

Female feeding regime and polyandry in the nuptially feeding nursery web spider, *Pisaura mirabilis*

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Abstract We examined the influence of female feeding regime on polyandry in the nuptially feeding nursery web spider (*Pisaura mirabilis*). In this species, the nuptial gift, a dead prey item wrapped in the male's silk, is physically separate from the ejaculate. We manipulated female feeding regime (starved or fed) and the presence or absence of a gift with three successive males to test direct-benefits hypotheses (nuptial gift or sperm supply) for the expression of polyandry. The presence of a gift was necessary for copulation, as no male without a gift successfully copulated. Female mating behavior most strongly supports polyandry due to the accumulation of gifted food items ("nuptial gift" direct-benefits hypothesis). Starved females that were presented with a gift accepted significantly more gifts and inseminations than fed females. Most starved females (74%) copulated two or more times, as opposed to only 3% of the fed females. Nearly all of the females that accepted a gift subsequently copulated. The nuptial gift item seems to function as male mating effort and females appear to receive multiple matings as part of a feeding strategy.

Keywords Polyandry · Nuptial feeding · Nursery web spider · *Pisaura mirabilis* · Mating effort

Introduction

Multiple mating by females is common in many animals (Ridley 1988; Birkhead and Møller 1998; Arnqvist and Nilsson 2000; Jennions and Petrie 2000; Simmons 2001a, 2005). Factors that drive polyandry are expected to reflect effects of material or genetic benefits on female fitness (Jennions and Petrie 2000; Shuster and Wade 2003). By mating with multiple males, females may accrue direct benefits, such as nuptial gift items (e.g., dead prey), replenishment of sperm supply, and/or ejaculate-derived nutrients (Vahed 1998, 2007; Arnqvist and Nilsson 2000). Genetic benefits include increasing the diversity of the female's offspring, "trading up" in mate quality, selecting for "sexy sperm" that are heritably superior in sperm competition, and avoiding genetic incompatibility between the female and any one mate (Keller and Reeve 1995; Eberhard 1996; Zeh and Zeh 1996, 1997; Jennions and Petrie 2000; Lorch and Chao 2003; Simmons 2001b, 2005; Bilde et al. 2007a).

The value of direct benefits (e.g., nutrients, sperm) may depend on a female's state, such as satiation level or sperm supply, at the time of mating. Given that empirical work (e.g., Thornhill 1984; Steele 1986a, b; Johnson et al. 1999; Takakura 2004; Edvardsson 2007) and theory (Boggs 1990; Newman and Elgar 1991) indicate that a female's acceptance of a mate can be driven by economic considerations, one can ask whether a female's nutritional status can drive polyandrous behavior. For example, if females mate multiply to gain nutrition via male donations, then food-limited females should accept more nuptial gifts and multiple matings than

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satiated females (Boggs 1990; Gwynne 1990; Simmons and Gwynne 1991; Gwynne 2008).

In this study, we examine the expression of polyandry among females of differing nutritional status. Our study species is the nuptially feeding nursery web spider (*Pisaura mirabilis*). This species is remarkable among spiders in that the male routinely offers a nuptial gift to the female (Bristowe 1958; Austad and Thornhill 1986). A male's mating behavior involves wrapping a prey item in silk, carrying it with his chelicerae, and displaying it to the female (Stålhandske 2001a). The female may accept the gift and insemination occurs while the female eats. In nature, individuals of both sexes have been observed copulating with multiple mates (Austad and Thornhill 1986). Given that a *P. mirabilis* female is more likely to accept a nuptial gift and to copulate when food-deprived (Bilde et al. 2007b), we ask whether female hunger can drive the expression of multiple gift acceptance and mating.

The present study has two goals. First, we test direct-benefit hypotheses for polyandry in the nursery web spider. We experimentally vary female feeding regime and expose females to successive males that offer or lack gift items. In the nursery web spider, the presence or absence of the gift item can be readily manipulated while controlling for the presence of sperm and ejaculate substances, which facilitates the testing of direct-benefit hypotheses (Engqvist 2007; Vahed 1998, 2007; Gwynne 2008). According to the “nuptial gift” hypothesis, females will mate multiply to accumulate gifted food items, so hungry females should accept more gifts than better-fed females. If gift acceptance necessarily entails copulation, then hungry females should copulate with more males as well. Thus, we also evaluate whether gift acceptance necessarily results in copulation. On the other hand, the “sperm supply” hypothesis posits that females will mate multiply to ensure sufficient insemination, so female mating rates should be equal across nutritional status. Second, we examine whether the offering of a gift item is a necessary precursor to copulation in this species, as previous studies appear to be in conflict over this question. Some studies indicate that insemination does not take place unless a gift is presented (Austad and Thornhill 1986; Prokop 2006), while Stålhandske (2001a) found that 50% of males without a gift were able to copulate.

