NOTES ON THE REPRODUCTIVE BIOLOGY AND SOCIAL BEHAVIOR OF TWO SYMPATRIC SPECIES OF *PHILOPONELLA* (ARANEAE, ULOBORIDAE)

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ABSTRACT. Populations of the facultatively communal species *Philoponella oweni* (Chamberlin 1924) and *Philoponella arizonica* (Gertsch 1936) (Uloboridae) occur sympatrically in the Chiricahua mountains of southeastern Arizona. This study compares reproductive biology, structure of communal groups, and feeding rates of the two species, and documents differences in their phenology, webs, web construction sites, egg-cases and spiderlings. I suggest environmental factors that may select for different reproductive strategies in the two species.

Many members of the spider family Uloboridae have been observed living in groups (Opell 1979; Muma & Gertsch 1964). For only a few of these species has the nature of their group-living behavior been investigated: the facultatively communal *Philoponella oweni* (see Smith 1982, 1983) and *P. semiplumosa* (Simon 1893)(see Lahmann & Eberhard 1979); *P. republicana* (Simon 1891), with its large, semi-permanent colonies (Smith 1985; Binford & Rypstra 1992); and a west African *Philoponella* Mello-Leitão which was observed in a very large colony (Breitwisch 1989).

This study compares reproductive biology, feeding rates and group-living behavior of two sympatric populations of group-living *Philoponella, P. oweni* (Chamberlin) and *P. arizonica* (Gertsch) (Uloboridae). Notes on the natural history of the two species are also presented, including structure of the egg-cases, the structure of the webs and substrates used for web-building in the two species.

Populations of *Philoponella oweni* and *P. arizonica* are broadly sympatric in the southwestern United States and northeastern Mexico (Muma & Gertsch 1964; Opell 1979). The basic life cycles of the two species are similar in southeastern Arizona. Field observations indicate that both are annual; sub-adults emerge from overwintering sites in the spring (early April to early June, depending on elevation). Mating takes place in late spring and early summer. In general, males are shorter-

lived than females and disappear from the population during the course of the summer. Females can lay eggs throughout the summer and may survive until early autumn, but in the populations studied no adult females overwintered for a second breeding season.

Immatures hatch and emerge from the egg-case during the summer. As is true of other uloborid spiders, the young can spin webs in the first post-emergence instar (Szlep 1961; Eberhard 1977). The newly emerged spiderlings lack a functional cribellum; and the orb webs they produce are distinctive, containing many hundreds of radial threads without a sticky spiral. Later instars possess a functional cribellum and produce webs that are similar or identical to those of adults in form (Szlep 1961; Eberhard 1977).

The young remain with the female for a variable length of time and attach their orbs to her web; during the course of the summer some or all of them disperse out of the maternal web and build independent webs (Smith 1982). Young spiders over-winter as sub-adults or younger immatures, and emerge the following spring to form the next generation of reproductives.

Both species are facultatively communal; that is, adult females of both species can be found living in small communal groups or as solitary individuals (Smith 1982, 1983). In the communal groups each female constructs her own orb web and defends it against other adult females. The orbs are joined by their support lines and space webbing.
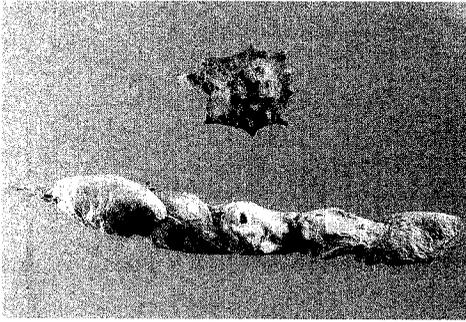
Figure 1.—Egg-cases of *Philoponella oweni* (above) and *Philoponella arizonica* (below).

Both species suffer from egg-parasitism by the chalcidoid wasp *Arachnopteromalus dasys* Gordh (Pteromalidae) (Gordh 1976), which greatly affects reproductive success of individual females. The female wasp oviposits in a uloborid spider's egg-case, and the larvae consume the contents of the spider's eggs, leaving behind empty spider egg shells. The wasp larvae then pupate inside the spider egg-case and emerge as adults. If an egg-case is parasitized, all of the spider eggs inside are killed (Smith 1982).

