European Arachnology 2003 (Logunov D.V. & Penney D. eds.), pp. 35–39.
© Arthropoda Selecta (Special Issue No.1, 2004). ISSN 0136-006X
(Proceedings of the 21st European Colloquium of Arachnology, St.-Petersburg, 4–9 August 2003)

Mating duration of *Pisaura mirabilis* (Araneae: Pisauridae) depends on size of the nuptial gift and not on male size

Продолжительность копуляции *Pisaura mirabilis* (Araneae: Pisauridae) зависит от размера брачного подарка, а не от размера самца

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ABSTRACT. The males of *Pisaura mirabilis* present a wrapped prey item as a nuptial gift to females prior to mating. Previous studies have shown that females favour males with large nuptial gifts by allowing them to copulate for longer. Thus, larger nuptial gifts mean that more eggs will be fertilized by the male. We hypothesized that male size might also be a factor in female choice, such that larger males would obtain a longer mating. We also predicted that males would show a preference for large prey when given a choice between prey items of different sizes. Laboratory experiments confirmed the earlier findings that males with a larger gift will obtain a longer copulation, but we found only weak (not significant) evidence for the effect of male body size. Males did not select the largest prey items for nuptial gifts, and the average prey size chosen by large males was not larger than that chosen by small males.

РЕЗЮМЕ. Самцы *Pisaura mirabilis* предлагают завернутую добычу самкам до копуляции. Прежние исследования показали, что самки позволяют более длительную копуляцию самцам с крупными брачными подарками. Таким образом, более крупный брачный подарок означает больше яиц, оплодотворенных самцом. Мы предположили, что размер самца может также быть фактором выбора самки, и более крупные самцы могут иметь более длительную копуляцию. Мы также преположили, что самцы могут препочитать более крупную добычу, когда есть выбор. Лабораторные эксперименты подтвердили прежние данные, что самцы с более крупными брачными подарками имеют более длительную копуляцию, но мы обнаружили очень слабые (не значимые) доказательства для эффекта размера самцов. Самцы не выбирали более крупную добычу для брачного подарка, и средний размер выбранной добычи у больших самцов не был больше, чем у мелких самцов.

KEY WORDS: Araneae, Pisauridae, sexual selection, nuptial prey, copulation duration.
КЛЮЧЕВЫЕ СЛОВА: Araneae, Pisauridae, половой отбор, брачный подарок, продолжительность копуляции.

Introduction

Pisaura mirabilis (Clerck, 1757) is peculiar among spiders in its mating behaviour because the male provides a nuptial gift (a prey insect wrapped in silk) to the female before he is allowed to mate [Bristowe, 1958; Nitzsche, 1988]. Austad & Thornhill [1986] found a pos-

itive correlation between copulation duration and the size of nuptial prey in *P. mirabilis*. Drengsgaard & Toft [1999] found that males having a longer copulation fertilized a higher percentage of eggs. Stålhandske [2001] confirmed these results and further demonstrated a preference of females for males with a larger nuptial gift. She argued that the male presenting a nuptial gift to the female during mating is maintained by sexual selection at two levels: the presence/absence of a gift (males without a gift have a very low chance of copulating), and the size of the gift (males with a larger gift have a higher reproductive success).

These studies have not yet considered the effect of male size, or the likely interaction between male and gift sizes. Larger males should be able to catch larger prey than smaller males. A large male size may also indicate a high viability, or a large male may show a more active copulatory courtship. Large male size may thus be a factor in female choice. The female preference for male size might also depend on the size of males with which she has previously copulated. Regardless, males should benefit from presenting a larger gift, and would be expected to select larger prey when given a choice. These are the questions we have addressed in the experiments described below.

Materials and methods

Spiders

More than 300 large juveniles and subadult specimens of *P. mirabilis* were collected in meadows at the Mols Laboratory, eastern Jutland, Denmark, during the period 24 April – 13 May 2002. They were raised to adulthood at room temperature (*c*. 20°C) and ambient photoperiod in half-litre glass jars with wet, live *Sphagnum* moss as a substrate. Twice weekly they were fed five house flies (*Musca domestica*) obtained from a laboratory culture. After the maturity moult feeding rations were reduced to three flies twice weekly.

