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Fitness effects of nuptial gifts in the spider *Pisaura mirabilis*: examination under an alternative feeding regime

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Abstract. Nuptial feeding has variable effects on fitness within a species, partly driven by variation in female diet. We investigate nuptial feeding in the spider *Pisaura mirabilis* (Clerck, 1757) under a feeding regime that has not been explored: starvation after mating and gift consumption. We vary gift size and gift number to examine the effects on mating behavior and components of female fitness. With regard to gift size, copulation duration increased with larger gift size, but no component of female fitness was affected (time to oviposition, egg sac mass, female lifespan). These results corroborate other examinations of gift size in *P. mirabilis*. Given a likely male benefit (prolonged copulation) for larger gift size and no demonstrated female benefit, sexual conflict stands as a likely explanation for male benefits due to large nuptial gift size. With regard to gift number, components of female fitness were not affected by the consumption of one or two extra gifts. This agrees with other studies, although we note that some experiments have found the consumption of extra gifts to increase female fitness. As for males, they were more likely to copulate when they had gifts, as in other studies. We conclude some support for sexual congruence with regard to gift number, as males and females stand to benefit simultaneously from the mere presence of the gift, and females might benefit from the consumption of multiple gifts. Thus, both sexual conflict and sexual congruence appear to be at work regarding the evolution of nuptial gifts in *Pisaura mirabilis*.

Keywords: Congruence hypothesis, nuptial feeding, sexual conflict

Nuptial feeding, a male's provision of nourishment to his mate, occurs in many arthropods (Thornhill & Alcock 1983; Zeh & Smith 1985; Parker & Simmons 1989; Simmons & Parker 1989; Boggs 1995; Vahed 1998, 2007), as well as some vertebrates (Tryjanowski & Hromada 2005; Mougeot et al. 2006). This nourishment (nuptial gift) has been observed in various forms, including food items captured by the male, glandular secretions by the male, edible spermatophores, and even the male's body parts (reviewed in Gwynne 1997; Vahed 1998, 2007). Two classes of hypothesis have been proposed for the evolution of nuptial feeding: sexual congruence and sexual conflict. Sexual congruence posits that nuptial feeding offers some combination of direct and indirect benefits to the male and female (Gwynne 2008; Ortíz-Jiménez & Castillo 2015). In contrast, sexual conflict posits that nuptial feeding manipulates the behavior of one sex (typically the female), thereby providing fitness benefits to the manipulator sex (typically the male) and little to none to the manipulated sex (Sakaluk 2000; Arnqvist and Rowe 2005; Vahed 2007). Thus, to distinguish between these hypotheses, one must determine how nuptial feeding affects male and female fitness.

Research over the past few decades points to male mating benefits via nuptial feeding, as well as potential male paternal investment (Gwynne 1997; Vahed 1998, 2007). Nuptial feeding shows variable effects on female fitness (Boggs 1995; Vahed 2007; Lewis & South 2012). While many studies have demonstrated nuptial feeding to increase components of female fitness, including the number and size of eggs (e.g., Gwynne 1984, 1988; Simmons 1990; Simmons et al. 1993; Wedell 1996; Wiklund et al. 1998; Voigt et al. 2005; Engqvist 2007; Immonen et al. 2009; DiRienzo & Marshall 2013), numerous studies have failed to detect such increases in female fitness (e.g., Wedell & Arak 1989; Heller & Reinhold 1994; Will & Sakaluk 1994; Vahed & Gilbert 1997; Perry & Rowe

2008;). Such differences in results between studies present challenges when attempting to distinguish between competing hypotheses on nuptial feeding.

Differences between studies on nuptial feeding's effect on female fitness may be attributable to interspecific differences in nuptial gift composition and female metabolic and feeding rates (Boggs 1995; Vahed 1998; Jarrige et al. 2015). To evaluate a hypothesis regarding the evolution of nuptial gifts, then, it may be more appropriate to remove interspecific differences by restricting one's examination to processes within a species. Within a species, however, the effect of nuptial feeding has been found to be variable, with nuptial gifts increasing fitness components for food-limited, but not well-fed, females (e.g., Steele 1986; Boucher & Huignard 1987; Butlin et al. 1987; Fox 1993; Immonen et al. 2009). Because an arthropod's metabolism and utilization of nutrients are influenced by its feeding regime (Slansky & Scriber 1985; Slansky & Rodriguez 1987; Mayntz & Tøft 2006; Tøft et al. 2010), assessing the effects of nuptial feeding on fitness for a given species should include a broad array of feeding regimes for the females.

