

# Hydration benefits to courtship feeding in crickets

Tracie M. Ivy\*, J. Chadwick Johnson† and Scott K. Sakaluk

*Behavior, Ecology, Evolution and Systematics Section, Department of Biological Sciences, Illinois State University, Normal, IL 61790-4120, USA*

The spermatophore transferred by male decorated crickets (*Gryllobates sigillatus*) at mating includes a large gelatinous spermatophylax that the female consumes after copulation. Although previous studies have shown that *G. sigillatus* females gain no nutritional benefits from consuming food gifts, there may be other benefits to their consumption. We examined potential hydration benefits to females by experimentally manipulating both the availability of water and the number of food gifts that females consumed, and by measuring their effect on female fitness. Analysis of the number of nymphs produced by females revealed a significant interaction between the number of spermatophylaxes consumed and water availability. When spermatophylaxes were not provided, females given water *ad libitum* produced significantly more nymphs than females subjected to water stress. Female longevity was significantly affected by water availability, with an increase in the availability of water corresponding to a significant increase in female longevity. These data suggest that female *G. sigillatus* accrue fitness benefits by consuming spermatophylaxes when alternative sources of water are unavailable. In addition, females appear to allocate water contained in spermatophylaxes towards reproduction as opposed to survival.

**Keywords:** crickets; courtship food gifts; *Gryllobates sigillatus*; life-history trade-offs; sexual selection

## 1. INTRODUCTION

Courtship food gifts are offered by males of numerous insect species, and occur in various forms. These include insect prey that are captured by the male and presented to the female at mating, specialized glandular secretions, regurgitated food, and in certain unusual cases, portions of the male's body that are consumed by the female at copulation (Vahed 1998). The effects of food gifts on female reproduction and offspring survival, and the ensuing benefits to males, vary greatly across species. Nowhere is this more apparent than in the ensiferan Orthoptera (crickets and katydids) (see the review in Brown & Gwynne 1997). In these insects, food gifts often take the form of a spermatophylax, a large gelatinous mass forming part of the spermatophore and consumed by the female after mating. The spermatophylax surrounds a smaller sperm-containing ampulla, both of which remain attached outside the female's body. After the female has consumed the spermatophylax, she typically removes and eats the ampulla, and this terminates the transfer of any remaining sperm (Sakaluk 1984; Simmons 1986).

In some species, consumption of the spermatophylax leads to a significant increase in female fitness, whereas in others, courtship feeding appears to have no effect on

female reproductive success. These conflicting results have led to considerable debate over the function of the spermatophylax and other courtship food gifts (see Wickler 1985; Sakaluk 1986; Simmons & Parker 1989). Some investigators view the spermatophylax as a form of prezygotic paternal investment, functioning to enhance female reproduction (Gwynne 1984; Gwynne & Simmons 1990), whereas others view the spermatophylax as a sperm-protection device, the principal function of which is to deter the female from prematurely removing the ampulla and terminating sperm transfer (Sakaluk 1984; Wedell 1991; Heller & Reinhold 1994; Vahed & Gilbert 1996).

Gwynne (1984) suggested that spermatophylax consumption may benefit only those females which are experiencing food stress, and previous studies have sought to test this hypothesis by varying the food quality available to females while measuring the effects of spermatophore consumption on female fitness (Gwynne 1984; Wedell & Arak 1989; Vahed & Gilbert 1997). Although protein-deprived females may gain benefits from spermatophore consumption in some species, the current emphasis on the nutritional quality (i.e. protein content) of food gifts may be misplaced for others. Rather than deriving nutritional benefits through the consumption of the spermatophylax, females may instead secure a vital source of water. In decorated crickets, *Gryllobates sigillatus*, for example, the water contained in the spermatophylax constitutes 82% of its mass. Previous studies have shown that female *G. sigillatus* gain no nutritional benefits through consumption of the spermatophylax, in terms of either increased longevity or an

\*Author for correspondence and present address: Department of Biology, New Mexico State University, Las Cruces, NM 88003-8001, USA (traivy@nmsu.edu).

†Present address: Center for Ecology, Evolution and Behavior, T. H. Morgan School of Biological Sciences, University of Kentucky, Lexington, KY 40506-0225, USA.

increase in the number and mass of eggs produced (Will & Sakaluk 1994; Kasuya & Sato 1998). Nonetheless, members of both sexes steal spermatophylaxes from mated females and consume them; this observation suggests that there is some benefit to their consumption (Sakaluk 1987). In these and other studies, however, females were provided with water *ad libitum*, such that any benefits brought about by the intake of additional water via courtship feeding may have been obscured.