Experiment 1. Female choice experiment

Females were mated twice, first at the age of nine days post maturity. They were weighed and randomly assigned to one of six mating treatments (see Table), which combined male size (large/small) and gift size (large/small) in different combinations over the two matings. The available adult males were weighed and divided into two groups: small (< 72 mg) or large (> 80 mg). Crickets (*Gryllus bimaculatus*) were obtained from a laboratory culture and used as prey items, divided into two size groups: small (5–15 mg) and large (37–47 mg). The small prey fell within the lower range of natural gift size [S. Toft, unpubl. data], whereas the large prey were heavier than most natural gifts. Each male was offered one prey according to the treatment it was assigned to. Males were at least five days post maturity and each was used only once.

Table.
Design of female choice experiment.
Experimental series A–F represented different combinations of large/small males with large/small gifts in first and second mating of a female, respectively. Initial N = 10 in each series.

Таблица.
Схема эксперимента по выбору самки.
Экспериментальные серии A–F представляют собой различные комбинации крупных/мелких самцов и крупных/мелких подарков в первой и второй копуляции самки. Начальное число повторов 10 в каждой серии.

Series	1. mating male – gift	2. mating male – gift
A	Large – Large	Large – Large
B	Large – Large	Large – Small
C	Small – Large	Small – Large
D	Large – Small	Large – Large
E	Large – Small	Large – Small
F	Small – Small	Small – Small

Females were transferred to mating cages (15 × 21 × 12 cm) 24 hrs before an experiment [cf. Stålhandske, 2001]. These cages had paper tissues on the bottom and the spiders were supplied with drinking water via a cotton-stoppered glass tube. Shortly before an experiment, males were introduced to the glass jar of its mate and offered the prescribed prey. Stimulated by the lingering female silk pheromones the males immediately wrapped up the prey as a gift rather than eating it themselves [Nitzsche, 1988]. Having wrapped the gift, each male was introduced to the female in its mating cage and the duration of copulation was measured. The female was returned to her jar for 48 hrs, then the procedure was repeated with a second male. Initially, ten females were

used in each mating group, but because some females laid an egg-sac before the second mating, the final sample sizes were slightly smaller.

Experiment 2. Prey size selection by males

Males were weighed and divided into four categories: < 72 mg; 72–80 mg; 80–100 mg; 100–120 mg. Similarly, the crickets (*Gryllus bimaculatus*) were divided into three categories: small 2.3–7.7 mg; medium 10.4–15.4 mg; and large 22.7–29.1 mg. Each male (N = 10 in each size group) was simultaneously offered one cricket from each of the three prey size groups.

The choice experiments took place in the mating cages with female silk. One cricket from each of the size categories was added. A tube with a male spider was placed in the middle of the cage. The lid of the tube was removed after a few minutes when the spider had calmed down. The size group of the first prey caught and wrapped was noted. If no prey had been caught within 60 mins, the test was cancelled.

Statistical analyses

After an initial check of homogeneity of group variances using Levene's test, results of Experiment 1 were analyzed in three different ways. First, 2-way ANOVAs were run on the duration of the first and second matings, with male size category (large/small) and prey size category (large/small) as factors. Preliminary analyses included both the interaction term and female weight (covariate), but none of these were significant and they were deleted from the final analyses. Second, comparable multiple regression analyses were performed using the exact values of male size and gift size. Third, repeated measures MANOVA were run with duration of first and second mating as the repeated response and the mating groups A–F (Table 1) as the factor. This was followed by contrasts between specific groups.

Results

Experiment 1. Female choice experiment

Fig. 1 combines the results from all mating groups and indicates that the large gift size increases the mating duration compared to small gift size for both male sizes and first and second matings. ANOVA on duration of the first mating (overall analysis: $F_{2,74} = 3.68$, P = 0.030) gave a highly significant effect of gift size ($F = 7.36$, P = 0.0083), but no effect of male size ($F = 0.041$, P = 0.84). A similar, but not significant trend was observed for the second mating (overall $F_{2,41} = 2.15$, P = 0.13). Multiple regression analyses confirmed these results (duration of the first mating: gift size P = 0.0023, male size P = 0.90; duration of the second mating: gift size P = 0.071, male size P = 0.67). Repeated measures MANOVA gave a marginally significant effect on mating duration of the mating groups ($F_{5,34} = 2.13$, P = 0.086). Two contrasts were significant (group A vs. group F: P = 0.0038, group B vs. group F: P = 0.0214); both comparisons involved differences in both gift size and male size.

