996.

Immature *P. prominens* usually went through five to six molts to become adults. Like most other spiders, the first molt occurred inside the egg case in *P. prominens*. The body color of the second instars was nearly black, while those of the third to fifth instars were generally dark brown. Adult males after five molts were brown, while adult females after six molts were yellow.

Association

A majority of *P. prominens* began their lives as commensals in the webs of other species when they emerged in the spring (Fig. 2). From mid-May, however, the number of commensal spiders started to decrease and by 9 June no more spiders were observed in commensal associations (Fig. 2). Host spiders for commensal *P. prominens* in spring included *Neriene nigripectoris*, *N. radiata* (Linyphiidae), and *Agelena difficilis* and *A. limbata* (Agelenidae). *Neriene nigripectoris* and *N. radiata* built sheet-webs, while both *Agelena* species built funnel-webs. The number of commensals per host ranged from 1 to 8, but a majority of the hosts (80.5±13.1%, n=5 quadrats) harbored only 1 or 2 commensals (Fig. 3).

On 5 May 19.5% and 13.3% of the spiders were colonial and solitary, respectively (Fig. 2). The numbers of both colonial and solitary spiders increased steadily throughout May and maintained relatively high densities until early June (Fig. 2). Some colonial and solitary spiders survived until early to mid-August when the new generation peaked in its population density (Fig. 2). Colonial spiders used neighbors barrier-web threads as supports for their orb webs (Fig. 4).

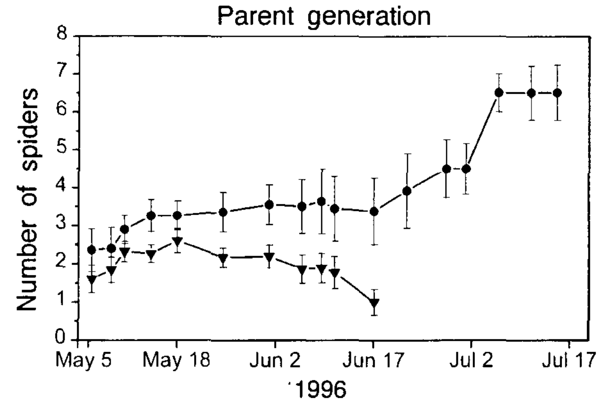

Fig. 3. Seasonal change in colony size (●) and the number of commensals per host (▼) from the time of emergence to the end of the parent generation in 1996. Vertical bars represent 95% confidence limits.

Most colonies (80.5±13.1%, n=5 quadrats) consisted of less than 4 individuals, although the largest colony had 23 spiders in all (Fig. 3). Group size of colonial spiders began increasing from mid-June and remained high throughout the mating season (Fig. 3).

Newly-hatched spiderlings formed predominantly colonial associations in the beginning (Fig. 2). The number of colonial spiders peaked around 10 August and then started to decrease, whereas commensal spiders maintained fairly high numbers from mid-August to early September (Fig. 2). Both commensal and colonial individuals began disappearing rapidly around 24 September (Fig. 2). Solitary spiders were found in low numbers in August but moderately increased in number toward the end of the season (Fig. 2). The mean number of spiders per colony remained above 7 until mid-August and then dropped to 3-4 per colony for the rest of the season (Fig. 5).

Fig. 4. Colonial webs of *Philoponella prominens*.

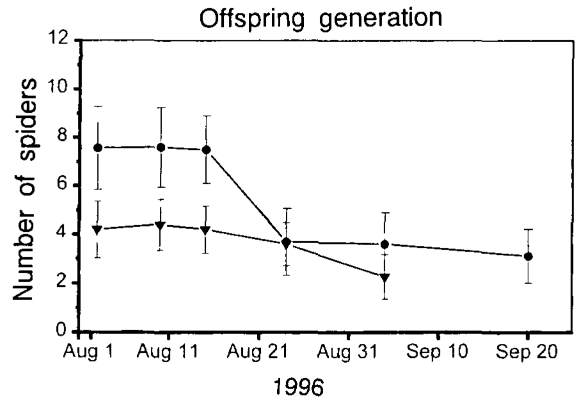

Fig. 5. Seasonal change in colony size (●) and the number of commensals per host (▼) from when newly-hatched spiderlings appeared to when they disappeared for overwintering in 1996. Vertical bars represent 95% confidence limits.

