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Reproductive Success of Solitary and Communal *Philoponella oweni* (Araneae: Uloboridae)

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Summary. *Philoponella oweni* (Uloboridae) is a facultatively communal orb-web spider found in arid regions in the southwestern United States. Within one habitat solitary adult females and communal groups of adult females coexist.

This study compared the reproductive output (egg production) and reproductive success (production of live offspring) of solitary and communal females. There was no significant difference in the mean number of egg-cases produced by solitary and communal females, but communal females produced significantly more eggs per egg-case. However, communal females suffered significantly higher rates of egg-case parasitism from the pteromalid wasp *Arachnopteromalus dasys*. As a result, the mean number of live offspring produced by solitary and communal females did not differ. Thus, both strategies led to roughly equal reproductive success. The advantages of aggregation of adults may be significant in the evolution of social behavior in spiders.

Introduction

Philoponella oweni (Uloboridae) is a facultatively communal spider. In one habitat, and within one population, both solitary individuals and communal groups can be found. This allows comparison of the costs and benefits of solitary and communal behavior without the complications introduced by cross-species comparisons, and makes possible investigation of the ecological factors promoting solitary and group life. This study measures the reproductive output (egg production) and reproductive success (production of live offspring) of solitary and communal females of *P. oweni.*

Subsocial behavior or care of offspring after hatching is widespread among spiders. *Communal* behavior occurs when two or more adults live together in a semi-permanent group, but do not cooperate in any aspect of group life. This does not include mating pairs or females with several courting males. *Cooperative* behavior occurs when individuals live together in semi-permanent groups and cooperate, e.g. in capturing large insects, sharing large prey items, caring for one another's young, or constructing webs used by the entire colony. There have been no long term studies of the reproductive output of individual females or of division of labor in cooperative groups.

The family Uloboridae is predominantly tropical and subtropical in distribution, though members of this group are found throughout the world (Opell 1979). Like members of the family Araneidae many members of the Uloboridae, including species of *Philoponella,* spin orb webs.

Social behavior appears to be widespread among the Uloboridae (Buskirk 1981). *Zosis geniculatus,* found in the West Indies and South America, and the Australian *Uloborus congregabilus* may form aggregations (Muma and Gertsch 1964; Butler 1933). In the genus *Philoponella* behavior ranges from solitary or aggregated in *P. semiplumosa* (Lahmann and Eberhard 1979) and *P. arizonica* (Buskirk 1981), to facultatively communal in *P. oweni,* and obligately communal in *P. tingena* (Struhsaker 1969), *P. vittata* (personal observation in Suriname), and *P. fasciata* (personal observation, Trinidad). *Philoponella republicana* is highly communal or perhaps cooperative (Simon 1891; Lubin 1980; personal observations).

Philoponella oweni is found in the arid foothill regions of the southwestern United States and northwestern Mexico (Muma and Gertsch 1964; Opell 1979). The spiders spin their webs in pro-

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tected places. Solitary females spin a prey capture orb and an irregular tangle of threads above and below the orb. In communal groups, which may contain 2 to 40 adult females, each female constructs her own prey-capture orb; the orbs typically share support lines and the irregular tangle of threads. Solitary females and communal groups usually have a retreat area. Although a communal group may have more than one retreat area, each retreat is used by many colony members.

Materials and Methods

This study was carried out between 1976 and 1980 in the Chiricahua Mountains, Cochise County, Arizona, USA. Data were collected from two populations of *Philoponella oweni* inhabiting riparian vegetation in mountain canyons at elevations of 1,500–1,800 m. The Cave Creek population was studied from July through mid-September 1976 and June through mid-September 1977. The South Fork population was studied from late May through mid-September 1979 and July and August of 1980.

Adult females in the study populations were individually color-marked with fast-drying enamel paints and classified as solitary or communal. A female was solitary if her web was not connected by silk to that of another adult female. Females were classed as communal if their webs were attached to those of one or more adult females.

The study populations were censused 2–5 times per week over the course of the 1977 and 1979 field seasons. At each census the following data were recorded: presence of color-marked females, presence of unmarked females (most of whom were then marked), identity and location of females with egg-cases, and approximate numbers and size classes of immatures present. The total number of egg-cases produced by each female was also noted. When females with egg-cases were discovered the egg-case was marked with a color code corresponding to that of the mother. The discarded egg-cases were collected, and their contents examined in the laboratory under a dissecting microscope. Discarded, unparasitized egg-cases contained empty egg-shells, occasionally a few dead eggs, and the cast-off exuviae of first stadium spiderlings. The egg shells and unhatched eggs were counted and used as a measure of the reproductive output of individual females.