Materials and methods

Collection and female treatments

Juvenile and subadult spiders were collected in April–May 2006 from various grasslands and small woods near Trnava, Slovakia (N 48°37', E 17°58'). Each spider was individually

kept in a ventilated 0.3-l glass jar in a room maintained at 20°C and exposed to natural photoperiod. Spiders were fed house flies (*Musca domestica*) and medflies (*Ceratitis capitata*) ad libitum three times per week (c. five to ten flies per feeding). Spiders were misted with water once per day.

In total, 109 females and 103 males molted into adulthood during May 2006. All males were fed ad libitum throughout the experiment. Each female was fed ad libitum until day 4 after the final molt. On day 4 post-molt, the female was randomly assigned to four treatments: Fed×No Gift (F×NG, $n=10$), Starved×No Gift (S×NG, $n=15$), Fed×Gift (F×G, $n=34$) and Starved×Gift (S×G, $n=42$). Treatments with no gifts (NG) were assigned lower sample sizes because previous work indicated low mating success for males without nuptial prey items (Prokop 2006). Females of the “Fed” treatments were maintained on the ad libitum feeding regime. Females of the “Starved” treatments received two houseflies on days 5–6 post-molt, and then remained unfed over the following 10 days. This starvation period was designed to generate the effects of food deprivation, as used by other authors (e.g., Drengsgaard and Toft 1999). “No gift” and “Gift” treatments refer to whether each female was offered a dead prey item by each of her prospective mates during three consecutive mating trials on days 14–16 post-molt. Females in the “No gift” treatments were faced with males that were not provided with dead prey items during any of the three consecutive trials. Females in the “Gift” treatments were faced with males that were each provided with one dead prey item during each of the three consecutive trials. Females of all treatments were not offered any other food during days 14–16 post-molt.

Mating trials

Each female was exposed to a different male on days 14–16 post-molt (i.e., one mating trial per day, three trials per female). The trials were conducted between 23 May and 3 June, 2006. For each female's first trial, a virgin, sexually inexperienced male was randomly assigned to her. Before the first trial, the female and male were anesthetized with CO₂ and body mass (to 0.001 g), maximum prosoma width (to 0.01 mm), and right foreleg length (tibia-patella, to 0.01 mm) were measured. For the second and third trials, previously used, experienced males were randomly assigned to the females. Each experienced male was used only once per day, with a minimum interval of 2 days before reuse in another trial.

Each mating trial was conducted in a glass terrarium (30×20×20 cm). Starting time for each trial was c. 0730. The female was placed inside the terrarium and was allowed 30 min to habituate and to construct drag lines. The male was then introduced, at least 10 cm from the

female. All males showed courtship behavior after 1–5 min, which included touching the females' drag lines, trembling of the palps and abdomen, jerking of the body, and rapid rubbing of the legs (Lang 1996). Once a male exhibited courtship behavior, we placed one dead housefly (*Musca domestica*) near him if his female was assigned to the "Gift" treatment. Dead houseflies were of standardized size (random sample of house flies: mean±SE body mass=11.9±0.2 mg, $n=15$). These flies were of comparable mass to those used in other studies on *P. mirabilis* (e.g., range=2.3–29.1 mg in Stålhandske 2001a, mean=15.5 mg in Stålhandske 2002), as well as gift items reported in nature (Nitzsche 1988, Stålhandske 2001a, b). Upon the addition of the dead prey item, the male typically immediately seized and wrapped it. For "No gift" trials, we simulated the motion of placing a dead housefly near the male, but did not leave a prey item.

Each trial was observed by the same experimenter (PP). The following behaviors were recorded to the nearest 1 min, from the time of the male's introduction: female acceptance of wrapped gift, start of copulation, copulation duration, and attacks between the male and female. The male and female were allowed to interact for 120 min after the male's introduction. During a given day, up to ten mating trials were conducted simultaneously. We randomly assigned order of treatments and females within a given day. To visually isolate male–female pairs, we attached white paper to the external sides of each terrarium.