The spider *Pisaura mirabilis* (Clerck, 1757) stands as a model system in which to test the robustness of emerging patterns regarding nuptial feeding and fitness, as a solid body of literature on nuptial feeding exists for this species (reviewed in Nitzsche 2011; Ghislandi et al. 2014), and the number and size of nuptial gifts can be easily manipulated. In *P. mirabilis*, the male typically wraps a prey item in silk, carries it with the chelicerae, and presents it to the female (Bristowe 1958; Austad & Thornhill 1986; Nitzsche 1988). The female may accept the nuptial gift item, and insemination occurs while the female eats. Nuptial gifts have been found to consistently benefit the male by increasing the likelihood of mating (Stålhandske 2001; Albo et al. 2011b; summarized in Table

1), with larger gifts prolonging mating duration (Stålhandske 2001; Bruun et al. 2004; summarized in Table 1a). Whether sexual congruence or conflict is more applicable to nuptial feeding in *P. mirabilis*, then, depends on how female fitness is affected.

Empirical results on the effects of nuptial gifts on female fitness are mixed in *P. mirabilis*. Several fitness components have been examined, including time to oviposition, egg number, and egg hatching success (Stålhandske 2001; Albo et al. 2011b, 2013; Tuni et al. 2013; Tøft & Albo 2015; summarized in Table 1). While an individual male does not present multiple gifts to the female during a mating encounter, females may encounter successive males in nature (Austad & Thornhill 1986), and therefore may accrue successive gifts. In some studies (Albo et al. 2011b, 2013), the experimental provision of one extra gift item to the female increased one component of fitness (i.e., egg hatching success), but not other components such as egg number (Table 1b). Stålhandske (2001) found the provision of one extra gift did not increase several measures of female fitness (i.e., time to oviposition, number of eggs in first egg sac, total fecundity). Tøft & Albo (2015) found that increasing the daily number of gifts over a period of exposure to males decreased time to oviposition and increased egg number. In other studies, some effects of gift number were revealed under relatively restricted feeding regimes. In Tuni et al. (2013), females that consumed two extra gifts had higher egg hatching success when maintained on one meal per week (Table 1b). This effect of two extra gifts was not seen in females that were maintained on two meals per week. Comparing results across studies reveals a similar effect. For females that were maintained on three prey items per week, one extra gift increased copulation duration (Albo et al. 2011b), while one extra gift failed to affect copulation duration in females that were maintained on a more food-abundant regime of seven prey items per week (Stålhandske 2001). We further note that examinations of the effect of gift size on fitness components have been conducted on females maintained on six or seven prey per week, with no effect on female fitness being detected (Stålhandske 2001; Bruun et al. 2004; Table 1a). As indicated for gift number, we ask whether effects of gift size on female fitness might be revealed under a more restricted feeding regime.

Given these indications that a more restricted feeding regime can unmask fitness effects of nuptial gifts in *P. mirabilis*, we examine nuptial feeding under a regime that involves starvation after copulation and gift consumption. We examine this feeding regime for several reasons. First, the starvation period focuses on the effect of the male-donated gift *per se*, removing the possible confounding influence of background feeding after the consumption of the gift, as noted by Tøft & Albo (2015). The goal of the starvation period is to standardize recent feeding to first oviposition (Maxwell 2000; Barry et al. 2008), with the nuptial gift serving as the female's last feeding opportunity before oviposition. Second, a regime that includes severe food limitation adds to the ecological scope of nuptial feeding studies in *P. mirabilis*. At some point after mating, food limitation appears to be common and rather extreme, as females do not feed while carrying egg sacs in nature (Austad & Thornhill 1986; P. Prokop, personal observations), although we acknowledge

that it is not clear as to how long after mating starvation begins. Third, this regime tests the robustness of previous examinations of nuptial feeding on fitness, all of which allowed for continued feeding after copulation and gift consumption (Table 1). Exploration of an alternative feeding regime will help to test the robustness of emergent patterns in the literature on this species.

The present study examines the effects of varying gift size and gift number on components of male and female fitness that have been examined in *P. mirabilis*, such as copulation duration, time to oviposition, egg sac mass, and female lifespan. Our examination under a rather extreme feeding regime (i.e., starvation after copulation) contributes towards a more comprehensive assessment of the effects of nuptial feeding in this species. A demonstration of consistent benefits to males and females would support the sexual congruence hypothesis for the evolution of nuptial feeding. Consistent male benefits and a lack of female benefits would support the sexual conflict hypothesis. In addition to examining these alternate hypotheses, this study's approach adds to the growing recognition of the importance of study replication (Kelly 2006; Jasny et al. 2011; Makel et al. 2012; Dal-Ré et al. 2016), through which the robustness of conclusions drawn from empirical studies can be evaluated.