When gift size was held constant there was no effect of male size with respect to the first mating, but there was a trend towards increasing mating duration for large males in the second mating. However, this was not significant in any of the analyses. A contrast between mating groups E and F (which differ in male size in both matings, but not in gift size) after the repeated measures ANOVA, gave a marginally significant effect (P = 0.087).

Second matings seemed to be shorter than first matings (Fig. 1). This, however, was not confirmed when mating groups with the same combination of male size and gift size in first and second matings (i.e., A, C, E and F) were compared (paired *t*-test, n.s.).

Experiment 2: Prey size selection by males

There was a significant difference in the prey sizes chosen by the male size groups (Fig. 2, ANOVA, $F_{3,38} = 3.113$, P = 0.039). However, there was no clear trend in the relationship and therefore no evidence that larger males select larger prey for nuptial gifts. Only males from one of the small male size groups took a substantial number of crickets from the large prey size group. Thus, there was no evidence that the males prefer the largest available prey for nuptial gifts.

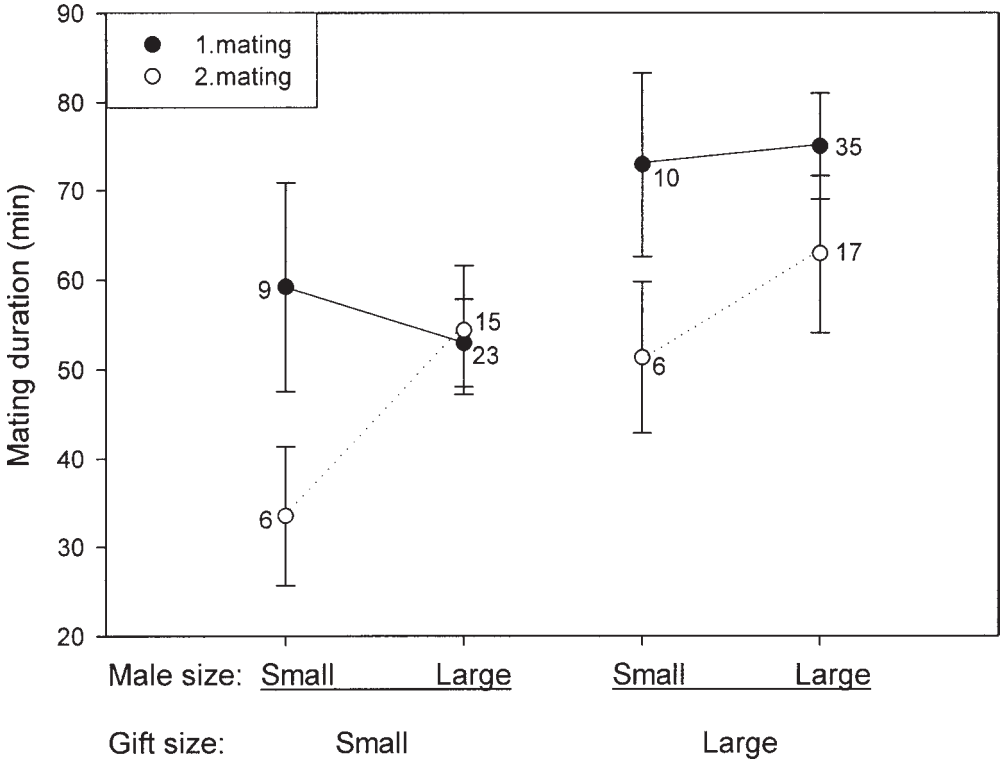

Fig. 1. Duration (mean ± SE) of first and second mating in *Pisaura mirabilis* as a function of male and nuptial gift size. For definition of size categories, see Materials and methods. Numbers indicate sample sizes.

Рис. 1. Продолжительность (средняя ± SE) первой и второй копуляции *Pisaura mirabilis* как функция размеров самца и брачного подарка. Определение размерных групп дано в Материалах и методах. Номера обозначают размеры образцов.

