Effects of the Consumption of Male Spermatophylax on the Oviposition Schedule of Females in the Decorated Cricket, Gryllodes sigillatus

Authors: Kasuya, Eiiti, and Sato, Nobuyo

Source: Zoological Science, 15(1) : 127-130

Published By: Zoological Society of Japan

URL: https://doi.org/10.2108/zsj.15.127

ZOOLOGICAL SCIENCE **15**: 127–130 (1998)

Effects of the Consumption of Male Spermatophylax on the Oviposition Schedule of Females in the Decorated Cricket, *Gryllodes sigillatus*

Eiiti Kasuya[1]*† and Nobuyo Sato†

Laboratory of Biology, Faculty of Education, Niigata University, 2-8050 Ikarasi, Niigata 950-21, Japan

ABSTRACT—The effects of the consumption of the spermatophylax produced by males on female fitness were studied in the decorated cricket, *Gryllodes sigillatus*. An increase in the number of spermatophylaces presented to females did not increase the total number of eggs made by females, the number of eggs laid, or the hatchability of eggs laid by females, but increased the number of eggs laid in the early stage of adult life of females. The duration of the egg stage decreased with the number of spermatophylaces presented to females. The implication of the results on the sham hypothesis that the spermatophylax does not have nutritional value is discussed.

INTRODUCTION

Courtship feeding, in which a male gives food to a female during or prior to mating, has been reported in diverse animal taxa (Alcock, 1987). The selective significance of courtship feeding has been documented in two ways that are not mutually exclusive. The first is that the transfer of prey or nutritional materials to the female ensures the transfer of sperm from the male to his mate (e.g., Thornhill, 1976; Sakaluk, 1984). The second is that courtship feeding increases the fecundity of the female or improves the offspring fitness, and is thus a kind of paternal investment (e.g., Gwynne, 1984).

Both types of the selective significance of courtship feeding have been demonstrated empirically in orthopteran insects. Sakaluk (1984) showed that sperm transfer occurred during the feeding on spermatophylax by the female in the decorated cricket, *Gryllodes sigillatus*. Gwynne (1984) reported the consumption of spermatophylax increased the fecundity of the female in the katydid *Requena verticalis*.

Several authors reported no effect of spermatophylax consumption on female fecundity in orthopteran insects (Wedell and Arak, 1989; Reinhold and Heller, 1993). Will and Sakaluk (1994) argued that the spermatophylax of some orthopteran insects including the cricket, *G. sigillatus*, is a sham gift in its nutritional value. This sham hypothesis predicts that there is no increase in the fecundity of females that consume more spermatophylaces. However, no effect of spermatophylax consumption on fecundity could be observed even when the spermatophylax has a nutritional value. For example, if spermatophylax consumption increases the number of eggs laid in a short period but does not increase that in other periods, the variation in the daily number of eggs laid may mask the effect of spermatophylax consumption.

In the present study, we examined the effects of the feeding of the spermatophylax on the oviposition schedule and on other fitness components of females in the cricket, *G. sigillatus*. These results are used to test predictions from the sham hypothesis by Will and Sakaluk (1994).

MATERIALS AND METHODS

Insects

We used the decorated cricket, *G. sigillatus* maintained in the Entomological Laboratory, Hirosaki University, Hirosaki, Japan. The crickets used were almost entirely brachypterous (S. Masaki, personal communication, and our personal observation). The crickets were reared at 16L8D, 30°C and 70–78% RH. RH was controlled by saturated solutions of sodium bromide and sodium chloride. The crickets were given ample food (food pellets for insects, Oriental Yeast Company). Prior to the experiments, the observed mating behavior of the crickets was, in general, similar to that reported by Sakaluk (1986). However, the duration of a mating (87.3 ± 37.4 sec, mean $\pm$ SD) was shorter than the durations reported by Sakaluk (119.2 sec) and Alexander and Otte (1967, 2 or 3 min). Females laid eggs without mating.