Completely different spiders served as host species for commensal *P. prominens* of the new generation. The most common host species was *Achaearanea japonica* (Theridiidae), followed by *Nephila clavata* (Tetragnathidae) and *Agelena difficilis* and *A. limbata* (Agelenidae). *Achaearanea japonica* built frame-webs (Fig. 6), while *Nephila clavata* and *Agelena* built orb- webs and funnel-webs, respectively. The numbers of commensals per host were generally higher than those in the parent generation (Fig. 5). Host spiders with large webs such as *Nephila clavata* and *Agelena* spp. sometimes supported more than 10 commensals per web.

Commensal *P. prominens* built their webs mostly inside or outside of the vertical lines above the flat sheet of the host spider's web (Fig. 6). The commensal webs are also found occasionally near barrier lines of orb-webs with many irregular lines. Commensal *P. prominens* used vertical, barrier, or irregular lines of host webs as supporting substrates.

Reproduction and sex ratio

On 1 May there were 39 males and 37 females in all five quadrats, and thus the sex ratio was relatively even (Chi-square test, $\chi^2=0.026$, $P>0.87$). In the midst of the mating season, however, the sex ratio became highly female-biased. In the survey conducted on 20 July, there were 19 females, but only 1 male in all five quadrats. Males were often killed in the process of approaching females and even successfully mated males died soon after mating.

When *P. prominens* females produced egg cases, they disassembled their orb-webs and built structurally irregular webs where most of the threads were connected to the egg case. The egg case of *P. prominens* was relatively long and flat, forming a trapezoid shape in a sideview. It was 11.5±6.52 mm (n=21) in length and 0.72±0.32 mm (n=21) in width. The color of the egg case ranged from light yellow to dark brown, with or without dots. The total number of eggs per egg case was 35.6±18.7 (n=32). Eggs took 13.6±5.1 d (n=17) to hatch and the mother protected the egg case by holding it with her fourth legs. Females generally produced multiple egg cases and the refractory period from one egg case to the next was 8.5±5.3 d (n=16).

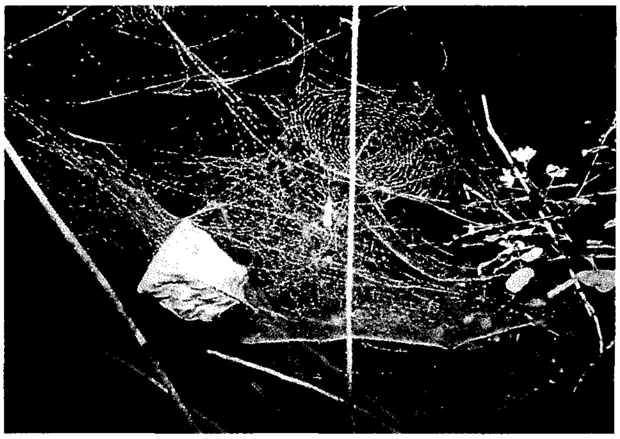

Fig. 6. Commensal webs of several subadult female *Philoponella prominens* connected to the upper barrier-web threads of *Achaearanea japonica.*

Discussion

Philoponella prominens clearly preferred to build their webs onto the webs of other species when they emerged from winter hibernation. Unlike spiders in the tropics where prey is available throughout the year, *P. prominens* has to survive more than half the year without food. They are probably in a state of near starvation when they first emerge from winter hibernation, as do most other temperate spiders (Nakamura, 1987; Vollrath, 1987). Thus, commensalism in such cases may be an adaptation to reduce the web-building cost (Lubin, 1986). As the cost of silk production, web construction, and maintenance is relatively high for solitary spiders, and it constitutes the majority of the spider's energy budget (Lubin, 1986; Jakob, 1991; Uetz and Hieber, 1997), the evolutionary transition from solitary to group living or commensal association may have been favored in some species (Uetz and Hieber, 1997).

The same can be said for the newly-hatched spiderlings that tended to build their webs in connection with the mother's web. Individuals were observed to switch between different life patterns (T. S. Park and J. C. Choe, in prep.). A majority of the overwintered individuals started as commensals to other species, but gradually shifted to either colonial or solitary life, as the season progressed. In the offspring generation, however, colonial individuals later became mostly commensal and partly solitary before they went into winter hibernation.

It appears that newly-hatched *P. prominens* spiderlings stay around their mother to form a colonial group more or less naturally. When they emerge from hibernation, however, their mothers or siblings are not around. Thus, they tend to become commensals to other spiders that are already out in the field.

