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The ultimate function of nuptial feeding in the bushcricket *Poecilimon veluchianus* (Orthoptera: Tettigoniidae: Phaneropterinae)

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Summary. During mating the males of the bushcricket *Poecilimon veluchianus* transfer a large spermatophore of about a quarter of their body weight to the female. Such nuptial feeding is often thought to function as paternal investment by increasing the fitness of the male's offspring. According to an alternative, though not mutually exclusive, hypothesis, the size of the spermatophore is maintained because of its function as a sperm protection device. In this case the cost to the male should be classified as mating effort. To discriminate between these two hypotheses we measured the duration of sperm transfer into the female spermatheca and the time taken for spermatophore consumption. A comparison of durations revealed that spermatophore consumption interferes with the process of sperm transfer (Fig. 4). There was no significant effect of spermatophore consumption on number of eggs laid, weight of eggs or absolute weight of hatched larvae. The relative dry weight of hatched larvae, however, was increased as a result of spermatophore consumption (Table 1). Thus spermatophylax size is adjusted in accordance with a sperm protection function and the spermatophylax therefore represents mating effort. The increase in relative dry weight indicates that there may also be a paternal investment effect of the spermatophylax, if the offspring that benefit from spermatophylax materials are fathered by the donating male.

Introduction

In groups of insects as varied as bushcrickets, butterflies, empedids, hangingflies and scorpionflies the males offer nuptial gifts during or after courtship (for a review see Gwynne 1991). One possible explanation of such nuptial feeding is that the males exchange the gifts for the opportunity to mate and thereby increase the number of offspring they will father. The costs, measured as reduced number of future offspring, of such behaviour, directed to maximisation of the number of the male's offspring, have been defined as mating effort (Low 1978). Alternatively these nuptial gifts are thought to function as paternal investment (Trivers 1972), at least in bushcrickets, because they potentially can increase the fitness or the number of the female's offspring (see Gwynne 1990).

There has been considerable debate about these two hypotheses (Gwynne 1984a, b, 1986a, b; Quinn and Sakaluk 1986; Sakaluk 1986; Wickler 1985, 1986). To support the paternal investment hypothesis it has to be shown that the offspring benefit from the nuptial gift and are, at least in part, fathered by the donating male (Wickler 1985). If the nuptial gift is larger than necessary for successful insemination this shows that its size is maintained through a paternal investment function. Alternatively the size of the nuptial meal may be adjusted to its mating effort function. In this case increased offspring fitness may result as a side-effect of the mating effort function with no additional costs to the male.

In *Requena verticalis*, egg-weight, a measure that probably is positively correlated with fitness, was increased by feeding females with spermatophylaxes (Gwynne 1984a). Given the nearly complete first-male advantage in fertilization (Gwynne 1988b) only the first male a female mates with will invest parentally. In the bushcricket *Decticus verrucivorus,* however, Wedell and Arak (1989) and Wedell (1991) found no evidence of paternal investment. They concluded that in this species the spermatophylax serves only as a device for successful insemination.

The aim of this study was to examine the function of the spermatophore and the reasons for its maintenance in the bushcricket *Poecilimon veluchianus*. In this species spermatophore production is so costly to males (Heller and Helversen 1991) that it results in a relatively balanced operational sex ratio in the field, only weakly biased in favour of males. During copulation males of *P. veluchianus* transfer a spermatophore that weighs about a quarter of the male's body weight and consists of a small sperm-containing ampulla and a large spermatophylax (about 85% of spermatophore weight). Some

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minutes after copulation the female bends over and begins to feed on the spermatophylax. This jelly-like part of the spermatophore is thought to deter the female from consuming the ampulla before the sperm have reached the female's spermatheca.

The experiments were designed to discriminate between the two hypotheses (paternal investment versus mating effort) and to answer the following questions: (1) Is the size of the spermatophylax as large as necessary for successful insemination or larger? (2) Do females lay more or heavier eggs after consumption of the spermatophore?