METHODS

Observations and collections were made at several sites in the Chiricahua Mountains in southeastern Arizona: the Southwestern Research Station of the American Museum of Natural History; South Fork Canyon, Cave Creek Canyon, and Herb Martyr Reservoir in the Coronado National Forest; and the town of Portal (Cochise County).

Population censuses: Adult females and some males were individually color-marked with dots of fast-drying enamel paints (Testor's model airplane paint) and censused 2–5 times per week. From 25 April–20 August 1977 I censused a marked population of *P. oweni* in Cave Creek Canyon at an elevation of approximately 1695 m. This population was destroyed by a flood in 1978. From 3 June–18 September 1979 I censused marked populations of *P. oweni* and *P. arizonica* in South Fork Canyon. The *P. arizonica* population was located in the lower part of the canyon (1525–1660 m) while the *P. oweni* population was in the upper part of the canyon (1630–1730 m). At each census visit I noted the presence of adult females, males, immatures or egg-cases.

Reproductive biology: When a female produced an egg-case it was given a color mark corresponding to that of the mother. To determine mean clutch size (number of eggs per egg-case) for each species I collected the egg-cases after the young had emerged and examined their contents with a dissecting microscope. As is true of most spiders, the young of *Philoponella* do not emerge from the egg-case immediately upon hatching from the egg; they remain in the egg-case for one instar, molt, and emerge as second instar spiderlings leaving behind both empty egg-shells and cast-off exoskeletons. In healthy egg-cases I used the number of egg shells as a measure of the number of eggs laid in the egg-case (Smith 1982). A parasitized egg-case can be recognized by the absence of exoskeletons from first instar spiderlings and presence of wasp pupal skins. Although all the spider eggs are killed in a parasitized egg-case, the egg-shells are still visible and were used to infer the original clutch size.

Colony structure: I noted the size and organization of all communal groups formed by each species in several locations: *P. oweni* in Cave Creek Canyon (1977), South Fork Canyon (1979, 1980) and Herb Martyr (1980); *P. arizonica* in South Fork Canyon (1979, 1980).

Feeding rates: From 21–27 August 1979, I compared feeding rates of solitary and communal females of the two species in South Fork Canyon using a trapline census method. Censuses were carried out from 0600–1800 h. Daily census periods were 4–6 h long, for a total of 29 h of observation. Every hour I visited each female in the study area and recorded whether or not she was feeding or engaged in prey capture.

Web structure: In July and August of 1980 I measured the webs of all adult females found in the South Fork Canyon study area: 22 webs of *P. oweni* and 19 webs of *P. arizonica*. I measured longest diameter of the orb webs and deviation (to the nearest 10°) of the plane of the orb webs from horizontal, and counted number of radii and number of spiral turns along the longest radius. I also noted the amount and position of "space webbing" (irregular tangles of threads), the presence or absence of a stabilimentum and the general appearance of the webs.

Habitat: To evaluate the distribution of the two species with respect to elevation I located

Table 1.—Phenological data for *Philoponella oweni* and *Philoponella arizonica*. * Still active when field observations ended.

	oweni (1977) Cave Creek	oweni (1979) South Fork	arizonica (1979) South Fork
Date census began	26 April	3 June	3 June
First adult female seen	5 May	3 June	3 July
First adult male seen	5 May	3 June	3 July
First egg-case seen	16 June	12 June	3 July
First hatchlings seen	28 June	2 July	5 July
Last adult male	4 July	27 June	21 July
Last adult female	20 August*	11 July	18 September*
End of census	20 August	18 September	18 September

all collection sites (eight for *P. oweni,* six for *P. arizonica*) on a topographical map. I also recorded the substrates used for web attachment by members of each species. In July and August 1977 I recorded the substrates used for 25 *P. oweni* webs in Cave Creek Canyon, and in August 1979 I recorded the substrates of 36 *P. oweni* and 31 *P. arizonica* webs in South Fork Canyon (in each case, this represented all adult webs present in the study sites).