Some egg-cases were parasitized by the chalcidoid wasp *Arachnopteromalus dasys* (Pteromalidae) (Gordh 1976). Several parasitized egg-cases were opened and raised in the laboratory so that the course of the wasps' development could be observed. The wasp larvae feed externally on the contents of the spider's eggs, leaving behind the empty egg-shells. The larvae pupate inside the spider egg-case and then emerge as adult wasps. If an egg-case is parasitized, all the spider eggs are killed.

When a discarded, parasitized egg-case is collected after the wasps have emerged, it contains the empty spider egg-shells, exuviae of the wasp pupae, but no exuviae of the spiderlings. Once again the egg-shells were counted and used as a measure of the number of eggs the spider laid in the egg-case.

Data on the numbers of eggs per egg-case were analyzed with the t-test. Data on numbers of live spiderlings produced per egg-case were not normally distributed, since no spiderlings were produced from a large number of parasitized egg-cases. These data were analyzed with the Mann-Whitney *U*-test.

There are several potential sources of error in using number of egg-shells as a measure of the number of eggs a female lays in an egg-case. As spiderlings emerge through the case's exit hole they sometimes drag a few egg-shells out as well. It is possible to mistake an egg-shell for an exuvium or vice versa. Finally, sibling cannibalism in the egg-case has been reported for some spiders. To verify that my count of egg-shells gave a good estimate of the number of eggs laid in an egg-case, 13 unparasitized egg-cases were reared in the laboratory. Both the number of egg-shells left behind in the egg-case and the number of live spiderlings emerging from the egg-case were recorded.

Results

Subadult *P. oweni* emerge from their overwintering sites with the advent of warm spring weather – in my study area in southeastern Arizona, late April or early May. Mature individuals appear in late May and early June. Mating takes place in June and the short-lived males die by mid-July. The females begin to construct egg-cases in late June and early July, and continue to lay eggs through September. The behavior of a female allows the identification of the mother of an egg case even in large communal groups. A female *P. oweni* moves to the retreat area to construct her egg-case. The mother remains in the retreat area, the egg-case attached to her spinnerets and held by the fourth pair of legs. She spins no orb until the young emerge, approximately 20 days later. After the young spiderlings hatch and emerge from the egg-case the female discards the case, leaves the retreat and spins a new prey capture orb.

Hatchlings and immatures remain in the maternal web or colony for a variable length of time, adding their own orbs to those already present. Tiny spiderlings sometimes spin orbs within the meshwork of adult orbs, and females tolerate the presence of the young of other females as well as their own. Over the course of the summer some immatures disperse out of the web while others remain. Those that remain in the parental web or colony overwinter there and emerge the following spring and occupy the same site.

Data from egg-cases reared in the laboratory showed that counting egg-shells gave a reliable measure of the number of eggs laid in an egg-case. A regression of number of live spiderlings against the number of egg-shells gave an r^2 value of 0.94.

Census data showed no significant differences in the average number of egg-cases produced by solitary and communal females of *P. oweni*. In 1977 solitary females produced an average of 1.3 ± 0.47 ($n=11$) egg-cases per female and communal females produced an average of 1.6 ± 0.66 ($n=45$) egg-cases. In 1979 solitary females produced an average of 1.6 ± 0.76 ($n=22$) egg-cases each and communal females produced 1.4 ± 0.79 ($n=23$) ($t=0.92$, n.s.).

However, solitary and communal females differed significantly in the average number of eggs per egg-case. In 1977 egg-cases produced by solitary females contained an average of 26.9 ± 13.0 eggs ($n=12$); those of communal females contained an average of 37.3 ± 15.1 eggs ($n=38$; $t=2.17$, $P<0.05$). In 1979 egg-cases of solitary females contained an average of 44.3 ± 15.3 eggs ($n=26$) while egg-cases of communal females contained an average of 56.1 ± 17.0 eggs ($n=24$; $t=2.57$, $P<0.05$).

However, communal females suffered much higher rates of parasitism than did solitary females. Combining 1977 and 1979 data, 28%, or 16 out of 57 of the egg-cases produced by communal females were parasitized, while only 10% (4 out of 40) of the egg-cases produced by solitary females were parasitized ($P<0.05$, $\chi^2=4.8$).