To answer the first question the duration of sperm transfer (experiment 1) was compared with the duration of spermatophore consumption (experiment 2), to reveal whether spermatophylax size is adjusted to the time needed for sperm transfer (mating effort) or to a larger size evolved through selection for increased paternal investment. To address the second question we prevented some females from feeding on the spermatophores (experiment 3) and compared their egg-number and different measurements of offspring quality with those of control females.

Methods

Species and study site. Poecilimon veluchianus Ramme is a medium-sized herbivorous bush-cricket endemic in central Greece (Willemse 1985). Males and females are brachypterous and therefore flightless. The insects are active mainly at night. Females lay their eggs in the soil at sunset, males call almost exclusively during the night and mating takes place from about 2000 to 0600 hours with a peak between 2300 and 0300 hours.

All experiments were conducted in spring 1989 and 1990 some kilometers north of Vitoli (near the village of Makrakomi, Nomos Fthiotis, Greece, about 330 m above sea level), either in the natural habitat of the species (experiment 2) or in cages at that place (experiments 1 and 3). The animals were fed with flowers and buds of *Spartium junceum*, their main foodplants at this locality. For details on the study site and its vegetation see Heller and Helversen (1991).

Experiment 1. Duration of sperm transfer. To estimate the time required for transfer of sperm from the ampulla to the female spermatheca, 76 virgin females were mated and their ampullae removed at different time intervals [2, 3, 4.25 (4 and 4.5 combined), 6, 7.5, 9, 12, 15 h]. The spermatophore was removed with forceps and the content of the ampulla was suspended in 4 ml water by repeatedly passing it through a fine syringe. After dissection of the female we handled the spermatheca similarly. For determination of sperm concentration we used a haematocytometer (Neubauer, improved). For each sample we counted the number of sperm in a volume of 50 nl (or up to 16 times that volume if we found fewer than 100 spermatozoa) and calculated the absolute number of sperm in every sample. From this we derived the percentage of sperm transferred to the spermatheca for every copulation.

Experiment 2. Duration of spermatophore consumption. On 27 May 1990, 120 females were marked individually with reflective tape and adheasive labels (for details of method see Heller and Helversen 1990) and released at the place of capture. During two arbitrarily choosen days (28 May and 5 June) we searched for the marked animals every 1–2 h and examined them for the presence of spermatophores. The duration of spermatophore consumption was calculated from the time between the first and the last observation of an individual female with a spermatophore. This value was adjusted by adding half of the interval between the last observation without and the first with a spermatophore, and between the last observation with and the first without a spermatophore. On two nights (4 and 6 June), the same experiment was repeated with 24 and 10 caged virgin females (caught as subadults, at the time of the experiment about 10 days adult) and the same number of males. In this experiment females and males were weighed before placing them together in a large cage ($1.5 \times 1.5 \times 1.5$ m) and copulating pairs were identified so that the duration of spermatophore consumption could be related to the weight of males and females.

Experiment 3. Effect of spermatophore consumption on oviposition. In order to determine fitness effects of spermatophore consumption, 40 virgin, newly moulted females were assigned to two groups at random. All females had been collected as subadults and reared to adults in a 120-l cage. About 3 days after their moult, the animals were marked individually with adheasive labels. The adults were housed individually in transparent plastic containers of 400 ml volume filled with about 60–80 ml fine sieved sand from the natural environment serving as oviposition substrate. All females were weighed to the nearest milligram and the length of one hindfemur was measured with dial calipers to the nearest 0.1 mm.