Egg-cases: In July 1980 I collected 24 empty *P. oweni* egg-cases and 33 empty *P. arizonica* egg-cases and measured maximum width and length to the nearest mm using dial calipers, and noted their color, shape and ornamentation.

RESULTS

Population censuses: Table 1 gives the dates of first sightings of age and sex classes of both species. These data are limited by the starting and finishing dates of the censuses, but still show differences between adjacent populations of *P. oweni* and *arizonica. P. oweni* adults appear sooner (at a given altitude) and adult *P. oweni* males disappear from these populations by late June and early July. Adults of *P. arizonica* appear later, and the adult males persist in populations until late July. There was little temporal overlap between *P. oweni* males and *P. arizonica* females in adjacent populations.

Reproductive biology: Table 2 presents data on reproductive parameters for all females in the study areas, whether or not complete records of their reproductive history could be made. In 1979 I had complete reproductive histories for 31 *P. oweni* females and 25 *P. arizonica* females. These data are presented in

Table 3. Both tables show that *P. oweni* females produce fewer egg-cases per female and lay more eggs per egg-case than do *P. arizonica* females. The behavior of females with egg-cases also differs between the two species.

A female *P. oweni* about to construct an egg-case leaves her prey-capture orb and moves to the retreat area, a protected area near the orb usually under a rock or log, and constructs the egg-case there. There she remains, holding the egg-case and (presumably feeding little or not at all) until the young emerge, a period of approximately 20 days. After the young emerge the mother discards the egg-case, leaves the retreat, and spins a new prey capture-orb. *P. oweni* females usually have one or at most two egg-cases at a time. The time interval between successive egg-cases produced by a female is more than a week, typically 2–3 weeks.

In contrast, females of *P. arizonica* were never seen to leave the orb with their egg-cases. These females suspend their spindle-shaped egg-cases from the hub of their horizontal orbs. As new egg-cases are constructed, at intervals of 4–10 days, they are attached to the egg-cases already hanging in the web to form a long, slender stick (Fig. 1). The female continues feeding while the eggs and young mature. *P. arizonica* females sometimes have as many as 8 egg-cases in the web at once. Egg-case parasitism by the wasp *A. dasys* (Fig. 2) is a major source of mortality in both species. In general, a higher proportion of the egg-cases of *P. arizonica* than of *P. oweni* are attacked by egg-case parasites. In 1979, 14% of the egg-cases produced by *P. oweni* females and 27% of the egg-cases pro-

Table 2.—Reproductive parameters for *Philoponella oweni* and *Philoponella arizonica*, Cave Creek Canyon in 1977 and South Fork Canyon in 1979. Statistical tests are for differences between adjacent *Philoponella oweni* and *Philoponella arizonica* populations in South Fork Canyon in 1979. [a] = Mann Whitney U-test; [b] = two-tailed t-test for samples with equal variance, $t = 13.5$; [c], $\chi^2 = 3.21$, 1 df; [d], $\chi^2 = 7.10$, 1 df; [e], Mann Whitney U-test.

		Year	Mean	SD	Range	n	P
Egg-cases per female	*oweni*	1977	1.29	0.50	1–3	49 females	
	oweni	1979	1.5	10.8	1–4	44	<0.001[a]
	arizonica	1979	3.2	2.0	1–8	50	
Clutch size	*oweni*	1977	35.2	15.6	10–85	51 egg-cases	
	oweni	1979	50.0	17.0	14–89	50	<0.001[b]
	arizonica	1979	21.8	8.9	6–49	112	
Egg-cases parasitized	*oweni*	1977	23.5%			51 egg-cases	
	oweni	1979	14.0%			50	0.073[c]
	arizonica	1979	27.0%			112	
Females with ≥ 1	*oweni*	1977	40.0%			30 females	
egg-case parasitized	*oweni*	1979	22.0%			32	<0.007[d]
	arizonica	1979	55.0%			27	
Live young per egg-case	*oweni*	1977	27.1	20.1	0–79	51 egg-cases	
	oweni	1979	42.5	21.5	0–88	50	<0.001[e]
	arizonica	1979	15.8	12.0	0–41	112	

duced by *P. arizonica* females were parasitized (this difference is not significant; $\chi^2 = 3.21$, 1 df, Table 2). For females for whom complete reproductive histories were recorded (Table 3), significantly more egg-cases of *P. arizonica* than of *P. oweni* were parasitized. Similarly, for all females and for females with complete reproductive records, a higher proportion of *P. arizonica* females than *P. oweni* females lost at least one egg-case to parasites.