METHODS

General methods: spider collection, maintenance, and mating trials.—For both experiments, we captured over 170 juvenile and subadult spiders from mixed woodlands near Trnava, Slovakia in April–May 2009 (Experiment 1, gift size) and April 2011 (Experiment 2, gift number). In both years, we isolated the spiders in ventilated 0.3-L glass jars, maintained at 20°C, provided with wet cotton, protected from direct sunlight and checked daily for adult emergence. We fed the spiders cricket nymphs (*Gryllus assimilis*) three times per week (c. five crickets per feeding), and misted them with water once per day. These crickets were also used as nuptial prey items in both experiments. For Experiment 1, 87 females and 85 males molted into adulthood in May 2009; for Experiment 2, 85 females and 182 males molted into adulthood in May 2011. We fed adult males cricket nymphs *ad libitum* throughout both experiments. For adult females, we fed each female *ad libitum* for the first 4–11 days after adult emergence.

We followed the following common protocol for mating trials in both experiments. Adult males and females were virgin and sexually inexperienced. Males were 10–15 days as adults at the mating trial. Females were 12–13 days (Experiment 1) or 6–9 days (Experiment 2) as adults at their first mating trial. Two days prior to each female's first mating trial, the female was starved to encourage mating behavior, as starved or food-limited *P. mirabilis* females are more likely to mate than satiated females (Bilde et al. 2007; Prokop & Maxwell 2009). Before the trial, we anesthetized the male and female with CO₂ and measured them for body mass (to 0.0001 g) and prosoma width (to 0.01 mm). We quantified body condition as the residual values of a linear regression of body mass on prosoma width (Jakob et al. 1996; Prokop & Maxwell 2012). We conducted each mating trial in a glass terrarium (30×20×20 cm), observed by the same experimenter (PP). We placed the female inside the terrarium and allowed her 30 min

Table 1a.—Review of effects of nuptial gift size on components of fitness in *Pisaura mirabilis*. “Positive” and “Negative” refer to the effect of increasing gift size on the variable in question. “No”: no effect detected. “—”: effect not measured. In column headers, “cop” = “copulation.”

Adult ♀ feeding regime			Treatments	Occurrence of cop	Cop duration	Time to oviposition	Egg number	Egg sac mass	Egg hatching success	Total fecundity	Female lifespan	Reference
Before cop	After cop											
1 cricket/day	1 cricket/day	No, Small, Medium, or Large gift (range = 2.3 – 29.1 mg/gift)	No	Positive	No	No	—	—	No	—	Stålhandske (2001)	
6 flies /week	6 flies /week	Small or Large gift (range = 5 – 47 mg/gift)	—	Positive	—	—	—	—	—	—	Bruun et al. (2004)	
<i>Ad libitum</i> crickets	Starved	Small gift (30 mg/gift) Large gift (100 mg/gift)	No	Positive	No	—	No	—	—	No	This study	

to habituate and to produce drag lines while walking. This procedure is important to elicit male courtship (Lang 1996; Stålhandske 2001). We then placed the male c. 10 cm in front of 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 gift item (freshly killed cricket nymph, *G. assimilis*) near him in Experiment 1 and for “Gift” (G) trials in Experiment 2. Upon the addition of the gift item, the male typically seized it immediately.

We recorded the following behaviors to the nearest 1 min, from the time of the male’s introduction: male’s wrapping of the gift with silk (binary measure – whether silk wrapping occurred), female’s acceptance of the gift, occurrence of copulation (binary measure – whether at least one pedipalp insertion occurred), and beginning and ending of a given pedipalp insertion. We defined copulation as the insertion of the male’s pedipalps into the female’s reproductive opening (Foelix 1996). We defined copulation duration as the total amount of time spent by the male in pedipalp insertions (Stålhandske 2001; Albo et al. 2011b; Tuni et al. 2013), as

Table 1b.—Review of effects of number of nuptial gifts on components of fitness in *Pisaura mirabilis*. “Positive” and “Negative” refer to the effect of an increase in number of gifts on the variable in question. “No”: no effect detected. “—”: effect not measured. In column headers, “cop” = “copulation.”