The genus *Philoponella* contains more 'social' species than any other genera (Uetz and Hieber, 1997). Prevalence of sociality in *Philoponella* may be in part due to the way of building webs common among the members of the Uloboridae. Risch (1977) showed that the orb-web of an Uloborid *Zosis geniculatus* contains almost twice the length of silk per milligram of body weight as that of a silimar-sized Araneid *Neoscona domiciliorum* that builds about the same-sized web of similar shape. Several thousand cribellate silk glands are involved in the Uloboridae to produce many fine threads (Friedrich and Langer, 1969), whereas only two pairs of aggregate glands are used to produce the sticky spiral in the Araneidae (Opell, 1982; Lubin, 1986). Uloborids rarely recycle the silk protein and lack the poison gland (Lubin, 1986). *Philoponella prominens* appears to have evolved to reduce the web-building cost through the formation of colonies or commensal associations.

Philoponella prominens is a 'social' spider recorded for the first time in a non-tropical region. Our observations revealed that most individuals were in colonial or commensal associations, although solitary individuals were nearly as common as colonial ones during the mating season. When some authors (e.g. Avilés, 1997) go so far as to discuss possible reasons for the exclusive tropical distribution of social spiders, factors responsible for the social evolution of *P. prominens* in a temperate region are worthy of further investigation.

Acknowledgements

We are most grateful to Tadashi Miyashita of Tokyo University for providing helpful comments and advice throughout the project. We also thank William Eberhard, Brent Opell, Ann Rypstra, Deborah Smith, and George Uetz for providing their reprints and valuable advice. This work was supported by a grant (No. 961-0508-069-2) from the Korea Science and Engineering Foundation.

References

Avilés L (1997) Causes and consequences of cooperation and permanent-sociality in spider. In: Choe JC and Crespi BJ (eds), The Evolution of Social Behavior in Insects and Arachnids, Cambridge University Press, Cambridge, pp 476-498.

Binford GJ and Rypstra AL (1992) Foraging behavior of the communal spider, *Philoponella republicana*. *J Insect Behav* 5: 321-335.

Bösenberg W and Strand E (1906) Japanishe spinnen. *Abh Naturfor Göritz* 30: 106-108.

Bradoo BL (1979) *Uloborus ferokus* n. sp. (Araneae: Uloboridae), a commensal of *Stegodyphus sarasinorum* Karsch. *Bull Br Arachnol Soc* 4: 353-355.

Bradoo BL (1986) Feeding behaviour of a non-poisonous spider *Uloborus ferokus* Bradoo (Araneae: Uloboridae). *Zool Anz* 217: 75-88.

Bradoo BL (1989) Advantage of commensalism in *Uloborus ferokus* Bradoo (Araneae: Uloboridae). *J Bombay Nat Hist Soc* 86: 232-328.

Burgess JW (1978) Social behavior in group-living species. *Symp Zool Soc Lond* 42: 69-78.

Burgess JW and Witt PN (1976) Spider webs, design, and engineering. *Interdisc Sci Rev* 1: 322-355.

Burgess JW and Uetz GW (1982) Social spacing strategies in spiders. In: Witt PN and Rovner JS (eds), Spider Communication: Mechanisms and Ecological Significance. Princeton University Press, Princeton, pp 317-351.

Buskirk RE (1981) Sociality in the Arachnida. In: Hermann HR (ed), Social Insects, Vol 2, Academic Press, New York, pp 281-367.

Choe JC and Crespi BJ (1997) The Evolution of Social Behavior in Insects and Arachnids. Cambridge University Press, Cambridge.

Crespi BJ and Choe JC (1997a) Introduction. In: Choe JC and Crespi BJ (eds), The Evolution of Social Behavior in Insects and Arachnids. Cambridge University Press, Cambridge, pp 1-7.

Crespi BJ and Choe JC (1997b) Explanation and evolution of social systems. In: Choe JC and Crespi BJ (eds), The Evolution of Social Behavior in Insects and Arachnids. Cambridge University Press, Cambridge, pp 499-524.

Crespi BJ and Yanega D (1995) The definition of eusociality. *Behav Ecol* 6: 109-115.

Eberhard WG (1972) The web of *Uloborus diversus* (Araneae: Uloboridae). *J Zool Lond* 166: 417-465.

Elgar MA (1994) Experimental evidence of a mutualistic association between two web-building spiders. *J Anim Ecol* 63: 880-886.

Fincke OM (1981) The association between two neotropical spider (Araneae: Uloboridae and Tengellidae). *Biotropica* 13: 301-307.

Friedrich VL and Langer M (1969) Fine structure of cribellate spider silk. *Am Zool* 9: 91-96.

Jakob EM (1991) Costs and benefits of group living for *Pholcid* spiderlings: losing food, saving silk. *Anim Behav* 41: 711-722.

Lahmann EJ and Eberhard WG (1979) Factores selectivos que afectan la tendencia a agruparse en la araña colonial *Philoponella semiplumosa* (Araneae: Uloboridae). *Rev Biol Trop* 27: 231-240.