After each trial, the male and female were returned to their housing jars. Males were continued on ad libitum feeding. Females were not offered food after each trial. On day 17 post-molt (i.e., after the three mating trials), each female was fed one medfly daily for the next 6 weeks. All spider adults were released near their sites of capture by early August 2006. For analysis, all statistical tests are two-tailed and calculated with Statistica (Version 6, StatSoft 2001, Tulsa, OK, USA, <http://www.statsoft.com>). Means are presented with standard errors (SE).

Results

Adult spider biometry

Adult female body condition on the day of the first mating trial (day 14 post-molt) significantly differed among treatments (Table 1). Body condition was assessed through ANCOVA (Garcia-Berthou 2001), with body mass as dependent variable, treatment as categorical factor ($F_{3,96}=74.30$, $p<0.001$) and prosoma width as covariate ($F_{1,96}=64.78$, $p<0.001$). Pairwise comparisons reveal that the Fed treatments significantly differed from the Starved treatments (Tukey tests, group-wise $\alpha=0.05$; Table 1). With

Table 1 Female body measurements on the day of the first mating trial (mean±SE)

Treatment	Number	Prosoma width (mm)	Body mass (g)
F×G (Fed, Gift)	34	3.46±0.04	0.1582±0.0057 a
F×NG (Fed, No Gift)	10	3.58±0.09	0.1428±0.0157 a
S×G (Starved, Gift)	42	3.53±0.03	0.0949±0.0023 b
S×NG (Starved, No Gift)	15	3.35±0.07	0.0864±0.0042 b

Different letters indicate significant differences in body mass while controlling for the effect of prosoma width (ANCOVA followed by Tukey multiple comparisons, group-wise $\alpha=0.05$)

regard to males, body condition did not differ among treatments (ANCOVA, $F_{3,96}=0.36$, $p=0.78$).

Mating behavior, female feeding regime, and nuptial gifts

Female mating behavior differed markedly among treatments (Table 2). Females in treatments in which no gift was presented (F×NG and S×NG) did not copulate with any of the three consecutive males. Most starved females presented with a gift copulated at least once (37/42=88% of S×G females), with 31 (74%) copulating two or more times (Table 2). Half of the fed females presented with a gift copulated at least once (17/34=50% of F×G females), with only one (3%) copulating two or more times (Table 2). Number of copulations was significantly higher for starved females presented with a gift (S×G females; Kruskal–Wallis, chi-square approximation, $H=58.55$, $df=3$, $p<0.001$; Table 2).

Further analysis of copulatory behavior is restricted to females presented with a gift, as only these females copulated (i.e., S×G and F×G females). For these two

Table 2 Copulations by feeding treatment

	<i>n</i>	Number of females with				Number of copulations per female (mean±SE)
		0 cop.	1 cop.	2 cop.	3 cop.	
S×G (Starved, Gift)	42	5	6	16	15	2.0±0.2 a
F×G (Fed, Gift)	34	17	16	1	0	0.5±0.1 b
S×NG (Starved, No Gift)	15	15	0	0	0	0.0±0.0 b
F×NG (Fed, No Gift)	10	10	0	0	0	0.0±0.0 b

For number of copulations per female, treatments with different letters significantly differ (Kruskal–Wallis test followed by Dunn multiple comparisons, group-wise $\alpha=0.05$). In all cases, copulation entails consumption of gift item and insemination
n refers to number of females per treatment

treatments, 54 females copulated at least once, for a total of 101 copulations. In the vast majority of copulations (92% = 93/101), the female took the gift item from the male and insemination began soon afterwards. In the remaining eight copulations, some fighting between the female and male occurred wherein the male typically resisted the female's first grab at the gift, but the female eventually took the gift and copulated with the male. All of these brief fights occurred with starved females (S×G) (Starved vs. Fed trials with gifts: 8/42 vs. 0/34, Fisher exact test, $p=0.007$).

Of the females presented with a gift (S×G and F×G females), only rarely did a female accept the gift without copulating with the male. Gift acceptance without copulation occurred in three trials with starved females (S×G). Thus, of the 104 trials in which a gift was accepted, copulation occurred in 101 of them (101/104=97%).