Experimental design

Virgin female crickets of 8 days after the final eclosion were used for the experiments. The spermatophore produced by the male crickets consists of two parts: the ampulla, which contains sperm, and the spermatophylax, which consists of a jelly-like material and which does not contain sperm. Female crickets were subjected to one of five treatments. Females were either mated with a male but given no spermatophylax (Treatment 0), mated with a male and given one spermatophylax (Treatment 1), mated with a male and given three

* Corresponding author: Tel. +81-92-642-2624/2623; FAX. +81-92-642-2645.
[1] Present address: Department of Biology, Faculty of Science, Kyushu University, Hakozaki, Fukuoka 812-81, Japan.
† Alphabetical order.

spermatophylax (Treatment 3), mated with a male and given seven spermatophylax (Treatment 7), or not mated and not given spermatophylax (No mating). In Treatment 0, the spermatophylax was removed within 5 min after the beginning of copulation (before consumption of the spermatophylax. This was determined by a preliminary observation). The female was confined in a small vial ($1 \times 1 \times 4$ cm) to prevent her from removing the ampulla. The ampulla was removed by tweezers after 1 hr in Treatments 1, 3 and 7. Males that were used to be mated with the females are unmated ones of 6 to 9 days after the final eclosion.

In Treatment 1, we fed one spermatophylax to the female during the confinement in the vial. In Treatments 3 and 7, we fed two or six additional spermatophylax to the female during the following 14 days. The time schedule was as follows. In Treatment 3, the first additional spermatophylax was given between the 3rd and 6th day (3.9 ± 1.0, mean $\pm$ SD in days, $n = 14$), and the second additional spermatophylax was given on the 9th or 10th day (9.7 ± 0.5). In Treatment 7, the first additional spermatophylax was given on the 2nd or 3rd day (2.9 ± 0.3, $n = 14$), the second additional one was given on the 4th day, the third additional one was given on the 6th or 7th day (6.4 ± 0.5), the forth additional one was given between the 9th and 11th day (10.1 ± 0.5), the fifth additional one was given on the 11th or 12th day (11.8 ± 0.4) and the sixth additional one was given on the 13th or 14th day (13.1 ± 0.3). We did not feed more than one spermatophylax on a single day in both of treatments.

We fed the spermatophylax to females while females were confined in the vial. All the females (under all the treatments) experienced the same number of the confinements in order to avoid any effects the confinement might have on the condition of the females.

Female body lengths (excluding antenna and ovipositor) were measured. That of males were also measured in Treatments 0, 1, 3, and 7.

Individual females were allowed to oviposit in a plastic container and, to correspond with the high food condition of Will and Sakaluk (1994), were given food in excess. Eggs oviposited by each female on sand in a small vessel during a single day were separately incubated at 30°C and 70–78% RH. The number of newly oviposited eggs and that of newly hatched eggs were recorded daily. The status of females (dead or alive) was recorded daily for 30 days. After the period of 30 days, the females were then dissected under anesthetization and the number of eggs within the body were counted. Hereafter, "total eggs" refers to the number of eggs oviposited plus the number of eggs found in the body after dissection.

Statistical analysis

To analyse the effect of the consumption of multiple spermatophylaces, we made two statistical comparisons. The first was a comparison of a particular variable between Treatment 0 and Treatments 1, 3, and 7 (contrast, hereafter). This was tested by the analysis of variance of ranks (Meddis, 1980). The second comparison was the correlation between the number of spermatophylax and a particular variable (trend, hereafter). This was tested by isotonic regression. By restricting the analyses to these two, we were able to refrain from testing a large number of post-hoc hypotheses and finding statistical artifacts. These two types of tests may reveal the mode of the effect of the materials transferred from the male to the female. For example, when the material is used as a direct source of nutrition, a trend that the number of eggs increases with the number of spermatophylaces is predicted. When the material acts as a catalyzer or essential microelement, the number of eggs under Treatments 1, 3, and 7 is likely to be larger than that under Treatment 0.

The score used in the statistical analysis is the mean (or another representative value) for an individual female and the mean $\pm$ SD of this score is shown. It is noteworthy that this is probably a conservative procedure. The sample size is the number of females if not otherwise mentioned.

RESULTS AND DISCUSSION

First, we analysed the confounding effect of body size on the two variables that showed a significant effect among the different treatments. This was tested by examining a partial regression. The body length of both sexes did not affect the first quantile of the date of oviposition ($t = 0.270$ and $P > 0.05$ for the female body length, and $t = 0.087$ and $P > 0.05$ for the male body length). The body length of both sexes did not affect the duration of eggs ($t = -1.472$ and $P > 0.05$ for the female body length, and $t = -0.787$ and $P > 0.05$ for the male body length).