Adult ♀ feeding regime			Treatments	Occurrence of cop	Cop duration	Time to oviposition	Egg number	Egg sac mass	Egg hatching success	Total fecundity	Female lifespan	Reference
Before cop	After cop											
1 cricket/day	1 cricket/day	0 or 1 gift (range = 2.3 – 29.1 mg)	Positive	No	No	No	—	—	No	—	Stålhandske (2001)	
3 flies/week	3 flies/week	0 or 1 gift (low to high quality)	Positive	Positive	—	No	—	Positive	—	—	Albo et al. (2011b)	
3 flies/ week	1 fly/day	0 or 1 gift	—	—	—	—	—	Positive	—	—	Albo et al. (2013)	
2 feedings/ week	2 feedings/ week	1 or 3 gifts	—	Positive	Negative	No	—	No	No	No	Tuni et al. (2013)	
1 feeding/ week	1 feeding/ week	1 or 3 gifts	—	Positive	Negative	No	—	Positive	No	No	Tuni et al. (2013)	
2 flies/ week	see Treatments	1 prey /day; 2 prey /day ¹	— ²	—	Negative	Positive	—	Negative	—	—	Toft and Albo (2015)	
<i>Ad libitum</i> crickets	Starved	0, 1, or 2 gifts (10 mg/ gift)	Positive	No	No	—	No	—	—	No	This study	

¹ In Toft & Albo (2015) Experiment 1, females were fed two flies per week until exposure to males. Then, females were exposed to males daily until egg sac construction. During the period of exposure to males, females were provided with one prey item per day (nuptial gift = fly), or two prey items per day (nuptial gift plus one extra fly).

² Females that received one prey per day showed higher number of copulations than females that received two prey per day. This is a different measure of “Occurrence of copulation” than in the other studies, which examined whether copulation occurred or not.

males may perform multiple insertions during an encounter with a female. We allowed the male and female to interact for 120 min after the male's introduction, after which time we returned them to their housing jars. We fed the males *ad libitum* until the conclusion of the trials in late May 2009 or 2011, after which we released them at their sites of capture.

For Experiment 1, we conducted mating trials between 7–22 May 2009; for Experiment 2, mating trials were between 26 April–4 May 2011. During a given day, we conducted up to ten separate trials simultaneously. Mating trials began during 0800–0900. To visually isolate male–female pairs, we attached white paper to the external sides of each terrarium. We randomly assigned the order of treatments within a day. After a female's mating trial(s), we returned her to her housing jar to lay egg sacs (egg sacs weighed to nearest 0.0001 g). We daily sprayed the females with water, but did not offer them food until oviposition.

Experiment 1: effect of gift size.—At each mating trial, we paired the virgin female with a virgin male who was randomly assigned to one of two gift treatments: large gift (male given a cricket nymph of 0.10 g; $n = 40$ trials) or small gift (male given a cricket nymph of 0.03 g; $n = 35$ trials). Neither male nor female body measurements (body mass, prosoma width, body condition) significantly differed between treatment groups (t -tests: all $t_{73} < 1.95$, all $P > 0.05$).

Experiment 2: effect of gift number.—To vary the number of gifts offered to a female, we paired each female with two virgin males in succession. Female polyandry in nature is indicated for *P. mirabilis* by Austad & Thornhill (1986), and previous experimental studies have presented successive males to females (Drengsgaard & Tøft 1999; Prokop & Maxwell 2009; Tuni & Bilde 2010; Tuni et al. 2013; Tøft & Albo 2015). For a given trial, we randomly provided the male with a cricket nymph as a gift item (Gift, G; gift size = 0.01 g) or no gift item (No gift, N). We randomly assigned each female to one of four treatment groups: Gift-Gift (GG, $n = 22$), Gift-No gift (GN, $n = 21$), No gift-Gift (NG, $n = 19$), and No gift-No gift (NN, $n = 21$). Thus, each female was presented with either zero, one, or two gifts, while the number of encountered males was held constant. In total, we used 166 males in the trials (i.e., 2 males per female, 83 females), with each male being virgin, sexually inexperienced, and used once. All females were virgin at their first trial. In trials where the female received a gift, we standardized gift consumption by the female by returning the gift item to the female in cases where the male escaped with it before it was eaten by the female. After the first trial, the female remained in the mating terrarium. The second trial began with the introduction of a new male c. 60 minutes after the end of the first trial.

Female body measurements (body mass, prosoma width, body condition) did not significantly differ among the four treatment groups (ANOVA tests: all $F_{3,79} < 1.00$, all $P > 0.4$). Male body measurements did not differ among treatment groups (ANOVA main effects, treatment: all $F_{3,158} < 1.95$, all $P > 0.1$). Overall, males used in the second trial were heavier than those in the first trial (mean \pm SE, body mass (g): trial 1 = 0.099 ± 0.002 , trial 2 = 0.104 ± 0.002 ; ANOVA main effect, trial: $F_{1,158} = 5.53$, $P < 0.05$), as well as wider (mean \pm SE, prosoma width (mm): trial 1 = 3.73 ± 0.04 , trial 2 = 3.86 ± 0.04 ; ANOVA main effect, trial: $F_{1,158} = 6.53$, $P < 0.05$).

Males did not differ in body condition between trials (ANOVA main effect, trial: $F_{1,158} = 0.05$, $P = 0.83$).