Beginning on the 8th night after moult, every night (with the exception of three nights of heavy rainfall during which only very few animals copulated in the field) individually marked males that had not copulated for at least 2 days were placed into the female cages (one by one, from about 2300 to about 0300 hours). During this time the females were monitored every 30 min to check whether they bore spermatophores. The females of one group (−SP, group B) were prevented from feeding on their spermatophores by sprinkling the spermatophylaxes with fine sand (the egg-laying substrate). This did not prevent the insemination process, as was confirmed later by the production of fertile eggs and spermatheca dissection. After this treatment the females rarely tried to feed on the spermatophore and never succeeded in consuming a substantial part of the spermatophylax. Some spermatophores treated in this way did not fall off until about 1800 hours the next day and were therefore removed with forceps at that time. The females of the other group (+SP, group A) served as a control and were allowed to consume their spermatophores. The egg-laying substrate was sieved daily and the eggs were kept and counted later in the laboratory. Most of the females survived until 20 June and were then, about 30 days post-moult, killed and preserved in 70% alcohol. Four females were excluded from the analysis because of early death or inability to mate or lay eggs.

In October 1989, the eggs were cleaned from the adhering material and put on moist sand in petri dishes for 10 days at room temperature (about 22° C) and then held for 14 days in a refrigerator (at 5° C). After this procedure groups of 5 eggs (with larvae of stage 23 after Ingrisch 1978) were weighed to the nearest 0.1 mg. The larvae that hatched from 2 to 20 March 1990 were weighed and up to five per female were dried at 80° C. One dried larva of each female (the first hatched) was weighed with a Cahn electro balance to the nearest 0.001 mg.

Results

Duration of sperm transfer

The time necessary for sperm transfer was surprisingly variable. For example, one spermatophore attached to the female for only 3 h contained less than 20% of its original number of sperm cells, while six others after the same time still contained more than 80%. Even after 12 h some spermatophores contained more than 50% of their initial sperm (see Fig. 1). It seemed that 2 h was not long enough for any sperm to reach the spermatheca but within 15 h all spermatophores transferred more

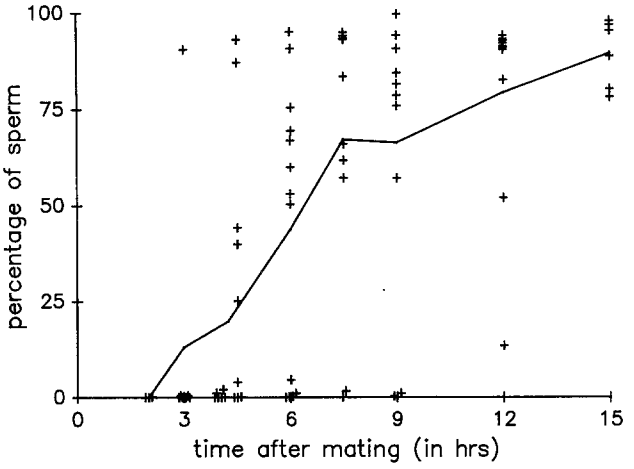

Fig. 1. Percentage of sperm transferred to the female spermatheca as a function of different spermatophore attachment durations. Time (h):n, 2:4, 3:7, 4.25:15, 6:13, 7.5:11, 9:10, 12:10, 15:6. The *solid line* connects the means for the different durations

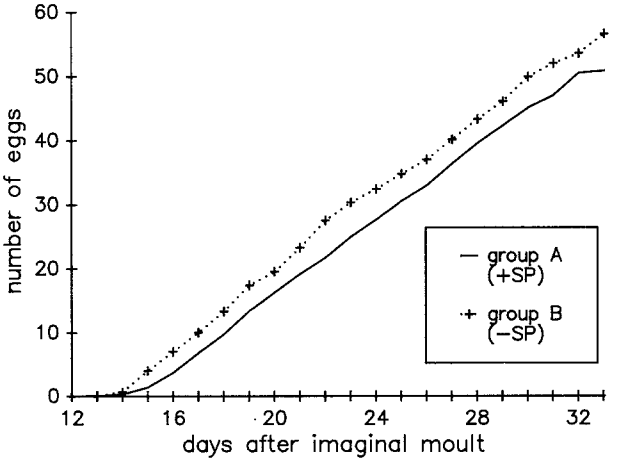

Fig. 2. Cumulative mean daily number of eggs per female in relation to female age. The crosses connected with a *dotted line* are the values for experimental animal (group B; −SP; deprived of spermatophore consumption); the *solid line* represents the values of the control animals (group A; +SP, allowed to consume the spermatophore)