During the first mating trial, the starved females were more likely to copulate (86% = 36 of 42 females, S×G) than were the fed females (21% = 7 of 34 females, F×G; Fisher exact test, $p=0.0001$). In the first mating trial, the starved females tended to have shorter latencies to copulate (mean ± SE = 6.9 ± 1.5 min., $n=36$; S×G) than fed females (mean ± SE = 11.9 ± 3.4 min., $n=7$; F×G), but this difference was not statistically significant (Mann–Whitney, $U=175$, $p>0.10$). During the first trial, copulation duration was longer for starved females (mean ± SE = 43.8 ± 3.6 min., $n=36$; S×G) than for fed females (mean ± SE = 27.7 ± 8.1 min., $n=7$; F×G; Mann–Whitney, $U=186$, $p=0.05$). In the first trial, 58% (21/36) of the starved females finished eating before copulation terminated; 29% (2/7) of the fed females finished eating before copulation terminated (Fisher exact test, $p=0.22$). All of these females consumed the entire gift.

The effect of multiple copulations on latency to copulate and copulation duration was examined in multiply-mated females of the S×G treatment (16 females copulated two times, 15 females copulated three times). Figure 1 shows average latencies and copulation durations for all first, second, and third copulations in this treatment. Within-female paired tests examine changes in behavior with respect to number of copulations. Separate paired tests compare copulation 1 vs. copulation 2, then copulation 2 vs. copulation 3, then copulation 1 vs. copulation 3 ($\alpha=0.05/3$ for both latency to copulate and copulation duration). This approach is adopted because females that copulate exactly once or twice become removed from a test that spans all three trials. For latency to copulate, no significant difference was detected ($\alpha=0.05/3$) between copulation 1 and 2 (paired t test, $t_{30}=-2.09$, $p=0.05$), copulation 2 and 3 (paired t test, $t_{14}=1.46$, $p=0.17$), or copulation 1 and 3 (Paired t test, $t_{14}=-0.094$, $p=0.36$). For copulation duration, no significant difference was detected ($\alpha=0.05/3$) between copulation 1 and 2 (Wilcoxon paired test, smallest $T=137.5$, $n=31$, $p=0.03$), copulation 2

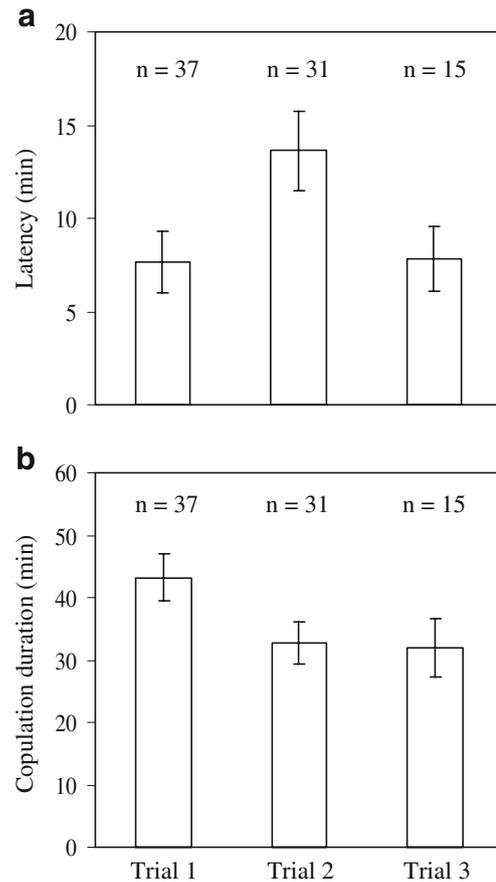


Fig. 1 Copulatory behavior over all three mating trials for starved females presented with gifts (S×G treatment). For each trial, overall mean ± SE is shown for those females that copulated. **a** Latency to copulate (minutes). **b** Copulation duration (minutes)

and 3 (Wilcoxon paired test, smallest $T=47.5$, $n=15$, $p=0.48$), or copulation 1 and 3 (Wilcoxon paired test, smallest $T=53.0$, $n=15$, $p=0.69$).

Sexual conflict: fights and intersexual cannibalism

Conflict over the receipt of the nuptial gift was observed both before and after insemination occurred. In three trials with starved females (S×G), the female took the gift from the male and consumed it without copulating with him. Across all treatments, insemination was terminated before the female had completely consumed the gift in 63 of the 101 total copulations. In these 63 cases, the female and male typically grappled with the first pair of legs while each attempted to gain hold of the gift with the chelicerae. In 45 trials (71%), the female successfully retained control of the gift and consumed the remainder. In the other 18 trials, the male seized the gift and crawled away with the remainder. In the 38 remaining trials with copulation, the female completely consumed the gift before the termination of insemination.