Statistical analyses.—We analysed the effects of gift size (Experiment 1) and gift number (Experiment 2) on various mating behaviors and components of female fitness. For continuous dependent variables (time to copulate, copulation duration, time to first oviposition, egg sac mass, female lifespan), analysis was through parametric tests. For dichotomous dependent variables (occurrence of copulation, occurrence of egg laying), analysis was through logistic regression. Statistical tests were performed with Statistica (Version 8, StatSoft 2007, Tulsa, OK, USA, online at <http://www.statsoft.com>). We assessed normality via Shapiro-Wilks test. For time to copulate, we achieved normality via Box-Cox ($x+0.1$) transformation. All tests are two-tailed.

RESULTS

Experiment 1: effect of gift size.—Upon being presented with a prey gift item, 74 of 75 males seized it. Of the males that took the small gift, 54% wrapped it (19 of 35 males); 49% of males that took the large gift wrapped it (19 of 39 males). Gift size did not significantly affect whether a male wrapped the gift item (Logistic regression: Wald's $\chi^2 = 0.34$, $P = 0.56$). For the 74 trials in which the male seized the gift item, 56 trials resulted in gift consumption and successful copulation, and 15 trials did not result in copulation (8 trials without copulation in the large gift treatment, 7 trials without copulation in the small gift treatment). Three trials resulted in the female's cannibalism of the male during copulation. Because sperm transfer was likely interrupted in these three trials, they were excluded from further analysis.

With regard to the occurrence of copulation in the 71 trials for analysis, neither gift size nor the wrapping of the gift with silk showed a significant effect (Logistic regression, main effects: Wald's $\chi^2 = 0.16$ and 0.60 , $P = 0.90$ and 0.44 , respectively). For 56 trials with copulation, duration was longer for males with large gifts, and for males who wrapped their gifts in silk (Figure 1; ANOVA: whole-model test $F_{3,52} = 4.09$, $P < 0.05$, gift size $P < 0.01$, gift wrapping $P < 0.05$, interaction $P = 0.1$). Time to copulate was not significantly affected by gift size or gift wrapping (ANOVA: whole-model test $F_{3,52} = 0.04$, $P = 0.99$).

With regard to female fitness, 42 of the 56 females that copulated produced one egg sac; no female produced two or more egg sacs. For the occurrence of oviposition, neither gift size nor the wrapping of the gift with silk showed a significant effect (Logistic regression, main effects: Wald's $\chi^2 = 1.99$ and 0.92 , $P = 0.16$ and 0.40 , respectively). We found no significant effect of gift size or gift wrapping on the time to first oviposition (ANOVA: whole-model test $F_{3,38} = 0.48$, $P = 0.69$; Table 2). We found no significant effect of gift size or gift wrapping on the mass of the first egg sac (ANOVA: whole-model test $F_{3,38} = 1.92$, $P = 0.14$; Table 2). Female lifespan was not affected by gift size, gift wrapping, or egg sac mass (multiple linear regression: adj. $R^2 = 0.05$, $F_{3,52} = 1.87$, $P = 0.17$; Table 2); this result remains when females that did not produce an egg sac are removed from analysis (multiple linear regression: adj. $R^2 = 0.01$, $F_{3,38} = 1.10$, $P = 0.34$).

Experiment 2: effect of gift number.—All males presented with a prey gift item seized it. In the first mating trials, 40 of

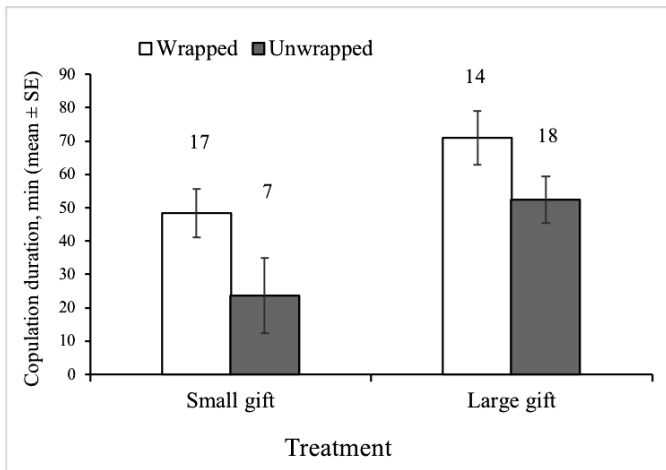


Figure 1.—Experiment 1 (gift size): copulation duration for small and large gift items, when the male wraps the gift (white bars) or does not wrap the gift (dark bars). Numbers above bars are sample sizes.

the 43 males wrapped the gift with silk (i.e., trial 1 of GG and GN treatments); in the second mating trials, 38 of the 41 males wrapped the gift (i.e., trial 2 of GG and NG treatments). Exclusion of the six males that did not wrap the gifts did not affect the statistical significance of the following results. Looking at only the first mating trial, where both the male and female were sexually naive, all of the males with gift items successfully copulated (43/43 = 100%; trial 1 of GG and GN treatments), whereas only 28% of the males without gifts copulated (11/40 = 28%; trial 1 of NG and NN treatments; Table 3; Fisher exact: $P < 0.001$).