than 70% of their sperm. At nearly any chosen time from 3 h to 12 h after spermatophore attachment, we found spermatophores with more than 50% and others with less than 5% sperm transferred. In only 4 out of 59 cases were values between 5% and 50% transferred sperm found. In summary, sperm transfer from the ampulla to the spermatheca seems to be a rapid process with a long and variable delay after mating, resembling an all-or-nothing reaction with a variable delay before initiation.

Duration of spermatophore consumption

During the 2 nights, 104 and 62 of the surviving marked females were located in the field. A total of 24 females that were observed with a spermatophore took on average 9.4 h (SD = 2.3) to consume the spermatophore. There was no correlation between the calculated moment of copulation and duration of spermatophore consumption ($r = -0.15$, $P > 0.5$). The duration of spermatophore consumption was significantly longer in captive females (mean 12.2 h, $n = 33$, SD = 3.3 h, Mann-Whitney, $Z = 3.3$, $P < 0.001$). This difference in consumption time may be explained by captive females mating with males that had refrained from mating for a minimum of 2 days and therefore produced larger spermatophores than males that remated within a shorter period (Heller and Helversen 1991). In this experiment, the time taken for spermatophore consumption was not correlated with female weight ($P > 0.2$; multiple regression analysis), but it was correlated with male weight ($y = 0.023x - 3.5$, $r = 0.54$, $P = 0.01$), and therefore with the weight of the spermatophylax which is itself strongly correlated with male weight (unpublished results).

Effect of spermatophore consumption on oviposition

The number of eggs the females laid per day did not depend on their age, at least over the period from the beginning of oviposition until about 30 days after moult (Fig. 2). Therefore a measure of female fecundity (eggs/day) that is independent of female lifetime can be determined by dividing the total number of eggs laid during life by the number of egg-laying days (the days a female survived from the 14th day after its imaginal moult). A comparison of group A (+SP, control) and B (−SP, deprived of spermatophore) did not reveal any influence of spermatophore consumption on fecundity (Table 1 A). The number of eggs laid was even higher in the group not feeding on spermatophores (see Table 1 A, cf. Fig. 2), so there is no indication that spermatophore consumption results in an increase in female fecundity. The fecundity of the females is clearly correlated with female weight (Table 1 A, Fig. 3) but not with their size as estimated by hindfemur length (Table 1 A).

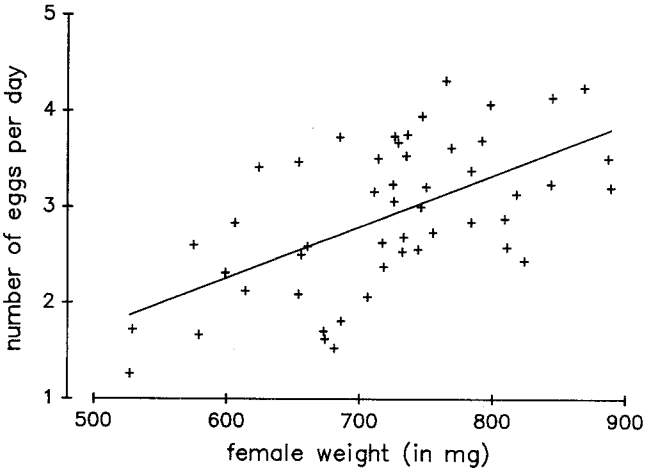

Fig. 3. Mean number of eggs laid per egg-laying day (the days a female survived from the 14th day after her imaginal moult) as a function of female body weight. (regression: $y = 0.0053x - 0.935$, $r = 0.592$, $P < 0.001$)