Because the average clutch size of *P. oweni* females is larger than that of *P. arizonica* females, the appropriate comparison of reproductive effort and reproductive success is lifetime egg and spiderling production of

individual females (Table 3). Mean lifetime egg production by *P. oweni* and *arizonica* females did not differ significantly, nor did mean lifetime production of live spiderlings (Mann Whitney U-test). However, 19% of *P. oweni* females (6 of 31) lost all of their eggs to parasites, while only 4% of the *P. arizonica* females (1 of 25) was similarly affected. While this difference is not significant ($\chi^2 = 2.9$, 1 df), it does suggest that *P. arizonica*'s habit of packaging lifetime egg production into many small clutches may reduce the risk of losing an entire lifetime of egg production to parasites.

A comparison can also be made between

Table 3.—Lifetime reproductive parameters for *Philoponella oweni* and *P. arizonica* for whom complete life histories are known (South Fork Canyon, 1979). [a] = Mann Whitney U-test; [b] = two-tailed t-test for samples with equal variance, $t = -1.73$; [c] $\chi^2 = 18.16$, 1 df; [d], $\chi^2 = 8.16$, 1 df; [e], Mann Whitney U-test.

		Mean	SD	Median	Range	n	P
Egg-cases per female	*oweni*	1.3	0.5	1.0	1–2	31 females	<0.001[a]
	arizonica	3.9	1.9	4.0	1–8	25	
Total eggs	*oweni*	66.3	21.4	68.0	30–100	31 females	0.09[b] (ns)
	arizonica	82.4	42.3	76.0	17–208	25	
Egg-cases parasitized	*oweni*	15.0%				40 egg-cases	0.00002[c]
	arizonica	54.0%				97	
Females with ≥ 1	*oweni*	16%				31 females	0.0043[d]
egg-case parasitized	*arizonica*	52%				25	
Total young	*oweni*	54.8	32.7	62.0	0–100	31 females	0.91[e] (ns)
	arizonica	58.0	36.2	55.0	0–159	25	

Figure 2.—*Arachnopteromalus dasys* on *Philoponella oweni* egg-cases.

the solitary and group-living members of each species. It was reported earlier (Smith 1982) that on average, communal females *P. oweni* produced more eggs per egg case than solitary females, though they did not differ in mean number of egg cases per female (1977: solitary females, 26.9 SD $\pm$ 13 eggs per egg case, $n = 13$ cases; communal females, 37.3 $\pm$ 15.1 eggs per egg case, $n = 38$ egg cases, $t = 2.17$, $P < 0.05$. 1979: solitary females 44.3 $\pm$ 15.3 eggs, $n = 26$ cases; communal females 56.1 $\pm$ 17.0 eggs, $n = 24$ cases, $t = 2.57$, $P < 0.05$).

In *P. arizonica,* no difference was observed in the number of eggs per egg case produced by solitary and communal females: solitary females, 21.5 $\pm$ 9.1 eggs per egg case, $n = 69$ cases; communal females, 22.2 $\pm$ 8.61 eggs, $n = 42$ cases. Because females in this species make a large number of egg cases, it is difficult to be sure all egg cases are noted and collected; thus estimating the mean number of egg cases per female is difficult. Given these caveats, there does not appear to be any significant difference in number of egg cases per female. For all females, the mean number of (observed) egg cases per female was 2.35 $\pm$ 1.9 for solitary females ($n = 40$ females), 2.6 $\pm$ 2.7 for communal females ($n = 25$ females; $t = 0.44$, $P < 0.66$, 63 df, two-tailed test, equal variances). For those females ob-

served with at least one egg case, the figures are 2.9 $\pm$ 1.6 egg cases per solitary female ($n = 32$ females), 3.61 $\pm$ 2.5 per communal female ($n = 18$ females; $t = 1.15$, $P < 0.26$, 48 df).

