Female reproductive variation in a nuptial-feeding spider, *Pisaura mirabilis**

Steven N. Austad** and **Randy Thornhill**
Department of Biology,
University of New Mexico,
Albuquerque,
New Mexico 87131, USA

Introduction

In recent years there has been a surge of interest in insect species in which males provide prey or other nutritional benefits to females as a necessary prelude to mating (e.g. Thornhill, 1976, 1979, 1981; Boggs & Gilbert, 1979; Gwynne, 1982). This behaviour is known as nuptial feeding. Nuptial-feeding species have proved to be fruitful research tools for understanding the detailed working of sexual selection, because they allow the partitioning of variation in male reproductive success into that component due to male-male competition and that due to female preference among males.

Only one spider species in the world, *Pisaura mirabilis* (Clerck), is known to exhibit nuptial feeding behaviour. Although the behaviour was first described nearly a century ago (Van Hasselt, 1889 — cited in Bristowe & Locket, 1926), until now there has been no detailed study of its reproductive significance. In this paper we provide data gathered during two seasons of field work and from various laboratory experiments on factors affecting female reproductive success in *P. mirabilis*. Our data suggest that nuptial feeding provides a direct reproductive benefit to females, and that the common assumption that nuptial feeding evolved as a device to reduce the probability of males being devoured during mating is probably erroneous.

Materials and Methods

Study site and census techniques

Our study site in 1984 was an irregularly-shaped 2000 square metre waste-lot near Wareham, England in the county of Dorset. Between 4 May and 28 July 1984 all adult *P. mirabilis* discovered within the study area were captured, measured (maximum cephalothorax width, total body length, and metatarsus length of either 1st leg), marked on the dorsal side of the abdomen with a unique colour pattern of hobby paint, and released at the site of first capture. A total of 189 females were marked in this period. During the same period, the study site was systematically and intensely surveyed daily (except in inclement weather during which spiders were not active). Every attempt was made to standardise the daily survey procedure. Resightings of any previously marked spiders were

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**Present address: Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Mass. 02138, USA.

recorded, as was the reproductive state (i.e. copulating or not, egg sac bearing or not, attending a nursery-web or not) of each sighted female.

After nursery-webs began to appear, the censuses of the study area were supplemented by censuses of the surrounding field as well. All nursery-webs, including those of unmarked females, were marked with plastic flags, and examined daily for presence of the female, presence and number of spiderlings outside the egg sac, and presence of parasites within the nursery-web. Nursery-webs are very conspicuous and we are confident that we discovered all webs in our study site and the surrounding field.

During 1985, in order to assess the role of female body size on reproductive success, we collected females with egg sacs and females guarding nursery-webs during the entire reproductive season. These females were measured as previously described and their progeny counted.

The effects of feeding rate

To examine the effects of feeding rate on timing and amount of reproduction, 20 penultimate instar females were captured and retained in the laboratory. These females were randomly assigned to 1 of 2 feeding regimes — 1 house-fly equivalent (all flies used were muscids of house-fly size although not necessarily *Musca domestica* L.) every day or 1 house-fly equivalent every 3 days. Five days after reaching maturity the females were mated with randomly chosen males, and the feeding regime continued. Date of egg sac deposition and number of eggs contained in each sac was recorded.

Results

Natural history and the phenology of female reproduction

Females were never observed to mate except with males bearing nuptial prey. However, females are not always receptive even to males with large prey. We saw both males and females copulating with more than a single mate during the course of the season. Females were still receptive as late as the day before egg deposition.

Adult females without eggs were seen over a 7-week period from early May until the beginning of July (Fig. 1). Beginning approximately one month after the first adult females were seen, females bearing egg sacs began to appear and they continued to be seen for about 2 months. Note that the number of newly observed females is distributed bimodally, suggesting that there are 2 emergence peaks about 3 weeks apart (Fig. 1). Approximately 15 days following each of these peaks, there is a peak in number of females seen with egg sacs. This period presumably corresponds to the modal interval between emergence and oviposition.

Like all pisaurids, female *P. mirabilis* carry their egg-sac in their chelicerae. In addition, females both in the laboratory and in the field build a silken retreat after egg-sac deposition and they remain within this retreat until nursery-web construction, except when

Timing of reproduction

Timing is often a critical factor influencing the likelihood of successful reproduction (e.g. Lack, 1966). In *P. mirabilis*, it is important in several senses. As previously mentioned (Fig. 1), late maturing female *P. mirabilis* are less successful at reproduction than are early maturers. If we divide our data on marked females into two halves, representing those which emerged during the first half of the 1984 season versus those emerging during the second half, we find that 17.5% of the early, but only 4.0% of the late, maturers survive gestation (chi-square = 7.7, $p < 0.03$).