Precisely how much of the water contained in the spermatophylax becomes available to females is unclear; for example, some of it may be used up in the process of hydrolysing spermatophylax proteins. Nonetheless, the potential hydration benefits to spermatophylax consumption may be substantial: when deprived of food, but given unlimited access to water, females typically live about two weeks, but when deprived of both food and water, they rarely live more than 48 h (Burpee & Sakaluk 1993; T. M. Ivy, unpublished data). Moreover, the species often occurs in xeric habitats (e.g. the south-western United States) where the availability of water is not always certain. For *G. sigillatus* and other gift-giving species, females may employ multiple mating as a tactic to obtain water contained in courtship food gifts, thereby enhancing their own survival (Reinhold & Heller 1993; Will & Sakaluk 1994). In this paper, we test the hypothesis that courtship feeding in decorated crickets provides important hydration benefits to females by experimentally manipulating the availability of water and the number of food gifts that females are permitted to consume.

## 2. METHODS

Experimental *G. sigillatus* were descendants of approximately 200 adult crickets that were collected in Tucson, Arizona, in October 1995. Adult crickets were housed in 75.7 l terraria, and provisioned with cricket chow, ample water, and egg cartons to provide shelter and increase surface area. Oviposition substrate, a mixture of sand and vermiculite, was also provided and moistened daily. Nymphs were reared in plastic shoe boxes (16.5 cm × 30.5 cm × 8.5 cm), and given food, water, and egg cartons. We placed newly moulted females (day 1 virgins) individually in 1 l plastic containers upon their eclosion. On day 3, experimental females were weighed to the nearest milligram. Newly emerged adult males, used in mating trials and as a source of spermatophylaxes, were housed together in shoe boxes. All crickets were maintained on a 12 L:12 D cycle at 28 °C.

Females from three successive generations were used as experimental subjects ( $n=92$ ). We permitted each female to mate twice to ensure her insemination. Matings were staged in 1 l plastic containers under red incandescent light. Virgin females were given three consecutive days, beginning at day four, to complete their initial mating. Twenty-four hours after the initial mating, mated females were given the opportunity to remate with a different male on two consecutive days. To ensure equal insemination across treatments, we prevented females from removing the sperm ampulla after each mating. Ampulla removal was prohibited by keeping females in narrow test tubes for a period of 50 min, the time that it takes for the ampulla to completely empty of sperm (Sakaluk 1984). After 50 min, we removed both the spermatophylax and the ampulla with forceps.

On completion of the second mating, we randomly assigned females to one of three treatments: provision of zero, one, or two spermatophylaxes per day, each day of the female's life. Females often mate twice in a single day, but rarely more than twice; thus, our provision of spermatophylaxes corresponds to the natural range of variation for this species (Sakaluk 1987; S. K. Sakaluk, A.-K. Eggert and W. A. Snedden, unpublished data). Spermatophylax treatments were replicated under three hydration regimes: (i) water provided *ad libitum*; (ii) no water provided; and (iii) water provided every second day (sample sizes are shown in figure 1). We obtained spermatophylaxes by removing them from males' spermatophoric pouches (Sakaluk & Smith 1988). Subsequently, spermatophylaxes were placed on the bottom of the females' cages, where they are readily found and consumed by females (Will & Sakaluk 1994; T. M. Ivy, personal observations).

Mated females, housed individually in 1 pint (ca. 0.5 l) containers, were maintained in incubators at 28 °C on a 12 L:12 D cycle. Position within the incubator was randomized daily. Experimental females were provided with egg cartons, water according to treatment, and food that was oven-dried to remove residual moisture. Female crickets will not oviposit unless the soil in which they deposit their eggs is kept moist. Therefore, we cut circular openings in the bottoms of the containers that held experimental females and affixed to the openings metal screens of the appropriate mesh size (1.2 mm × 1.8 mm). These containers were then placed inside slightly larger containers, which held oviposition dishes filled with moistened oviposition substrate. Thus, the mesh screen was positioned directly on top of the substrate, allowing females to insert their ovipositors through the screen and deposit eggs but preventing them from bringing their mouthparts into direct contact with the moistened substrate. Hence, eggs could be kept suitably moist, permitting normal development, without inadvertently supplying females with water.

We counted emerging nymphs daily and recorded total offspring production. We measured female longevity as the day of emergence to the day of death. We eliminated from the study females that produced fewer than five nymphs ( $n=5$ ). These females were probably sterile; the nymphs counted were probably a result of cross-contamination from other containers.