Colony structure: Both species occur in solitary webs and in aggregations. The aggregations of both species contain two or more adult females, each with her own prey capture orb. The aggregations formed by the two species differ in several respects.

Colonies of *P. oweni* attained larger size than those of *P. arizonica:* the largest *P. oweni* colony observed contained 44 adult females plus males and immatures. The mean number of females per web site at various locations were: Cave Creek Canyon 1977, 3.5♀ $\pm$ SD 8.6 (range 1–44, $n = 25$ web sites, 87♀); South Fork Canyon, 1979, 1.7♀ SD $\pm$ 2.0 (range 1–11, $n = 52$ web sites, 87♀); and Herb Martyr, 1979, 1.3♀ $\pm$ SD 0.6 (range 1– 4, $n = 40$ web sites, 53♀).

In *P. oweni* colonies, orbs of adults and immatures share support lines. The orbs are arranged side by side in loose sheets of orbs, and several orbs or sheets of orbs may be stacked one over the other. Retreat(s) are not specially constructed by colony members; they are simply protected areas near the web such as a cleft under a rock or log surrounded by old webbing. The retreat or retreats may be used in common by all colony members.

Aggregations of *P. arizonica* are smaller and simpler. The largest aggregation ever observed (in 1980) contained eight adult females. In 1979 the mean number of females/ web site in South Fork Canyon was: 1.7 $\pm$ SD 1.2 (range 1–6, $n = 45$ web sites, 76♀). Males and immatures may also be present in aggregations. The webs in an aggregation are side by side, joined by their space webbing. Retreats are usually absent.

Feeding rates: Females of *P. oweni* spent a greater proportion of time feeding during the census period. On average 41.7 $\pm$ SD 17.8% of *P. oweni* females and 26.5 $\pm$ SD 11.7% of *P. arizonica* females were feeding per census hour (29 h, 10–13 *P. oweni* females, 17–20 *P. arizonica* females, $P = 0.0009$, Mann Whitney U-test). These measurements can be broken down to compare the feeding rates of solitary and aggregated females. In *P. oweni* an average of 53.1 $\pm$ SD 22.9% of communal females were feeding per census hour (6–8 fe-

Table 4.—Web measurements for *Philoponella oweni* and *Philoponella arizonica*; $n = 22$ webs of adult female *Philoponella oweni*, 19 webs of adult female *P. arizonica*. (Significance determined by two-tailed *t*-test for samples with equal variance).

Parameter		Mean	SD	*P*
Longest diameter	*oweni*	27.8 cm	10.6	<0.001
	arizonica	12.4	3.8	
Number of radii	*oweni*	27.9	7.0	>0.05
	arizonica	29.2	9.0	
Number of spiral turns	*oweni*	25.6	10.5	<0.005
	arizonica	16.4	8.4	
Deviation from horizontal	*oweni*	51.9°	24.2	<0.001
	arizonica	6.8°	13.8	
Stabilimentum present	*oweni*	73%		
	arizonica	0%		

males). This is significantly more than the time spent feeding by any other class of females (29 h, $P = 0.001$ or less, Mann Whitney *U*-test). There was no significant difference among the other three classes ($P = 0.40$ or more, Mann Whitney *U*-test): solitary *P. oweni*, 22.9 ± SD 22.2% females feeding per hour, $n = 2$–5 females; aggregated *P. arizonica*, 28.7 ± SD 15.7% females feeding per hour, $n = 7$–10 females; solitary *P. arizonica*, 25.2 ± SD 15.4% feeding per hour, $n = 7$–11 females.

Web structure: Web measurements are presented in Table 4. Female *P. oweni* construct relatively large orbs which are closer to vertical than horizontal. There is a small quantity of space webbing below and around the orb, but there is seldom any above the orb. Stabilimenta are usually present. The web *P. arizonica* consists of a small horizontal orb surrounded above, below and around the edges with space webbing. The orb is sometimes drawn up in the center by threads attached to

the hub, giving it a slightly domed appearance. In many orbs the radials are not all in one plane, giving the orb a pleated appearance. None of these webs had stabilimenta.