Lubin YD (1980) Population studies of two colonial orb-weaving spiders. *Zool J Linn Soc* 70: 265-287.

Lubin YD (1986) Web building and prey capture in the Uloboridae. In: Shear WA (ed), Spiders, Webs, Behavior, and Evolution. Stanford University Press, Stanford, pp 132-172.

Michener CD (1974) The Social Behavior of the Bees. Harvard University Press, Cambridge.

Nakamura K (1987) Hunger and starvation. In: Nentwig W (ed), Ecophysiology of Spiders. Brühlsche Universitätsdruckerei, Giessen, pp 287-295.

Opell BD (1979) Revision of genera and tropical American species of the spider family Uloboridae. *Bull Mus Comp Zool* 148: 443-547.

Opell BD (1982) Cribellium, calamistrum, and ventral-comb ontogeny in *Hyptiotes cavatus* (Hentz) (Araneae: Uloboridae). *Bull Br Arachnol Soc* 5: 338-43.

Paik KY (1978) Illustration Encyclopedia of Fauna and Flora of Korea. Vol 21. Araneae, Samwha Publishing Co., Seoul, pp 1-193.

Platnick NI (1989) Advances in the spider taxonomy, 1981-1987. Manchester University Press, Manchester.

Riechert SE (1984) Why do some spiders cooperate? *Agelena consociata,* a case study. *Fla Entomol* 68: 105-116.

Risch P (1977) Quantitative analysis of orb-web patterns in four species of spiders. *Behav Genet* 7: 199-238.

Rypstra AL (1993) Prey size, social competition and the development of reproductive division of labor in social spider groups. *Am Nat* 142: 868-880.

Rypstra AL and Binford GJ (1995) *Philoponella republicana* (Araneae: Uloboridae) as a commensal in the webs of other

spider. *J Arachnol* 23: 1-8.
Shear WA (1970) The evolution of social phenomena in spiders. *Bull Br Arachnol Soc* 1: 65-76.
Simon E (1891) Observations biologiques sur les Arachnides. *Ann Soc Entomol Fr* 60: 5-14.
Smith DRR (1982) Reproductive success of solitary and communal *Philoponella oweni* (Aeaneae: Uloboridae). *Behav Ecol Sociobiol* 11: 149-154.
Smith DRR (1983) Ecological costs and benefits of communal behavior in a presocial spider. *Behav Ecol Sociobiol* 13: 107-114
Smith DRR (1985) Habitat use by colonies of *Philoponella republicana* (Aeaneae: Uloboridae). *J Arachnol* 13:363-373
Spiller DA (1992) Relationship between prey consumption and colony size in an orb spider. *Oecologia* 90: 457-466.
Smith K (1984) Rate of predation by a kleptoparasitic spider, *Argyrodes fissifrons*, upon a large host spider, *Agelena limbata* (Araneae). *J Arachnol* 12: 363-367.
Struhsaker TT (1969) Notes on the spiders *Uloborus mudiar* (Chamberlin and Ivie) and *Nephila clavipes* (Linneaus) in Panama. *Am Midl Nat* 82: 611-613.
Uetz GW and Burgess JW (1979) Habitat structure and colonial behavior in *Metepeira spinipes* (Araneae: Araneidae), an orb-weaving spider from Mexico. *Psyche* 86: 79-89.
Uetz GW and Hieber CS (1997) Colonial web-building spiders: balancing the costs and benefits of group-living. In: Choe JC and Crespi BJ (eds), The Evolution of Social Behavior in Insects and Arachnids, Cambridge University Press, Cambridge, pp 458-475.
Vollrath F (1986) Environment, reproduction, and the sex ratio of the social spider *Anelosimus eximius*. *J Arachnol* 14: 267-281.
Vollrath F (1987) Growth, foraging, and reproductive success. In: Nentwig W (ed), Ecophysiology of Spiders. Brühlsche Universitätsdruckerei, Giessen, pp 357-370.
Wilson EO (1971) The Insect Societies. Harvard University Press, Cambridge.
Wise DH (1982) Predation by a commensal spider, *Argyrodes trigonum*, upon its host: an experimental study. *J Arachnol* 10: 111-116.
Yoshida H (1980) Six Japanese species of the genera *Octonoba* and *Philoponella* (Aeaneae: Uloboridae). *Acta Arachnol* 29: 57-64.
Yoshida H (1991) A Note on the Japanese genera *Uloborus*, *Zosis*, *Octonoba* and *Philoponella* (Aeaneae: Uloboridae). *Atypus* (98/99): 21-26.

[Received April 3, 1999; accepted April 26, 1999]