The different treatments did not significantly affect the number of eggs laid by females (Table 1, $z = 1.043$ and $P > 0.05$ for contrast, and $z = 0.755$ and $P > 0.05$ for trend). Neither the total eggs of a female ($z = 1.379$ and $P > 0.05$ for contrast, and $z = 1.108$ and $P > 0.05$ for trend) nor the proportion of eggs laid (number of eggs oviposited/number of total eggs) ($z = 0.087$ and $P > 0.05$ for contrast, and $z = 0.299$ and

Table 1. Female fitness components under the different treatments (mean $\pm$ SD)

Treatment	No mating	0	1	3	7	statistical tests	
sample size (No. of females)	9	12	12	14	14	trend[1]	contrast[2]
fecundity	351.9 ± 175.7	456.3 ± 213.3	564.8 ± 247.6	525.6 ± 177.9	500.6 ± 266.4	0.755	1.043
egg production	692.3 ± 136.1	709.7 ± 154.5	803.7 ± 212.4	813.1 ± 146.8	749.8 ± 217.4	1.108	1.379
proportion of eggs laid (%)	51.4 ± 24.8	62.2 ± 23.8	67.0 ± 16.5	64.2 ± 18.2	63.7 ± 22.4	0.299	0.087
hatchability (%)	0	10.3 ± 10.6	6.7 ± 3.3	8.6 ± 5.1	6.2 ± 5.6	1.222	0.109
oviposition schedule							
median (day)	22.7 ± 4.8	17.4 ± 3.4	12.9 ± 6.5	12.8 ± 5.5	15.2 ± 8.2	1.496	1.716
first quantile (day)	21.5 ± 6.0	15.3 ± 7.0	10.3 ± 6.2	9.9 ± 4.3	12.7 ± 8.2	1.757	2.172*
duration of egg (day)	–	20.5 ± 1.5	21.5 ± 1.8	20.6 ± 2.0	19.3 ± 2.0	2.386*	0.608

[1] Value of z by isotonic regression.
[2] Value of z (0 vs 1, 3 and 7) by Meddis' (1980) ANOVA by ranks.
* $P < 0.05$

$P > 0.05$ for trend) was affected significantly by the number of spermatophylax consumed (Table 1). Females without mating had eggs comparable to those in Treatment 0 (Table 1).

A lack of difference in the number of eggs laid or in the total eggs among treatments does not necessarily mean that there is no difference in the oviposition (m_x) schedules. We tested for a difference in oviposition schedule by examining the following two measures. If a female lays a half of total eggs before a date and the other half after the date, the date is hereafter called the median. Similarly, if a female lays a quarter of total eggs before a date and three quarters after the date, the date is hereafter called the first quantile. We were able to examine the change in oviposition schedule of females by analysis of the median and first quantile. Though there was no significant difference in the median ($z = 1.716$ and $P > 0.05$ for contrast, and $z = 0.134$ and $P > 0.05$ for trend), that in the first quantile was significant ($z = 2.172$ and $P < 0.05$ for contrast, and $z = 1.757$ and $P > 0.05$ for trend) (Table 1). Consumption of the spermatophylax by the female shortened the first quantile. This was done by laying a large number of eggs during the first week ($z = 2.823$ and $P < 0.05$ for contrast).

There was no significant difference among treatments in hatchability of eggs laid (Table 1, $z = 0.109$ and $P > 0.05$ for contrast, and $z = 1.222$ and $P > 0.05$ for trend).

Our results show that the consumption of spermatophylax increased the number of eggs laid by females in their early life in *G. sigillatus*. However, the effects of spermatophylax consumption on the number of eggs laid or total eggs observed in several orthopteran insects (e.g., Gwynne, 1984; Simmons, 1988) were not found in the present study.

The sham hypothesis of Will and Sakaluk (1994) predicts spermatophylax consumption has no effect on oviposition in the early life of female adults. The present results do not support this hypothesis. However, it is noteworthy that the present results are consistent with the results of Will and Sakaluk in that both studies showed no significant effect of spermatophylax consumption on the total number of eggs laid. The present results show that a lack of difference in the number of eggs laid does not mean that there is no effect on oviposition or female fitness. To test the sham hypothesis, it is necessary to examine the oviposition schedule as well as the total number of eggs laid.