All data were analysed by means of the Statistical Analysis System (SAS) for personal computers (SAS Institute 1988). Data were transformed, when necessary, to meet the assumptions of statistical tests. When multiple comparisons were made, we controlled for type I error by employing the sequential Bonferroni method (Holm 1979). Because female age and mass are known to affect fecundity, female age at the time females were established on their respective treatments, and their mass three days after the imaginal moult, were entered as covariants in all analyses. Because females from three generations were used in the study, we also examined the effect of generation on all dependent variables.

## 3. RESULTS

Mean female body mass did not differ across treatments (one-way ANOVA,  $F_{8,83}=0.38$ , n.s.), nor was female body mass significantly correlated with the number of nymphs produced (Pearson correlation coefficient =  $-0.092$ , n.s.) or longevity (Pearson correlation coefficient =  $-0.067$ , n.s.). Age at second mating had no significant effect on number of nymphs produced

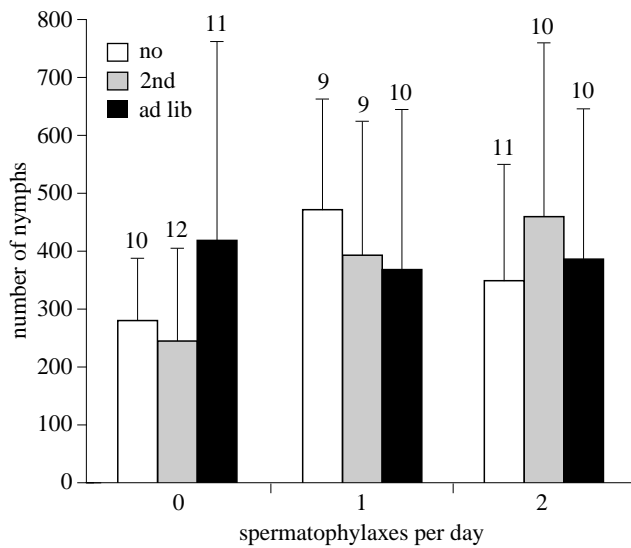


Figure 1. The least-squares mean number of nymphs at each level of water availability within spermatophylax consumption levels ( $\pm$  s.e.). Numbers above error bars represent sample sizes for each treatment. A three-way ANOVA revealed a significant interaction between the level of water availability and number of spermatophylaxes consumed on total offspring production ( $p=0.0218$ ).

(one-way ANOVA, square-root transformed,  $F_{8,83}=0.25$ , n.s.) or longevity (one-way ANOVA,  $\log_{10}$  transformed,  $F_{8,83}=0.30$ , n.s.). Generation had no significant effect on female longevity (one-way ANOVA,  $\log_{10}$  transformed,  $F_{8,83}=0.38$ , n.s.), but it did have a significant effect on the number of nymphs produced (one-way ANOVA, square-root transformed,  $F_{8,83}=7.24$ ,  $p=0.0012$ ). Consequently, we incorporated generation as a main effect in all subsequent analyses involving the number of nymphs.

#### (a) Number of nymphs

The least-squares mean number of nymphs produced in each treatment is shown in figure 1. A three-way ANOVA revealed a significant second-order interaction between the availability of water and the number of spermatophylaxes consumed on total offspring production ( $F_{4,83}=3.09$ ,  $p=0.0218$ ). The third-order interaction of water  $\times$  spermatophylax  $\times$  generation was not significant, nor were the remaining second-order interactions. Pairwise comparisons, using least-squares means within the zero-spermatophylax treatments, showed that both females deprived of water and females given water every second day produced significantly fewer nymphs than those females which were provided with water *ad libitum* ( $p=0.0182$  and  $p=0.0131$ , respectively). No other pairwise comparison within the remaining spermatophylax treatments were significant.

#### (b) Longevity

The least-squares mean female longevity for each treatment is shown in figure 2. A two-way ANOVA revealed that water availability had a significant effect on female longevity ( $F_{2,83}=12.98$ ,  $p=0.0001$ ). However, there was no significant effect of number of spermatophylaxes consumed ( $F_{2,83}=1.11$ , n.s.), nor was there a significant interaction effect ( $F_{4,83}=0.34$ , n.s.). Pairwise comparisons

showed that females provided with water every second day and females provided with water *ad libitum* survived significantly longer than females deprived of water ( $p<0.0001$  in each case). The longevities of females provided with water *ad libitum* and those provided with water every second day did not differ significantly.