Table 1. Means (not adjusted for effects of covariates) and analyses of A, number of eggs produced and B–F measurements of offspring weight (B, D and E in mg, F in %; further explanation see text) in experiment 3 (ANOVA)

Mean ± SE (*n*)	A Number of eggs per egglaying day				B Weight of groups of 5 eggs				C Residual of egg weight			
	Group A (+SP) 2.69 ± 0.19 (17)		Group B (−SP) 3.03 ± 0.21 (17)		Group A (+SP) 24.16 ± 0.33 (17)		Group B (−SP) 23.32 ± 0.30 (17)		Group A (+SP) 0.44 ± 0.32 (17)		Group B (−SP) −0.48 ± 0.31 (17)	
Analysis of variance												
Source of variation	*df*	MS	*F* ratio	*P*	*df*	MS	*F* ratio	*P*	*df*	MS	*F* ratio	*P*
Treatment	1	1.562	3.778	0.061	1	3.018	1.987	0.169	1	3.627	2.524	0.123
Covariates												
Female weight	1	7.967	19.272	0.000**	1	4.015	2.644	0.114	1	3.202	2.229	0.146
Female size	1	0.262	0.633	0.441	1	12.343	8.128	0.008*	1	13.541	9.425	0.005*
Residual	30	0.413			30	1.519			30	1.437		

Mean ± SE (*n*)	D Weight of hatched larvae (wet)				E Dry weight of hatched larvae				F Relative dry weight of larvae			
	Group A (+SP) 6.78 ± 0.20 (10)		Group B (−SP) 6.60 ± 0.10 (13)		Group A (+SP) 1.38 ± 0.04 (10)		Group B (−SP) 1.27 ± 0.02 (12)		Group A (+SP) 20.29 ± 0.47 (10)		Group B (−SP) 19.04 ± 0.17 (12)	
Analysis of variance												
Source of variation	*df*	MS	*F* ratio	*P*	*df*	MS	*F* ratio	*P*	*df*	MS	*F* ratio	*P*
Treatment	1	0.002	0.010	0.924	1	0.039	3.543	0.076	1	10.691	10.004	0.005*
Covariates												
Female weight	1	0.641	0.339	0.574	1	0.004	0.375	0.555	1	1.868	1.748	0.203
Female size	1	0.996	5.266	0.033	1	0.032	2.849	0.109	1	0.012	0.011	0.917
Residual	19	0.189			18	0.011			18	1.068		

Treatments: females prevented from consuming the spermatophore or not; covariates: female size (hindfemora length) and female weight

To correct for the inflation in the Type 1 error associated with multiple statistical tests, we adjusted the significance levels 0.05 and 0.01 to $P = 0.0085$ (*) and $P = 0.002$ (**). Regression lines for the covariates and dependent variables are not significantly different between the treatment cells

One other possible effect of spermatophore consumption could be an increase in egg or offspring size (measured as weight). We compared the mean weights of groups of 5 eggs (1–4 values per female) between the control and experimental group, controlling for female size and weight as covariates, and obtained no indication of an effect of spermatophore consumption (Table 1 B). In order to eliminate the correlation between female age at oviposition and egg weight (older females laid eggs of lower weight than younger ones, $n = 138$, $r = -0.25$, $P < 0.01$) we calculated the mean residual for every female and again compared groups A and B (residual of egg weight, Table 1 C). Both egg weights and residuals are correlated with the length of the female hindfemur but not with female body weight, indicating that female size affects egg size, whereas female nutrition (weight) seems to affect egg number but not egg size. Comparison of the wet weights of hatched larvae (one mean value for every female from 1–7 larvae) also yielded no difference between the groups A and B (Table 1 D). The dry weights of larvae from group A were slightly larger than those of group B (Table 1 E). Only the relative dry weight of the larvae (the proportion of dry weight in relation to wet weight, expressed as a percentage) was significantly influenced by the treatment (Table 1 F). This may indicate that the larvae did not grow bigger but retained more material during embryonic development if the females were allowed to feed on the spermatophores.