After the effects of egg-case parasitism are taken into account, there is no significant difference between solitary and communal females in the number of live spiderlings produced per egg-case. In 1977 solitary females had an average of 24.3 ± 14.4 live young per egg-case ($n=12$, median 20.5, range 0–33) and communal females had an average of 26.1 ± 21.8 young per case ($n=40$, median 28.5, range 0–59; Mann Whitney U-test, $P=0.62$). In 1979 solitary females produced an average of 40.2 ± 19.5 young per egg-case ($n=26$, median 42.5, range 0–78) and communal females produced 41.0 ± 26.8 young per egg-case ($n=24$, median 49.0, range 0–88; Mann Whitney U-test, $P=0.41$).

Discussion

The results of this study show one reason for the coexistence of both solitary and communal females in a single population of spiders. Both strategies lead to roughly equal reproductive success, at least at the level of production of live spiderlings.

There are at least two explanations for the higher rates of parasitism on the egg-cases of communal females. Communal groups, with more occupants and more webbing than solitary webs, may provide more effective cues to a searching wasp. The behavior of the communal spiders themselves may also contribute to their higher rates of parasitism. Female *P. oweni* generally remain in the retreat area with their egg-cases, and in communal groups all or most of the egg-case carrying females in the colony are gathered together in the same retreat. As a result, if a female *A. dasys* does discover the retreat of a communal group, she may have access to a large number of *P. oweni* egg-cases at once.

Table 1. Trends in clutch size and sociality among non-orb-weaving families of spiders

	Social system	Clutch size
Stegodyphus (Eresidae)		
pacificus	Solitary with maternal care for 1 instar	500–600 eggs
lineatus	Solitary with maternal care for 2 instars	120–250
sarasinorum	Cooperative	Variously reported 20–120
Agelena (Agelenidae)		
labyrinthica	Solitary	100
republicana	Cooperative	11
consociata	Cooperative	11
Achearanea (Theridiidae)		
tepidariorum	Solitary	130–379
disparata	Cooperative	20–30

Several authors (Kullmann 1972; Stern and Kullmann 1975) have noted an inverse relationship between level of social development and fecundity in spiders. Within some groups this certainly appears to be true (Table 1). Species of *Stegodyphus* (Eresidae) demonstrate a variety of social systems, from the solitary *S. pacificus* and *S. lineatus* to the cooperative *S. sarasinorum*. *Stegodyphus pacificus* lays a large number of eggs per egg-case, (Kullmann and Zimmerman 1974; Stern and Kullmann 1975), while the species with more developed social behavior lay fewer eggs per egg-case (Bradoo 1973; Jacson and Joseph 1973; Kullmann 1972; Millot and Bourgin 1942). Similar trends are seen in the genera *Agelena* (Agelenidae) (Darchen 1967; Krafft 1970) and *Achearanea* (Theridiidae) (Darchen 1968; Kaston 1948).

The sheet- and tangle-web spinners show trends which imply the evolution of communal and cooperative behavior from species with extended parental care. This is perhaps best documented in the genus *Stegodyphus*. Females of *S. pacificus* care for their young and feed them by regurgitation until the first post-emergence molt; the mother then dies. *S. lineatus* females feed their young both by regurgitation and later by giving them small, partially digested prey. The mothers remain alive with their brood until the young reach their second post-emergence molt. The immatures remain together for a time after the mother's death jointly attacking and feeding on small insects, and later disperse. *Stegodyphus sarasinorum* feed their young by regurgitation and by providing them with small insects. The young typically remain in the colony with the mother, who produces several batches of young in her lifetime (Kullmann 1972). Similarly, the solitary *Agelena labyrinthica* shows no prolonged maternal care, while females of the cooperative *A. consociata* care for both their own young and those of other females in the colony (Krafft 1970). Kullmann (1972) discusses these trends in maternal care, clutch size and sociality among theridiids.

Reduction in clutch size in these groups appears to be correlated with the development of extended parental care and greater investment in each offspring. This presumably reduces the total number of offspring a parent can produce, but increases the likelihood of survival for an individual offspring.

This would appear to be at variance with the results presented here, that solitary *Philoponella oweni* lay fewer eggs per egg-case than communal females. In fact, this points to the existence of two different types of spider societies, and to two different (though not mutually exclusive) routes to communal behavior among spiders.