Overall, 68 of the 83 females copulated at least once (Table 3). Each copulation involved the consumption of the gift item by the female. The number of copulations differed among the treatment groups (Table 3). Average number of copulations was highest for females that were presented with two successive males bearing gifts (GG treatment; ANOVA: whole model test $F_{3,79} = 58.17$, $P < 0.001$). These results were statistically equivalent when males that did not wrap the gifts were excluded from analysis (ANOVA: whole model test $F_{3,79} = 32.73$, $P < 0.001$). Females in trials with males without gifts often did not assume the typical mating position (i.e., elevated opistosoma), but rather remained with their opistosoma close to the ground, thereby blocking the males' insertions of the pedipalps into the epigyne.

Overall mean time to copulate was 13 min (SE = 1 min, $n = 99$ trials with copulation). Gift number did not affect time to copulate. For females presented with two gifts (GG treatment), time to copulate did not differ between trial 1 (first gift presented; mean \pm SE = 15 \pm 2 min, $n = 22$ trials) and trial 2 (second gift presented; mean \pm SE = 16 \pm 2 min, $n = 22$ trials; paired t-test: $t_{21} = 0.4$, $P = 0.75$). Across treatments, females presented with one gift (trial 1 in GN; mean \pm SE = 12 \pm 2 min, $n = 21$ females), one gift after previous exposure to a male (trial 2 in NG, mean \pm SE = 10 \pm 2 min, $n = 19$ females), or two successive gifts (trial 2 in GG) did not differ in time to copulate (ANOVA: whole model test $F_{2,59} = 2.29$, $P = 0.15$). Similarly, gift number did not affect copulation duration. Overall mean copulation duration was 46 min (SE = 3 min, $n = 99$ trials with copulation). For females presented with two gifts

Table 2.—Experiment 1 (gift size): female reproductive output and lifespan (mean \pm SE).

Treatment	Time to oviposition (days)	Egg sac mass (g)	Lifespan (days)
Large gift ($n = 26$)	29.1 \pm 1.3	0.0390 \pm 0.0055	84.7 \pm 2.8
Small gift ($n = 16$)	29.8 \pm 1.8	0.0402 \pm 0.0070	78.3 \pm 4.1

(GG treatment), copulation duration did not differ between trial 1 (first gift presented; mean \pm SE = 46 \pm 6 min, $n = 22$ trials) and trial 2 (second gift presented; mean \pm SE = 55 \pm 6 min, $n = 22$ trials; paired t-test: $t_{21} = 1.26$, $P = 0.27$). Across treatments, females presented with one gift (trial 1 in GN; mean \pm SE = 55 \pm 6 min, $n = 21$ females), one gift after previous exposure to a male (trial 2 in NG; mean \pm SE = 55 \pm 6 min, $n = 19$ females), or two successive gifts (trial 2 in GG) did not differ in copulation duration (ANOVA: whole model test $F_{2,59} = 0.002$, $P = 0.98$).

Four females cannibalized males during trial 1 or 2 (two females in GG, two females in NN). To focus on the effect of gift consumption on female fitness, these females were removed from further analysis. Over all treatments, twenty females produced an egg sac (Table 4); no female produced two or more egg sacs. The number of gifts consumed did not affect the occurrence of egg laying (Logistic regression: Wald's $\chi^2 = 3.02$, $P = 0.27$). For the 20 females that layed eggs, the number of gifts consumed did not affect the time to oviposition (linear regression: $R^2 = 0.004$, $F_{1,18} = 0.08$, $P = 0.74$), or the mass of the egg sac (linear regression: $R^2 = 0.01$, $F_{1,18} = 0.23$, $P = 0.66$). Female lifespan was not affected by the number of gifts consumed or the occurrence of egg laying (multiple linear regression: $R^2 = 0.015$, $F_{2,80} = 0.62$, $P = 0.57$). To examine whether the mass of the egg sac affected female lifespan, we removed females that did not produce an egg sac from analysis, and included egg sac mass as an independent variable. An overall significant effect resulted, but neither independent variable emerged as a significant effect on female lifespan (multiple linear regression: $R^2 = 0.32$, $F_{2,17} = 3.95$, $P < 0.05$; number of gifts $P = 0.07$; egg sac mass $P = 0.06$).