In the present study, spermatophylaces were presented during the early stage of adult life of females. An increase in the number of eggs in the early life of females would be predicted if some substance in the spermatophylax that is used as a nutritional source or that activates oviposition is consumed and depleted quickly by oviposition. Because we gave spermatophylaces to females only in their early life in each of the treatments, an effect would be found only in the early life if the substance contained in spermatophylax is consumed. Simmons (1988) argued that mating continually throughout the life of females is necessary to realize the beneficial effect of male-donated egg stimulants and proteins. The present results suggest that the consumption of spermatophylax in the later stage of adult life of females increases the number of eggs laid in the later stage and thus increases the total number of eggs laid.

Two types of differences among treatments, contrast and trend, were examined in the present study. Only contrast between Treatments 0 and 1, 3 and 7 was significant for the first quantile and the number of eggs oviposited in the first week. If the material in spermatophylax is used as a direct source of nutrition or energy, a linear increase with the number of spermatophylaces would be expected. The present results suggest that the material in spermatophylax acts as a catalyst or an essential microelement.

Duration of the egg, which is the time from oviposition to hatching of an egg, was measured for each of the eggs. As mentioned in Materials and Methods, we used the mean for an individual female as the score in this study. This procedure may lower the statistical power. A large number of spermatophylax consumed significantly shortened the duration of the eggs ($z = 2.386$ and $P < 0.05$ for trend) (Table 1).

Most studies, except Gwynne (1988), have examined the effects of the consumption of male-donated nutrition in orthopteran insects on female fitness only in relation to the total fecundity or egg size. In the present study, the duration from oviposition to hatching of *G. sigillatus* became shorter with the number of spermatophylax consumed by the female. This appears to be the first report of this kind of effect on female fitness in orthopteran insects. Though we did not weigh the eggs in the present study, the weight of an egg in this species could have been heavier in females that consumed a greater number of spermatophylax, as occurs in other orthopteran insects (e.g., Gwynne, 1984).

Wasserman and Asami (1985) found a similar shortening of the duration of eggs in a bruchid beetle, *Callosobruchus maculatus*, though they did not separate the effect of multiple copulations and the consumption of multiple spermatophores. The present study found no direct effect of multiple copulations itself, but rather an effect of the consumption of multiple spermatophores (spermatophylax, strictly).

ACKNOWLEDGMENTS

We are indebted to S. Masaki for providing the crickets used in these experiments and to D. T. Gwynne for his critical reading of an early draft of the manuscript. S. Masaki and S. K. Sakaluk provided advice on the scientific name of the cricket species. J. Raymond made suggestions on English expressions. This study was in part supported by a Grant-in-Aid (No. 07640838) from the Ministry of Education, Science, Sports and Culture, Japan.

REFERENCES

Alcock J (1987) Animal Behavior. 5th edition, Sinauer, Sunderland

Alexander RD, Otte D (1967) The evolution of genitalia and mating behaviour in crickets and other orthoptera. Misc Publ Mus Zool Univ Michigan 133: 1–62

Gwynne DT (1984) Courtship feeding increases female reproductive success in bushcrickets. Nature 307: 361–363

Gwynne DT (1988) Courtship feeding and the fitness of female katy-

dids. Evolution 42: 545–555
Meddis R (1980) Unified analysis of variance by ranks. British J Math Stat Psychol 33: 84–98
Reinhold K, Heller KG (1993) The ultimate function of nuptial feeding in the bushcricket *Poecilimon velchianus* (Orthoptera: Tettigoniidae: phaneropterinae). Behav Ecol Sociobiol 32: 55–60
Sakaluk SK (1984) Male crickets feed females to ensure complete sperm transfer. Science 223: 609–610
Sakaluk SK (1986) Is courtship feeding by male insects parental investment? Ethology 73: 161–166
Simmons LW (1988) The contribution of multiple mating and spermatophore consumption to the lifetime reproductive success of female field crickets. Ecol Entomol 13: 57–69
Thornhill R (1976) Sexual selection and paternal investment in insects. Am Nat 110: 153–163
Wasserman SS, Asami T (1985) The effect of maternal age upon fitness of progeny in the southern cowpea weevil, *Callosobruchus maculatus*. Oikos 45: 191–196
Wedell N, Arak A (1989) The wartbiter spermatophore and its effect on female reproductive output (Orthoptera: Tettigoniidae). Behav Ecol Sociobiol 24: 117–125
Will MW, Sakaluk SK (1994) Courtship feeding in decorated crickets: is the spermatophylax a sham? Anim Behav 48: 1309–1315

(Received August 27, 1996 / Accepted October 22, 1997)