Females of group B copulated at a faster rate (13 out of 17 remated within 5 days) than females of the control group (3 out of 17 remated within 5 days, $P < 0.001$, Fisher's exact test).

Discussion

Comparison of the durations of spermatophore consumption and sperm transfer is necessary to discriminate between the different hypotheses of spermatophylax function. In *Poecilimon veluchianus* sperm transfer seems to be an all-or-nothing process with a variable initiation delay. Therefore the proportion of spermatophores that have transferred a substantial part of their sperm (we considered more than 20% as substantial) into the spermatheca is the best measure of success in sperm transfer. This measure of the duration of sperm transfer can be compared with the period the females need for total consumption of the spermatophore. Comparing the two

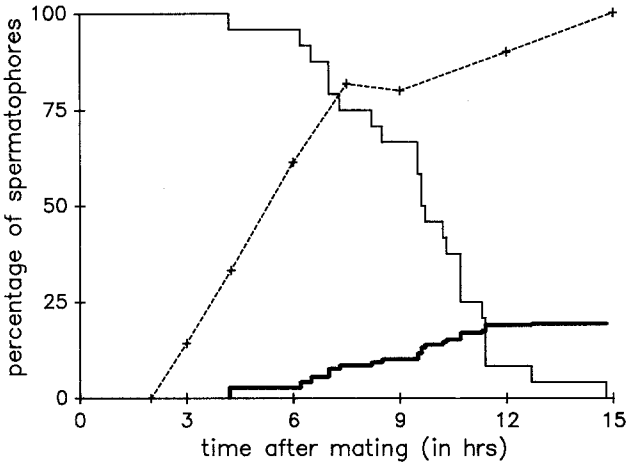

Fig. 4. Comparison of the proportion of spermatophores that have transferred more than 20% of their sperm into the female spermatheca [$f1(t)$, *dotted line*] and the proportion of spermatophores not completely consumed [$f2(t)$, *thin line*] as a function of spermatophore attachment duration. Assuming independence of these two curves, we calculated the cumulative percentate of prematurely consumed spermatophores [$f3(t)$, *bold line*] as follows:

$$f3(t) = \sum_{t=0}^{t} \Delta f2(t) * [1 - f3(t)]$$

curves (Fig. 4) it is evident that a small proportion of spermatophores is consumed before sperm transfer. For example, a spermatophore that is consumed 6 h after copulation will have a chance of only about 66% of transferring a substantial part of its sperm into the female spermatheca. An estimate of the percentage of spermatophores that are consumed before sperm transfer yields about 19% prematurely consumed and thus unsuccessful spermatophores (Fig. 4). The spermatophores eaten in less than 9 h are particularly at risk of being consumed prematurely, since the one curve (thin line, percentage of spermatophores not consumed) falls before the other (dotted line, percentage of spermatophores that have transferred more than 20% of their sperm) has reached the 100% level. Thus, assuming that consumption time and duration of sperm transfer are independent, spermatophore size seems to be rather small. However, spermatophore size in *P. veluchianus* depends on the time since the last copulation (Heller and Helversen 1991). A male may then profit more if it produces a small spermatophore that may be unsuccessful rather than delaying mating until it is able to produce a large spermatophore that is certain to be not consumed prematurely – otherwise it should not mate at that time. In summary, spermatophylax size in *P. veluchianus* seems to be adjusted to the sperm protection function, as it is in *Gryllodes supplicans* (Sakaluk 1984, 1986).

To see whether the spermatophylax could also act as incidental paternal investment one has to show that the progeny of the investing male benefit from spermatophylax consumption (Wickler 1985). There are two possible effects of paternal investment, which may either increase the fitness or the number of offspring (Gwynne 1990). Our experiments have revealed that there is no increase in the number of eggs produced after spermatophore consumption (Table 1A; cf. Fig. 2), contrary to the results for *Reguena verticalis* (Gwynne 1984a).