Although clutch size is unaffected by the timing of reproduction, females which reproduce late are also more likely to suffer from predation of their eggs (Fig. 4). The parasitoid wasp, *Trychosis* sp. (Ichneumonidae), deposits its eggs in *Pisaura* egg sacs. After hatching, the larvae consume the eggs and/or spiderlings within the sac before pupating. Usually all the spiderlings are consumed before pupation, so that *Pisaura* females often build nursery-webs containing nothing but the wasp pupae. The incidence of parasitism increases throughout the reproductive season (Fig. 4), so that toward the end of the season as many as 42% of the egg sacs found in nursery-webs are parasitised. Thus, it is important for females to reproduce as early in the season as possible because both their own survival is increased and the probability of egg sac parasitism is decreased.

Feeding rate

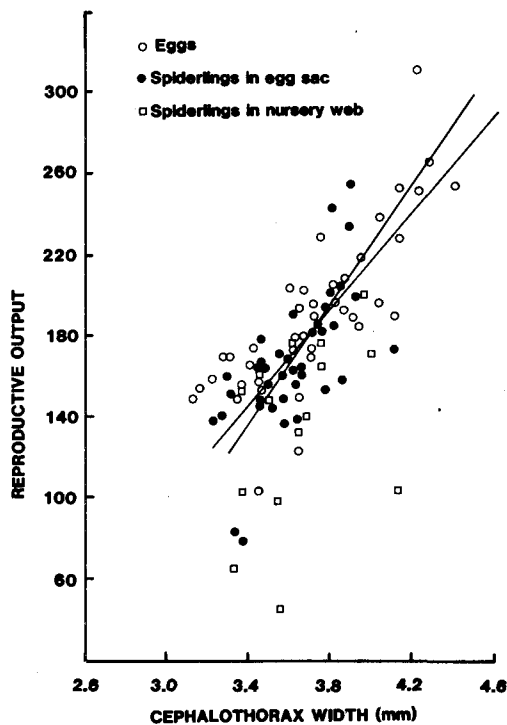The rate at which females acquire food has often been shown to affect fecundity in spiders (Kessler,

Stage	Mean cephalothorax width (mm)	Number of females
Eggs in egg sac	3.64 (±0.24)	44
Spiderlings in egg sac	3.71 (±0.30)	41
Nursery-web	3.62 (±0.25)	52

Table 1: Female body size at successive reproductive stages. Numbers in parentheses are standard deviations. There are no significant differences in body size between the stages (One-way ANOVA, $p > 0.4$).

1971; Wise, 1975, 1979; Van Wingerden, 1978). In our laboratory experiments, tripling female feeding rate nearly doubled fecundity (Table 2). The eggs in these two treatments also differed drastically in appearance. At the lower feeding rate, eggs were darker and obviously drier than at the higher rate. Note that even at the high feeding rate, mean fecundity (112 eggs) was significantly smaller (t-test, $p = 0.0001$) than the fecundity of field-captured females (170.4 eggs), suggesting that our laboratory feeding regime was inferior either in quantity, quality, or both to that of females in the field.

The difference in feeding regime also affected the interval between mating and egg-sac deposition (Table 2). The greater feeding rate reduced the mating-oviposition interval by more than five days.

In sum, an increased female feeding rate affects reproduction both by increasing fecundity and decreasing the interval until egg sac deposition.

Discussion

Our results indicate that there is a strong influence of female body size, time of maturation, and high feeding rate on female reproductive success in *P. mirabilis*. Adult body size and time of maturation has been shown to be a function of feeding rate during development in spiders (Turnbull, 1962, 1965; Miyashita, 1968), and is unaffected by adult behaviour.

However, adult female feeding rate can contribute to female reproductive success in two ways. First, fecundity is enhanced as feeding rate increases, as is the case in other spiders (Kessler, 1971; Wise, 1975, 1979; Van Wingerden, 1978; Austad & Kiklevich, ms). Second, reproduction is completed earlier with increased feeding rate. The potential advantage in completing reproduction early is that mortality is decreased for reasons which are not at the moment clear; although certainly, if predation is an important source of mortality and the probability of predation is constant or increasing as the reproductive season progresses, then individuals which reproduce as rapidly as possible will be at a selective advantage. Another advantage of rapid reproduction is a reduced probability of egg sac parasitism (Fig. 4).