Table 3.—Experiment 2 (number of gifts): copulations per female. Females were presented with two consecutive males that were bearing a gift (G) or without a gift (N). GG = Gift-Gift; GN = Gift-No gift; NG = No gift-Gift; and NN = No gift-No gift. Thus, each female was presented either zero, one, or two gifts, while number of encountered males was held constant. Treatments with different letters differ significantly (ANOVA followed by Tukey HSD post-hoc test; $p < 0.05$).

Treatment	# females	# females that copulated			# copulations/female (mean \pm SE)
		Trial 1 only	Trial 2 only	Trial 1 & 2	
GG	22	0	0	22	2.00 \pm 0.00 a
GN	21	21	0	0	1.00 \pm 0.00 b
NG	19	0	12	7	1.37 \pm 0.11 c
NN	21	2	2	2	0.38 \pm 0.15 d

Table 4.—Experiment 2 (number of gifts): female reproductive output and lifespan (mean \pm SE). Females were presented with two consecutive males that were bearing a gift (G) or without a gift (N). Abbreviations as in Figure 3.

Treatment	Time to oviposition (days)	<i>n</i>	Egg sac mass (g)	<i>n</i>	Lifespan (days)	<i>n</i>
GG	9.7 \pm 3.4	3	0.0144 \pm 0.0125	3	50.8 \pm 2.1	22
GN	8.2 \pm 2.7	5	0.0328 \pm 0.0097	5	52.4 \pm 2.1	21
NG	14.3 \pm 2.1	8	0.0171 \pm 0.0076	8	48.6 \pm 2.2	19
NN	11.3 \pm 3.0	4	0.0086 \pm 0.0108	4	52.6 \pm 2.1	21

DISCUSSION

Evaluation of alternate hypotheses for the evolution of nuptial feeding—sexual congruence and sexual conflict—requires an assessment of how male and female fitness are affected within a species. The present study contributes towards such an evaluation for the spider *Pisaura mirabilis*, as it corroborates several emergent patterns from the literature on male and female fitness (summarized in Table 1). Given the range of feeding regimes for the females in the various studies on *P. mirabilis*, finding consistent results across studies points to robust conclusions for this species.

With regard to gift size, copulation duration increased with larger gifts (Experiment 1), pointing to a likely male fitness benefit. This result agrees with previous examinations of gift size in *P. mirabilis* (Stålhandske 2001; Bruun et al. 2004), where copulation duration was found to increase with gift size. Longer copulation duration is associated with higher fertilization success in this species (Stålhandske 2001). When a female mates with two males, a male's fertilization success increases as his copulation duration increases relative to his rival's (Drengsgaard & Tøft 1999). Gift size failed to affect other mating behaviors, such as the occurrence of copulation and time to copulation. With regard to female fitness, gift size showed no effect on the occurrence of oviposition, time to oviposition, egg sac mass, or female lifespan in the present study. These results corroborate Stålhandske (2001), who similarly failed to find an effect of gift size on time to oviposition and measures of egg output. The lack of an effect of gift size on female fitness appears to be a robust result, as females were constantly fed before and after mating in Stålhandske (2001), in contrast to the post-mating starvation in the present study.

At present, empirical studies suggest that larger gift size benefits the male by prolonging copulation, but shows no effect on female fitness. This conclusion points to sexual conflict as the more likely explanation for male benefits due to large nuptial gift size. We note that a full evaluation of this hypothesis includes costs to the male when acquiring larger gifts. Such costs are not known, but larger gifts might involve heavier transportation costs, as Prokop and Maxwell (2012) have demonstrated reduced running speed for males when carrying gifts.

Gift number showed variable effects in the present study. The number of copulations per female increased with gift number (Experiment 2), as all females exposed to two gift-bearing males copulated twice, females exposed to one gift-bearing male copulated once on average, and most females exposed to no gift-bearing males did not copulate at all. Furthermore, for the first trial of this experiment, when both

the male and female were sexually inexperienced, males with gifts were significantly more likely to mate than males without gifts. This result is consistent with other studies that indicate that the presence of a gift is an important determinant of mating success in *P. mirabilis* (Austad & Thornhill 1986; Stålhandske 2001; Prokop 2006; Prokop & Maxwell 2009; Nitzsche 2011; Albo et al. 2011b, 2013). Thus, possessing a gift increases a male's chance of mating. Recent work points to another male benefit of gift possession: reduced risk of cannibalism. In Tøft & Albo (2016), males with gifts were less likely to be cannibalized by the females than were males without gifts.