Spermatophore consumption could also result in "better" offspring instead of a higher number of offspring. Fitness in offsping is difficult to measure directly, so we measured the weight of eggs and larvae, which is probably positively correlated with fitness (Capinera 1979; Harvey 1985; Gwynne 1988a). The weights of developed eggs and hatched larvae were higher if their mothers were allowed to feed on the spermatophores, but the differences were not significant (Table 1B–D). Spermatophore consumption yielded a significant increase in relative dry weight of hatched larvae (Table 1F). This result may indicate that the larvae did not grow to a larger size, but used the spermatophore materials to increase their energy reserves, sustaining them for longer while searching for food after eclosion.

To determine whether a nuptial gift that benefits a female's progeny can be viewed as paternal investment it is necessary to know whether the male fathers the offspring he benefits. The experiments here deal only with the question of the benefit of the spermatophore for the offspring and not with their paternity. However, we have some indication that the investing male will only rarely be the father of the progeny that benefit from nuptial feeding. Since about 90% of all eggs are fertilized by the last male to copulate with the female (Achmann et al. 1992), the interval between two matings should be considered as the critical period for nutrient incorporation. The inter-mating period most frequently observed in *P. veluchianus* is 2 days (Heller and Helversen 1991), which seems too short for incorporation of spermatophore materials into developing eggs, because there is a lag of about 7 days for the incorporation of spermatophore contents into the eggs of *Poecilimon affinis* (D. v. Helversen pers. comm.). In contrast, Simmons (1990) has reported that egg weight increases as little as 24 h after copulation in an undescribed member of the Zaprochilinae as a result of spermatophore consumption.

There may be, however, a very fast utilization of the main spermatophylax component, water, which consitutes about 88% of spermatophylax weight in *P. veluchianus* (unpublished results). It seems possible that water may enhance female or offspring fitness in the dry summer climate of Greece, but it is unlikely to result in higher relative dry weight of hatched larvae.

The females of *P. veluchianus* mate at a higher rate if they are prevented from consuming the spermatophore, which may be interpreted as an attempt to gain materials they are deprived of. This result, like the higher mating rate in an unnamed species of Zaprochilinae (Gwynne and Simmons 1990) and in *Requena verticalis* (Gwynne 1990) when females are undernourished, indicates that the females benefit from spermatophore consumption.

Taken together, our results reveal that spermatophylax size in *P. veluchianus* is maintained by selection on the male to increase the number of young he will father, and hence the spermatophylax represents mating effort.

In addition it may cause an increase in progeny fitness, which could be considered as incidental paternal investment if nutrients are incorporated in eggs laid before remating. The spermatophylax may even function as true paternal investment, but only in the rare case when the optimal spermatophylax size is almost equal for the mating effort and paternal investment functions.

In *Requena verticalis* the size of the spermatophylax seems to be larger than necessary for sperm protection, and spermatophylax consumption yields an increase in egg number and egg weight, so Gwynne (1986a) concluded that the spermatophylax represents paternal investment in this species. Wedell and Arak (1989) and Wedell (1991) found no evidence of paternal investment in the wartbiter *Decticus verrucivorus* and concluded that spermatophylax size is adjusted to a sperm protection function. Given such variation in bushcrickets it seems to be premature to label nuptial gifts as paternal investment in a given species of bushcricket without experimental confirmation.

Even the occurrence of a reversal in the typical courtship sex-roles, as has been observed in bushcrickets (Gwynne 1981, 1985; Simmons and Bailey 1990) cannot be taken as evidence for paternal investment. Courtship sex role reversal may also evolve if female reproductive success is limited by the female's ability to acquire spermatophores, even if this benefits the offspring of subsequent mates.

A relationship between the sexes similar to that in *P. veluchianus* has been found in brush-turkeys (Jones 1990) where the mounds that males build in a period of months serve mainly as a device for attracting females for copulations. The eggs that females lay in these mounds shortly after copulation have been fertilized some days earlier, mostly by other males.

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