How might these issues bear on the evolution of nuptial feeding in *P. mirabilis*? The received wisdom on this behaviour (e.g. Bristowe, 1958; Foelix, 1982) is that it evolved because it decreased the probability of males being eaten during mating. Our observations provide no support for this hypothesis. First of all,

Fig. 3: The effect of female body size on fecundity. Regressions are highly significant for both number of eggs (open circles) (r-square = 0.51, $p < 0.0001$) and number of spiderlings in egg sac (closed circles) (r-square = 0.60, p < 0.0001).

cannibalism is very rare among adult *P. mirabilis*. We have performed more than 70 experimental matings in the laboratory giving males nuptial prey of a wide variety of sizes. We have seen 3 instances of cannibalism; in one case a male killed the female, and in the other two the females killed the males. In two of these cases, the deaths occurred during a struggle for possession of the nuptial prey, suggesting that nuptial prey may actually cause a certain degree of cannibalism! We have also left many *P. mirabilis* male-female pairs together for several days after they mated without providing any prey for either of them, and in no single case have we seen cannibalism.

An alternative hypothesis is that nuptial prey evolved in the context of sexual selection, i.e. female preference for certain mates. Females *do* show mate preference in *P. mirabilis* in two ways. First, they do not mate with males which do not offer nuptial prey. Second, males with small nuptial prey are not allowed to mate for as long as males with large prey (Austad & Thornhill, unpublished data). Furthermore, because of the influence of feeding rate on female reproductive success, females presumably receive an important benefit from males every time they mate.

A possible scenario for the evolution of nuptial feeding might be as follows. Initially females only mated once, and were unreceptive after that. However, because of the reproductive benefits associated with high feeding rate, females which tried, and occasionally succeeded, in stealing prey from males in addition to their normal foraging would be at a reproductive advantage. Male *P. mirabilis*, on the other hand, would not often be overpowered by females (ignoring the swollen abdomens of females as a result of egg ripening, males of this species are at least as large as females in any linear dimension, and larger in some dimensions [Austad & Thornhill, unpublished data]), and the struggle for the prey might be energetically costly, time consuming, and risky for both. Therefore once a female succeeded in grasping the prey, it may have been selectively favoured for the sexes to share

Variable	Feeding rate (# House fly-equivalents/day)	
	1	⅓
Fecundity (# eggs)	112.0 (±26.8) *	64.9 (±22.1)
Mating-Oviposition interval (days)	13.5 (±1.4) **	18.6 (±4.0)

Table 2: Effect of feeding rate on female fecundity and the rapidity of reproduction. Numbers in parentheses are standard deviations. (* = $p < 0.01$; ** = $p < 0.001$ — Student's t-test).

possession of it rather than continue the struggle. At some point, a male sharing prey in this manner may have attempted to copulate while retaining his hold on the prey by attaching it to his spinnerets (as males invariably do today). The advantage to the female is obvious. She now gets more than half the value of the prey, because the male is no longer consuming it. For the male, if the number of eggs he fertilised as a result of his copulation exceeded the number he might expect to fertilise after sharing the prey but not copulating, then the behaviour would also be selectively favoured, hence evolution could proceed.

We put forward this scenario merely as a speculative hypothesis. However, it immediately raises the question "Why, if it is so beneficial for both sexes, has nuptial feeding behaviour not evolved in other spiders?" There are two answers to this question. The first is, "Perhaps it has." After all, the mating behaviour of very few of the world's spider species is known in any detail, and this behaviour may eventually be found in a diversity of species. The second answer is that our scenario requires the following conditions be met: (1) There must be a major advantage to females of increasing the feeding rate; (2) Males can somehow become involved in increasing the female feeding rate (such would not be true of most web-builders, in which the nonweb-building males do not capture prey except in female webs); (3) The spiders must exist at high enough densities so that females routinely encounter males with prey; (4) The sexes must be equal enough in body size and strength so that one does not quickly overpower the other; (5) The rate at which males encounter receptive females must be low enough so that the potential increase in male longevity associated with finishing their share of the prey would not result in more egg fertilisations than the male can get from mating with the female who is sharing his prey.