Discussion

The current study strongly supports earlier findings with *P. mirabilis* that males presenting a large nuptial gift obtain significantly longer copulations than those presenting a small gift. However, the study provides only very weak evidence for the idea that large males might be rewarded with a longer copulation, if gift size is accounted for. This weak evidence appeared only in the second mating of females. In *P. mirabilis* the females mate multiple times and available evidence indicates that late males will father more offspring than earlier males [Drengsgaard & Toft, 1999]. It is therefore possible that females become more and more selective once they have already mated a number of times. This selectivity is not expected to be revealed by complete rejection of small males, because even small males bring a nuptial prey that will contribute to female fecundity. But females may favour large males by allowing them a longer copulation and thus a relatively higher paternity than their actual nuptial gift should justify. Alternatively, since females often break the copulation by running away with a gift [see Stålhandske, 2001], it may be easier for them to do this when confronted by small, rather than large males.

Given the clear advantage to the males presenting a large gift, the lack of a male preference for large crickets may seem odd. The fact that males from the smaller size group were able to capture crickets of the largest prey size has demonstrated that the lack of preference for large prey in other male size groups was not due to the inability to subdue these prey. Possibly, it was the first prey males encountered that was

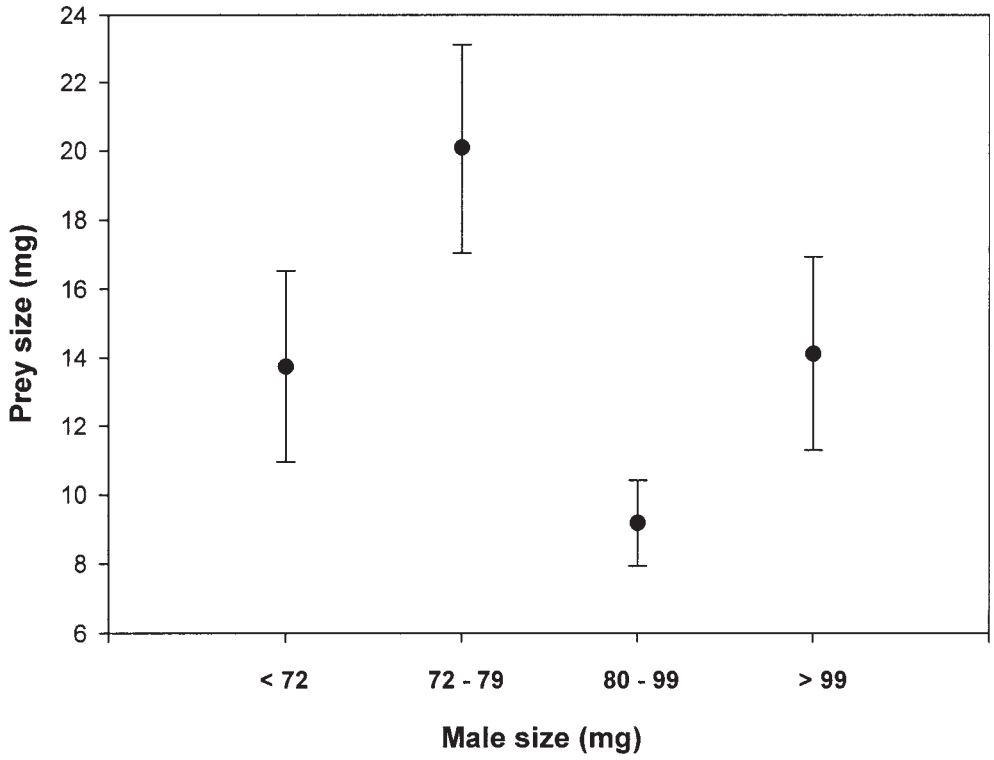

Fig. 2. Mean (± SE) prey sizes chosen by four male size groups of *Pisaura mirabilis* when given a choice between three sizes of crickets.

Рис. 2. Средние (± SE) размеры добычи, выбранной 4 размерными группами самцов *Pisaura mirabilis*, при выборе из трех размеров сверчков.

wrapped as a nuptial gift. This might have been the result of performing the experiment with the males under the influence of female pheromones to stimulate their decision to wrap prey into gifts. Under less stimulating conditions (i.e., without female silk), we suspect that males might have decided to eat small prey themselves and to use large prey for gifts.

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