Habitats: In August 1980 all populations of *P. oweni* sampled were found at an elevation of 1630 m or higher (1630–1950 m) while all populations of *P. arizonica* were below 1630 m (1460–1630 m). The *P. oweni* webs were usually built in protected locations such as hollow trees and clefts between rocks. The *P. arizonica* webs were built in more open areas, such as in brush, shrubs or grass (Table 5).

Egg-cases and immatures: The two species differ in the structure of their egg-cases. *Philoponella oweni* constructs large beige or cocoa-colored stellate egg-cases which are more-or-less flat on one side and domed on the other (Fig. 1). The mean length of the 24 egg cases measured was 6.7 mm (SD ± 0.96, range 5.2–5.8 mm); mean width was 4.4 mm (SD ± 0.61, range 2.9–5.4 mm). These cases are heavily decorated with small spikes of

Table 5.—Substrates used for web construction by *Philoponella oweni* and *Philoponella arizonica*: 1977, Cave Creek population; 1979, South Fork Canyon populations. [a] *Yucca schottii* absent from site.

			Rocks	*Yucca schottii*	Brush, shrubs	Herbs, grass	Base of trees	Along logs	Hollow trees	Total
1977	*oweni*	*n*	10	[a]	0	0	6	6	3	25
		%	40		0	0	24	24	12	100
1979	*oweni*	*n*	18	0	6	1	3	4	1	36
		%	50	0	17	3	8	11	3	100
1979	*arizonica*	*n*	3	15	6	6	1	0	0	31
		%	10	48	19	19	3	0	0	100

silk, especially on the curved side (spikes on flat side: median 5, range 0–22; spikes on curved side: median 13, range 5–24). *Philoponella arizonica* constructs pale smooth, whitish or bone colored egg-cases (Fig. 1). These cases are spindle-shaped, and there are usually no decorations or projections (of 33 egg-cases only eight were decorated with spikes, ranging in number from 7–12). Mean length of the 33 egg cases measured was 7.4 mm (SD ± 1.1, range 5.1–9.1 mm); mean width was 2.8 mm (SD ± 0.30, range 2.2–3.4 mm).

The immatures of the two species are also recognizably different. *P. oweni* immatures are black with white markings and *P. arizonica* immatures are yellow with brown markings.

DISCUSSION

Philoponella oweni and *P. arizonica* are found in close proximity in both time and space and occupy similar habitats. Although they are similar in appearance, they can easily be distinguished in the field by structure of the orb webs, nature of the communal groups (where they exist), the form of the egg cases and the coloration of second instar spiderlings. They also tend to use different substrates for web construction, with *P. oweni* making use of rigid substrates such as fallen logs, hollow trees, and niches under rocks, and *P. arizonica* making greater use of vegetation such as shrubs, grasses and yuccas as substrate.

An enhanced food supply (whether due to higher prey capture rate, reduced prey handling time, increased size of prey, or other factors) has often been proposed as a benefit of group-living behavior in spiders (e.g., Binford & Rypstra 1992, Buskirk 1975, 1981; Nentwig 1985; Rypstra 1979, 1990). This study showed an interesting difference in feeding rates of the solitary and communal females *P. oweni* and *P. arizonica*. As was reported earlier (Smith 1983), among *P. oweni* the proportion of females feeding per hour was greater for communal than for solitary females. Insect trapping at the sites of communal and solitary *P. oweni* webs indicated that insect abundance was greater at sites occupied by colonies than at sites occupied by single webs. This suggests that communal groups are feasible at sites where insect abundance is high enough to support several females.

Among *P. arizonica*, there was no difference in the feeding rates of solitary and communal females—both were similar to the feeding rates of solitary *P. oweni*. No insect trapping was done in the vicinity of *P. arizonica* colonies and solitary webs, so it is not possible to say if insect abundance differs between the sites of colonies and solitary webs.

The earlier report on communal behavior of *P. oweni* also showed that females in communal groups produced a greater number of eggs per egg case than did solitary females, though total live young per female was the same for the two groups due to higher rates of egg case parasitism in the communal groups (Smith 1982). One explanation for this difference could be the difference in feeding rates between solitary and communal females. We observed no significant difference between solitary and communal *P. arizonica* either in number of eggs per egg case or in egg cases per female, which dovetails with the feeding rates observed. However, as noted above, there are problems in collecting data on the number of egg cases per female in this species. Additional comparative study of the reproductive biology of communal and solitary *Philoponella* is warranted.