All in all, these are a complex set of conditions. However, the extent to which they might be met in other spider species is clearly open to empirical investigation.
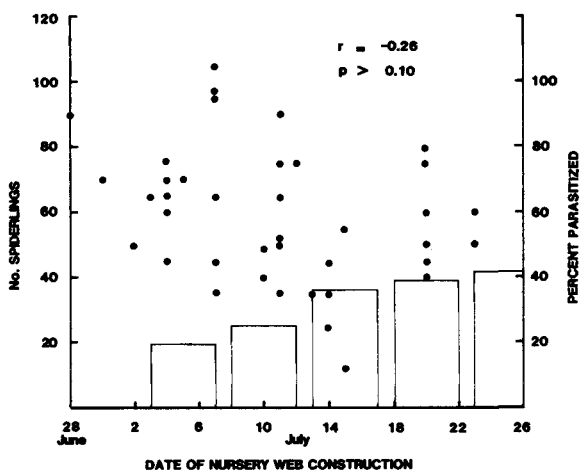
Acknowledgements

Fig. 4: Per cent nursery-webs with parasitised egg sacs as a function of time. Circles refer to numbers of spiderlings in egg sacs, and histograms to per cent egg sacs parasitised.

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Spiders from the Galápagos Islands. III. Miscellaneous families

L. L. Baert

Koninklijk Belgisch Instituut voor Natuurwetenschappen, Vautierstraat 29, B-1040 Brussel, Belgium

and

J.-P. Maelfait

Laboratorium voor Oecologie der Dieren, Zoögeografie en Natuurbehoud, K. L. Ledeganckstraat 35, B-9000 Gent, Belgium

Summary

Four new species are described from the Galápagos Islands: *Neozimiris santiago* sp.n. (Gnaphosidae), *Speocera jacquemarti* sp.n. and *Theotima galapagosensis* sp.n. (Ochyroceratidae) and *Theridion coldeniae* sp.n. (Theridiidae). The male of *Olios galapagoensis* Banks, 1902 (Eusparassidae) is described.

Introduction

This is the third paper concerning the results of our mission to the Galápagos Islands (February-May 1982) (Baert & Maelfait, 1983, 1984). Four new species are described, belonging to the Ochyroceratidae (2 species), Gnaphosidae (1 species) and Theridiidae (1 species). The male of *Olios galapagoensis* Banks, 1902 is described for the first time. All types are at the Institut royal des Sciences Naturelles de Belgique. All the material was collected by the authors, except where otherwise stated.

Family Gnaphosidae

Neozimiris santiago sp.n. (Figs. 1-2)

Material examined: ♂ holotype, Isla Santiago, transition zone, 260 m, 8 April 1982.

Description (Male holotype, ♀ unknown): Carapace and legs pale orange; abdomen dorsally yellowish, thickly mottled with grey, ventrally whitish and sparsely mottled with grey. Carapace longer than wide. Eye sizes and interdistances (mm): AME 0.07, ALE 0.08, PME 0.09, PLE 0.08, AME-PME 0.03, AME-ALE 0.01, PME-PME 0.02, PME-PLE 0.01, ALE-PLE 0.01. Median ocular quadrangle: length 0.27 mm, anterior width 0.17 mm, posterior width 0.19 mm. Palp with extremely long embolus, arising at base of tegulum; bulbus with prolateral strongly sclerotised small extension; strongly curved median apophysis; extremely sinuous palpal duct; excavated ventral side of cymbial tip with 7 lanceolate hairs; retrolateral tibial

they emerge to bask the sac in the sun. Females do not feed while carrying eggs.

About 25 days after the first peak of egg sac deposition there is a strongly defined peak of nursery-web construction (Fig. 1), which approximately corresponds to laboratory observations on the interval between egg sac deposition and egg hatching (mean = 21.6, range: 20-24, $n = 8$). Notice, moreover, that there is no second peak of nursery-web construction corresponding to the 2nd peak of egg sac appearance, suggesting that females from the 2nd emergence peak do not survive to the nursery-web stage as well as those from the first peak.

Females remain on the nursery-web for 4-7 days after it is built. During this time they resume feeding and have even been observed to mate. However, no female was ever found to survive long enough to reproduce twice, either in the field or in the laboratory. Thus *P. mirabilis* is semelparous in the strictest sense, i.e. it reproduces in a single episode.