Starved females (S×G treatment) were particularly successful in post-insemination fights over gifts. To control for the effect of fighting experience, we analyzed fights that occurred during each female's first mating trial. For starved females, 21 fights occurred after insemination. The females won 17 of these 21 fights (binomial test, $p=0.007$), despite being similar in size to males (mean±SE tibia–patella length, males, 6.38 ± 0.15 mm, females, 6.18 ± 0.10 mm; mean±SE difference between male and female tibia–patella length, 0.21 ± 0.18 mm; paired t test, $t=-1.14$, $df=20$, $p=0.27$). Fed females (F×G treatment) were not considered in this analysis, because only three fights occurred during the first mating trial.

Intersexual cannibalism was observed in one trial (F×NG treatment), wherein a male killed a female. In this trial, both adults were virgins, as it was the female's first mating trial. The male repeatedly attempted to copulate with the female, but he had no prey item to offer. The female stayed motionless, with her legs withdrawn. At 18 min after his introduction to the female, the male grabbed the female's prosoma with his chelicerae and wrapped her in silk. Once wrapping was complete, he crawled around the terrarium, carrying the wrapped female and performing the jerky body motions typical of courtship behavior.

Discussion

This study supports the notion that females mate multiply to accumulate direct benefits in the form of nuptial gift items. Poorly-fed (Starved) females accepted more nuptial gifts and more inseminations than better-fed females. These results are consistent with the “nuptial gift” direct-benefit hypothesis for polyandry, where females mate multiply to accumulate gifted food items (Vahed 1998; Arnqvist and Nilsson 2000; Gwynne 2008). From the female's perspective, gift acceptance typically lead to copulation, as nearly all (97%) gift acceptances resulted in copulation.

With regard to the nuptial gift as mating effort, the offering of a nuptial gift was a necessary precursor to copulation in the present study, as no male without a gift successfully copulated. This result agrees with earlier studies (Austad and Thornhill 1986; Prokop 2006). Stålhandske (2001a) reports near complete copulation success for males with gifts, yet 50% of males without gifts were still able to copulate. The causes of the differences between these studies are unclear, but they may lie in differences in feeding ecology and female preferences between spider populations. At minimum, differences in life cycle have been documented for Danish and Slovakian populations of nursery web spiders. In Denmark, populations are biennial (i.e., spiders overwinter twice before maturation; Stålhandske 2001b), whereas Slovakian populations are

annual (i.e., spiders overwinter once before maturation; Buchar et al. 1989). These differences in developmental schedules reflect environmental and ecological factors, one of which is likely prey availability. Prey availability would be expected to affect the importance of nuptial gift items to the female and therefore may contribute to behavioral differences between the populations.

Alternative hypotheses regarding polyandry in the nursery web spider are not strongly supported by the present study. First, an alternative “nuptial gift” direct-benefit hypothesis posits that females mate multiply to receive nutrition via ejaculate substances (Ivy et al. 1999; Edvardsson 2007). If this were the case, then starved females that encountered males without prey gift items (S×NG) should have mated so as to receive ejaculate-derived substances. No female mated with a giftless male, however. Second, the “sperm supply” direct-benefit hypothesis predicts that females would show similar numbers of matings across treatments so as to ensure insemination. Number of matings, however, differed markedly according to female feeding regime. We acknowledge that data on fertilization success (e.g., % eggs fertilized) and offspring quality (e.g., adult offspring reproductive success) would be necessary to provide more direct tests of the “sperm supply” hypothesis, as well as tests of indirect or “genetic” benefits hypotheses (Tregenza and Wedell 1998; Simmons 2001b, 2005; Fedorka and Mousseau 2002; Engqvist 2007).

The present study supports the “foraging” hypothesis for the maintenance of the nuptial gift in the nursery web spider (Bilde et al. 2007b). Bilde et al. (2007b) found that food-deprived virgin and singly mated females were more likely to accept a gift and copulate than were their food-satiated counterparts. By showing an effect of feeding regime on the female's response towards the gift, Bilde et al. (2007b) concluded that the offering of the gift item exploits the female's foraging motivation, rather than the female's maternal care instinct to accept an eggsac-like item. The present study indicates that foraging considerations can lead to polyandry among hungry females, but only if the males provide gift items. Giftless males appear to have very low mating success, certainly in our study population. The factors surrounding the expression of polyandry in this species, as well as possible behavioral differences between populations, deserve further study in this species.