Over their lifetimes, females of the two species produce the same average number of eggs and the same number of live second instar spiderlings. However the two species differ in the way they package their eggs and care for the egg cases. *P. oweni* females package their eggs in one or a few large packets and make what appears to be a large expenditure in parental care, in the form of guarding the egg-case without feeding. The females of *P. arizonica*, on the other hand, package their eggs into many small packets and continue to feed in their orbs while the egg-cases are suspended in the web.

Both species are subject to the same egg parasite, *Arachnopteromalus dasys*. It is not clear if the different egg-case tending behaviors of *P. oweni* and *P. arizonica* have any effect against egg parasites such as *Arachnopteromalus dasys*. One might suppose that the behavior of *P. oweni* affords more protection than that of *P. arizonica*. However another uloborid spider, *Uloborus glomosus* (Walckenaer 1841), also makes several small-egg cases which it attaches to the web. In this species, the female has been observed to jerk the

web and make leg sweeping motions in response to parasitoid wasps (and spiderlings) crawling on the egg-cases (Cushing 1989; Cushing & Opell 1990), though it is not clear how effective this is in deterring parasites. I have observed *A. dasys* crawling on the egg-cases of both *P. oweni* and *P. arizonica* with no obvious reaction from the mothers of eggs.

It is possible to make some testable hypotheses concerning the adaptive significance (or lack of it) of the *Philoponella* egg-case tending behaviors. These hypotheses fall into four categories: those dealing with uncertainties faced by the female, those dealing with uncertainties faced by the young, those which consider differences in clutch size as side-effects of other maternal behaviors, and non-adaptive explanations.

Hypothesis 1: P. arizonica females face more uncertainties in food supply than *P. oweni* females. When they gather enough resources for a small batch of eggs they produce a clutch right away; if they were to wait for additional prey they might use up their small reserve of energy in maintenance activities. This can be tested by measuring the feeding rates of marked individuals over time. *P. arizonica* females would be expected to have a higher variance in feeding rate than *P. oweni* females.

Hypothesis 2: P. arizonica females are subject to a high and constant probability of mortality over their adult lives, while *P. oweni* females have relatively low probability dying before the first clutch is laid. It doesn't pay a *P. arizonica* female to save up resources for a large clutch if there is a good chance she will die before it can be laid. Life history data, particularly from the early part of the breeding season, are needed to test this hypothesis.

Hypothesis 3: Females of *P. oweni* must guard their egg-cases because predators and egg-parasites are more common in their environment than in that of *P. arizonica*. It would be more economical to produce a single large clutch than many small ones, since it takes as much time and energy to guard a small egg-case as a large one. This assumes that the type of maternal care shown by the bag species actually is more effective than that of the *P. arizonica* females in preventing parasitism or predation. This can be tested by removing females from egg-cases, leaving the egg-cases *in situ,* and comparing the rates of

parasitism on unguarded *P. arizonica* and *P. oweni* egg-cases to rates of parasitism on unmanipulated egg-cases.

Hypothesis 4: P. arizonica is subject to a risky, unpredictable environment. The *P. arizonica* pattern of reproduction ensures that at least some of a female's offspring may hatch at a time when conditions are favorable. One obvious possibility is that spiderlings require a supply of very small prey, and that the availability of these insects varies unpredictably over time. Little is known about the feeding behavior and survivorship of spiderlings. A first step would be to examine feeding behavior and prey of hatchlings, record variation in juvenile feeding rates over time, and correlate fluctuations in feeding rate with fluctuations in environmental factors such as rainfall.

Hypothesis 5: The differences in reproductive behaviors are not adaptations to any differences in ecology, behavior or microhabitat. Each species is conservative in behavior and displays the maternal behavior typical of its closest relatives. The first step in testing this hypothesis would be to construct a phylogeny for species in the *Philoponella semiplumosa* species group (Opell 1979, 1987), and examine the maternal behavior of the closest relatives of *P. oweni* and *P. arizonica* species.

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