Factors affecting female reproductive success

Only a small percentage of *P. mirabilis* females survive long enough to reproduce (Fig. 2). Fewer than one-fifth of our marked females were resighted carrying egg sacs, only 12% survived to build nursery-webs, and fewer than 8% actually succeeded in producing independent spiderlings. Three factors which have been implicated in affecting female reproductive success are female body size, the timing of reproduction, and female feeding rate. We consider these separately.

Female body size

Within a spider species, the number of eggs deposited is sometimes a positive function of female
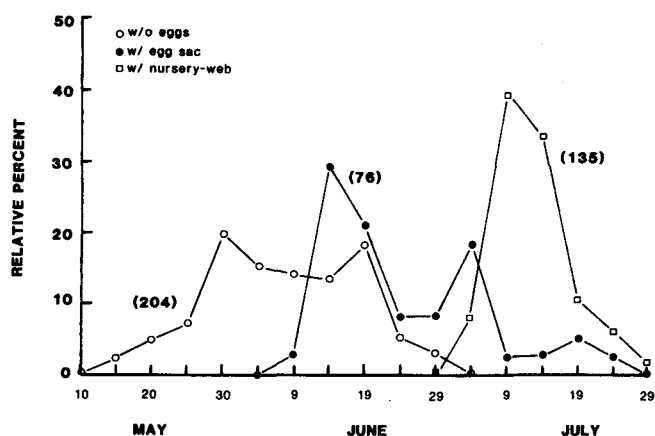

Fig. 1: Phenology of reproduction of *P. mirabilis* in southern England. Data represent the relative per cent of all adult females observed on the study site in 1984. Data were combined in 5-day periods, because inclement weather sometimes interrupted both spider activity and census taking for several consecutive days. Open circles = first sighting of mature females without egg sacs. Closed circles = first sighting of mature females bearing an egg sac. Open squares = first sighting of females on nursery webs. Numbers in parentheses represent sample sizes.
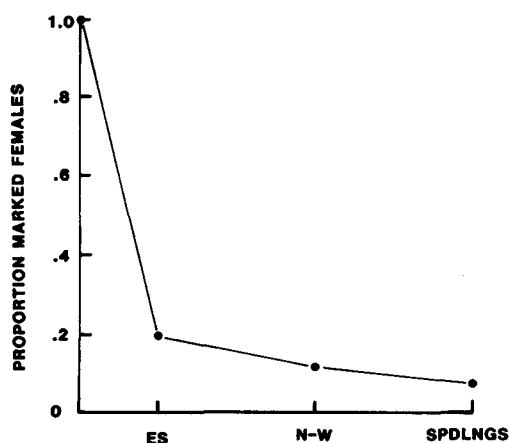

Fig. 2: Per cent of marked females surviving to various reproductive stages. ES = carrying eggsacs, N-W = with nursery-web, Spdlngs = produced independent spiderlings.

body size (Petersen, 1950). This is true for *P. mirabilis* (Fig. 3). The linear regression of both number of eggs and number of second instar spiderlings within the egg sac against female cephalothorax width is highly significant ($p < 0.0001$ in both cases) and explains more than 50% of the variance in female reproduction. However, this relationship deteriorates within 4 days after nursery-web construction (linear regression $r^2 = 0.16$, $p > 0.10$) for reasons which are unclear but which may reflect dispersal of some spiderlings from the nursery-web.

Because, as previously indicated, a major contributor to variation in female reproductive success is whether or not females survive gestation (We use "gestation" in its literal sense meaning "to carry". Therefore as applied to *P. mirabilis* the word pertains to the period from mating to when the egg sac is sealed in the nursery-web.), might female body size influence survival? Apparently so. In 1984, marked females which failed to survive gestation were significantly smaller than those which did survive (mean cephalothorax widths = 3.40 and 3.69 mm respectively; $t = 2.72$, $p < 0.01$).

To try to distinguish the phase at which selection had acted to favour larger females, in 1985 we collected and measured females at three reproductive stages: (1) bearing egg sacs containing only eggs, (2) bearing egg sacs containing second instar spiderlings, (3) guarding nursery-webs containing 2nd-instar spiderlings. Because these collections represented females which were increasingly close to the successful reproduction of independent young, we should have found a significant size difference between the stages at which selection was acting. However, there is no significant body size difference between any of the stages (Table 1), suggesting that selection has eliminated the smaller females during the period between maturation and oviposition.

Therefore, body size affects female reproductive success in two ways; larger females produce more eggs and spiderlings, and they are also more likely to survive long enough to produce independent young.