The present study did not find effects on female fitness for gift number. Gift number failed to affect the occurrence of oviposition, time to oviposition, egg sac mass or female lifespan. These results agree with some studies that have examined these fitness components in *P. mirabilis*, thereby allowing some conclusions to be drawn (summarized in Table 1b). In Stålhandske (2001), the provision of one extra gift did not affect time to oviposition, the number of eggs in first egg sac, or total fecundity. In Albo et al. (2011b), the provision of one extra gift did not affect clutch size or the number of spiderlings per egg sac. In Tuni et al. (2013), the provision of two extra gifts did not affect egg number or female lifespan, but the two extra gifts decreased time to oviposition. From these studies, gift number consistently fails to affect total fecundity and female lifespan (Stålhandske 2001; Tuni et al. 2013; this study).

For other measures of female fitness, the effects of gift number are complicated (Table 1b). For egg number and egg sac mass, the literature approaches a consensus in that most studies do not find an effect of gift number on either measure (Stålhandske 2001; Albo et al. 2011b; Tuni et al. 2013; this study). An exception is Tøft & Albo (2015), in which females were placed on two feeding regimes in one of the study's experiments. Females were supplied with either one or two prey items per day, and encountered a male daily. Females supplied with two prey per day laid more eggs than females supplied with one prey per day. In other studies, an effect on female fitness may emerge after a certain number of gifts have been consumed. For example, time to oviposition does not appear to be affected when one extra gift item is consumed (Stålhandske 2001). Time to oviposition can decrease when two or more extra gifts are consumed (Tuni et al. 2013; Tøft & Albo 2015), although we caution that we failed to find such an effect in the present study, where females consumed one or two extra gifts. Still other fitness measures remain difficult to evaluate. These include egg hatching success, where various studies report positive (Albo et al. 2011b, 2013), negative (Tøft

& Albo 2015), or no effect (Tuni et al. 2013) of the number of nuptial gifts.

The varied effects of gift number on components of female fitness point to sexual congruence as the more likely explanation of benefits derived from one or more gift. In the simplest case, a male with a gift is more likely to mate, and less likely to be cannibalized, than a male without a gift (Austad & Thornhill 1986; Stålhandske 2001; Prokop 2006; Prokop & Maxwell 2009; Nitzsche 2011; Albo et al. 2011b, 2013; Tøft & Albo 2016; this study; Table 1b). A female undoubtedly derives nutrients from a single gift, but significant fitness effects might not be seen until she consumes multiple gift items, as suggested by some results for time to oviposition (Stålhandske 2001; Tuni et al. 2013; Tøft & Albo 2015; but see this study; Table 1b). We caution that these benefits to males and females need to be weighed against the possible costs and constraints involved. For males, gift construction requires time spent foraging, expenditure in silk, and probable transportation costs (Albo et al. 2011a; Nitzsche 2011; Prokop & Maxwell 2012; Ghislandi et al. 2014). For females, the reproductive benefits of consuming multiple gifts might plateau or decrease after a certain number, as suggested by Tøft & Albo (2015).

An unexpected result in the present study was the lower incidence of gift wrapping by males in Experiment 1 (51% of males that took the gift) than by males in Experiment 2 (93% of males that took the gift). A likely explanation lies in the sizes of the gifts in the two experiments. The gifts in Experiment 2 were smaller (0.01 g) than those in Experiment 1 (0.03 and 0.10 g). Males given the small gifts in Experiment 2 may have wrapped the gifts to increase their size or volume (Ghislandi et al. 2014; Prokop & Semelbauer 2017). It is likely that females spend more time manipulating wrapped gifts, which appears to contribute to longer copulation durations. Indeed, gift wrapping increased copulation duration in Experiment 1, as in Lang (1996) and Andersen et al. (2008). Given that longer copulations correlate with higher fertilization success (Drengsgaard & Tøft 1999; Stålhandske 2001), gift wrapping evidently confers fertilization benefits to males. Furthermore, gifts wrapped with silk in nature are more frequently lighter and worthless (i.e., containing inedible prey) than unwrapped gifts (Ghislandi et al. 2014; Prokop & Semelbauer 2017), suggesting that males may mask the content of low-quality gifts through wrapping.

In sum, both hypotheses appear to be at work regarding the evolution of nuptial gifts in *Pisaura mirabilis*. Males and females both stand to benefit from the mere presence of the nuptial gift: the male is more likely to mate and the female obtains nutrients. This outcome supports the sexual congruence hypothesis. Females may benefit from the consumption of multiple gifts, but results are mixed, as multiple feeding positively affects some fitness components while not affecting others. With regard to gift size, males prolong copulation, and therefore likely increase fertilization success, by providing larger gifts to their mates. Females, on the other hand, do not appear to benefit by consuming larger gifts. This outcome supports male benefits via larger gifts as having arisen through sexual conflict.

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