Orb-spinning spiders such as *Cyrtophora* (Araneidae) and *Philoponella* (Uloboridae) show a different trend in clutch size (Table 2). Solitary species tend to have smaller clutches than communal species. *Cyrtophora cicatrosa* is found in solitary webs and in aggregations. Females lay egg-cases containing 25–50 eggs (Lubin 1974). *C. citricola* is communal (Rypstra 1979) and is reported to lay egg-cases containing about 200 eggs (Kullman 1972). *Cyrtophora moluccensis* forms very large, dense, communal groups (Lubin 1974). Females lay egg-cases containing 877 to 1,850 eggs (Lubin 1974, 1980; Sabath et al. 1974).

A similar trend is evident among uloborid spiders. As reported here, solitary females of *P. oweni* produced fewer eggs per egg-case than communal females. *Zosis geniculatus*, a related species similar in size to *P. oweni*, can be solitary or aggregated. Opell (1979) reports that it lays 40 to 80 eggs per egg-case. Two discarded egg-cases I collected in Arima, Trinidad, W.I. contained 40 and 85 egg shells. *Philoponella republicana* is an obligately communal (or perhaps cooperative) species which forms colonies of hundreds to thousands of individuals. I examined 5 egg-cases of *P. republicana* collected from the Arima Valley, Trinidad, and from Brownsberg, Suriname. The 3 unparasitized egg-cases contained 165, 163, and 168 eggs. Lubin (1980) reports that cases of *P. republicana* in Panama produced an average of 121 young per egg-case. Thus in these orb-weaving groups we see a tendency for clutch size to increase with increasing level of social development.

Table 2. Trends in clutch size and sociality among orb-weaving families of spiders

	Social system	Clutch size
Cyrtophora (Araneidae)		
cicatrosa	Solitary or aggregated	25–50 eggs per egg-case, up to 10–20 cases per female
citricola	Communal	200 eggs per case, ca. 5 cases per female
moluccensis	Communal	877–1850 eggs per case, up to 4–6 cases per female
Philoponella (Uloboridae)		
oweni	Facultatively communal: solitary	Mean of 26–44 eggs per egg-case
	Communal	Mean of 56–58 eggs per egg-case
republicana	Communal	88–166 eggs per egg-case

There are important differences between the societies of orb-spinning spiders such as *Cyrtophora* and *Philoponella* and the societies of sheet-web weavers such as *Stegodyphus*. While the communal and cooperative societies of *Agelena, Achearanea* and *Stegodyphus* appear to be derived from extended parent-offspring associations, the communal groups of *Philoponella* and *Cyrtophora* appear to be derived from aggregations of adults, related or unrelated. In *Philoponella* and *Cyrtophora* maternal care is not highly developed and investment in individual offspring is low, compared with the cooperative and communal sheet-web weavers. Benefits to colony members are in the form of increased number of eggs or young produced.

A complication is introduced into this analysis by the fact that clutch size and body size are, in general, positively correlated in spiders (Eberhard 1979; Peterson 1950; Wise 1975). Thus all comparisons of clutch size were made within a genus or between species in closely related genera, both to eliminate any possible taxon-related differences in clutch size, and to control to some extent for body size. None the less, body size differences have not been completely eliminated. For example, *Cyrtophora moluccensis* is larger than *C. citricola* (Lubin, personal communication); *Agelena consociata* is smaller than *A. labyrintheca* (Krafft 1970). However, the species of *Philoponella* discussed here have similar body sizes, ranging from 4.6–7.1 mm total body length for females of *P. oweni* to 6.3–8.4 mm for *Z. geniculatus* (Opell 1979). Some of the smaller spiders have the larger clutches, making the correlations between clutch size and level of sociality in this genus even more striking.

An interesting case of highly cooperative behavior in an araneid, *Eriophora bistriata,* was discussed by Fowler and Diehl (1978). These cooperative colonies may be groups of siblings that remain together for most of their lives. After females mature and mate, they leave the colony to construct their egg-case, and apparently never return to the colony. The clutch size (400–700 eggs per egg-case) corresponds roughly to the size of a single colony. It is possible that this species has developed a cooperative society from extended family groups, brought about by non-dispersal of siblings rather than by extension of maternal care.

These two routes to communal behavior in spiders – extended parental care and aggregation of adults – are similar to the subsocial route on one hand, and the parasocial and polygynous family group route on the other, which have been proposed for the evolution of sociality in some Hymenoptera (Evans 1958; Lin and Michener 1972; Michener 1958; West Eberhard 1975, 1978). The evolution of higher social behavior in arthropods is a two step process. The first step is the formation of semi-permanent aggregations. The second step is the development of communal, cooperative or even semisocial and eusocial behavior in these groups. It is possible that the ecological factors responsible for the initial formation of aggregations in spiders are similar to those that promote aggregation among Hymenoptera.

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