Intersexual conflict

Sexual conflict is evident in this species, both overtly in the form of intersexual fights and indirectly with respect to female remating frequency. With regard to physical contests, females grabbed and consumed the gift without copulating in a few trials and intersexual cannibalism occurred (Drengsgaard and Toft 1999; Stålhandske 2001a;

Bilde et al. 2007b). More conflict was observed near the end of copulation. When insemination ended before the female has finished eating the gift, the male and female grappled over control of the gift, with the female retaining control in the majority of these contests. Such fights have been reported not only in *P. mirabilis* (Drengsgaard and Toft 1999; Stålhandske 2001a) but also in hangingflies where males forcibly remove prey items at the termination of copulation if they are not completely consumed (Thornhill 1976). These contests over gift ownership suggest that the gift item has nutritional value.

The post-insemination fights over the gifts imply that the gifts represent male mating effort rather than parental effort. The males' attempts to recover the gifts, rather than allowing the females to completely consume them and thereby possibly contributing to offspring production, indicate that the males are interested in consuming the gifts or using them for future matings. Other lines of evidence point to the gifts as male mating effort in this species. In this and other studies (Austad and Thornhill 1986; Prokop 2006), the gift appears to be necessary to achieve insemination, although we note the mating success of giftless males in Stålhandske (2001a). Larger gifts result in longer copulation durations and presumably higher fertilization rates (Drengsgaard and Toft 1999; Stålhandske 2001a; Bruun et al. 2004), while female consumption of the gift and gift size fail to affect female fecundity and spiderling size in Stålhandske (2001a). Furthermore, the possibility of remating by females, observed in nature (Austad and Thornhill 1986) and evidenced in captivity (Drengsgaard and Toft 1999; Bilde et al. 2007b; this study), casts doubt on the paternity of gift-giving males. While first-mating males may achieve ~70% paternity of an eggsac when the female mates with two males ($P_1 \approx 70\%$ in *P. mirabilis*, Drengsgaard and Toft 1999), late-mating males, such as fourth-mating males, also have substantial fertilization success which reduces the first-mating males' paternity advantage.

Sexual conflict is also suggested through an examination of female remating behavior (Arnqvist and Nilsson 2000; Arnqvist and Rowe 2005; Gwynne 2008). No clear refractory period emerges from the present study. Only one well-fed female mated multiply over the 3-day mating period (F×G treatment), whereas most starved females (74%, S×G treatment) mated multiply. Two explanations are possible. First, mating might be costly to the female in the nursery web spider, in terms of risks of predation, injury, or disease transmission (Daly 1978; Arnqvist 1989; Rowe 1994; Hurst et al. 1995; Chapman et al. 2003; Schneider and Lubin 1998; Thrall et al. 2000; Ahtiainen et al. 2005). Starved females, however, may be willing to repeatedly incur these costs in order to receive multiple gifts and inseminations. Second, males may induce a refractory period in females, possibly through chemicals

in the ejaculate and/or silk (Simmons 2001a; Arnqvist and Rowe 2005; Vahed 2007). Yet, starved or food-limited females may be able to overcome or shorten this refractory period (Gwynne 1990; Simmons and Gwynne 1991; Gwynne 2008). A possible male-induced refractory period, along with female physiological responses, warrants further investigation in this species.

In the nursery web spider, females appear to demand the "payment" of a gift item before copulation and the coupling of matings and nuptial gifts may be part of a larger foraging strategy (Thornhill and Alcock 1983; Shuster and Wade 2003). In the nursery web spider, it is possible that food-limited females signal to attract males for the receipt of gift items. Mechanisms of mate attraction are poorly understood for the nursery web spider, although Drengsgaard and Toft (1999) suggest the use of contact pheromones in the female's silk. If females lure in males as a means of getting food, then males would be expected to assess a female's mated state before offering a prey item. This would be especially true if the prey item is difficult to capture or large. We did not observe indications of male rejection of mated females in the present study. We note, however, that the prey items (house flies) were of standardized size, and may have been perceived as "readily available" by the males (i.e., house flies were offered three times per week to the males). Alternative male tactics in response to polyandry include adding silk to prey items, thereby increasing the female's feeding time and copulation duration, as well as feeding on the prey item by the male before offering it to the female (Lang 1996; Bilde et al. 2007b; Vahed 2007). Such considerations of male and female reproductive interests will help illuminate the fitness consequences of gift giving and polyandry.

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