## 4. DISCUSSION

The results of this study suggest that when females are water stressed, they benefit from the consumption of spermatophylaxes in terms of an increased number of nymphs. Among females not permitted to consume spermatophylaxes, those that were either deprived of water or given water only every second day produced significantly fewer nymphs than those females given access to water *ad libitum*. There were no significant differences in nymph production among the other spermatophylax treatments; this result suggests that when females are experiencing water stress, the consumption of food gifts results in an increase in offspring production to levels comparable to those of females given water *ad libitum*. In addition, it appears that the consumption of just one spermatophylax per day is sufficient to produce this increase. Therefore, a water-stressed female need mate only once a day to attain normal reproduction. In some insect species, females apparently employ multiple mating to secure nutrients contained in male contributions at mating (Sakaluk & Cade 1980, 1983; Butlin *et al.* 1987; Simmons 1988). Female *G. sigillatus* may, under conditions of water stress, mate with multiple males to obtain the water contained in spermatophylaxes.

The extent to which female *G. sigillatus* obtain hydration benefits in nature through the consumption of spermatophylaxes depends on how frequently they experience water deprivation of the severity manifested in our experimental treatments. Our experimental subjects were descended from crickets originally collected at Tucson, located in the Sonoran Desert in southern Arizona. Here *G. sigillatus* often has to survive extended periods of little or no precipitation lasting several months, particularly during the dry fore-summer. Although the species breeds all year round, populations are severely depressed during periods of low precipitation even with favourable temperatures, but increase markedly after the onset of summer rains (Thomas 1985; Smith & Thomas 1988). During periods of drought, most or all of the water intake of crickets almost certainly comes from the food items they consume. In the present study, both females held without water and those given water every second day showed reduced reproduction when given no opportunity to consume spermatophylaxes. Even those females held without free-standing water undoubtedly were able to obtain water from moisture absorbed by their food, a situation that we could not entirely avoid owing to the high humidity in experimental containers arising from the daily watering of oviposition dishes. It seems likely, then, that *G. sigillatus* in natural populations are often subject to the kinds of water stress established in our experimental treatments, at least at certain times of the year, but exactly how pervasive such stress is must await long-term studies of water relationships in free-living individuals.

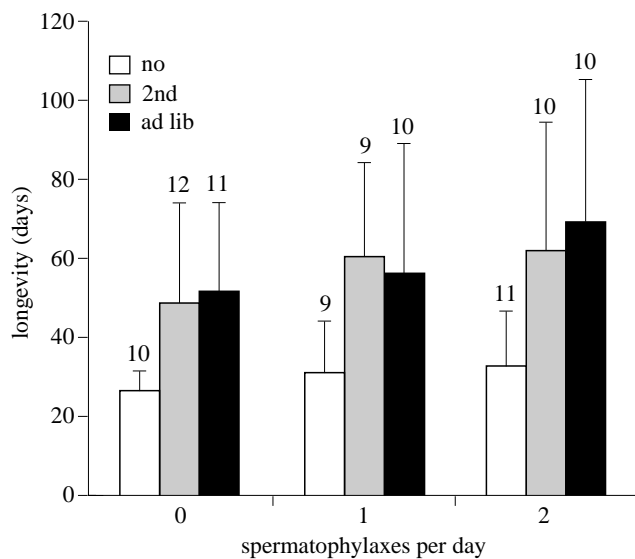


Figure 2. The least-squares mean female longevity for each level of water availability ( $\pm$  s.e.). Numbers above error bars represent sample sizes for each treatment. A two-way ANOVA revealed that water availability had a significant effect on female longevity ( $p=0.0001$ ). Females provided with water *ad libitum* (ad lib) did not show increased longevity relative to those females provided with water every second day (2nd) ( $p=0.0167$ ). However, females provided with water (both every second day and *ad libitum*) survived significantly longer than females deprived of water (no) ( $p<0.0001$ ).

Despite its benefits in terms of offspring production, spermatophylax consumption had no effect on female survival; only water availability significantly influenced female longevity. The differing effects of spermatophylax consumption on these life-history parameters suggest a trade-off between reproduction and survival when water is limited. This type of trade-off is well documented and forms the basis for much of the theory concerning life-history strategies (for reviews see Bell 1980; Partridge & Harvey 1985; Stearns 1989). When resources are scarce, organisms must often alter the allocation of resources between current reproductive effort and survival to avoid reproductive failure. Kaitala (1987, 1991) showed that female water striders exposed to food stress exhibited increased fecundity and decreased longevity relative to those females given unlimited access to food. However, *G. sigillatus* females appear to employ a different strategy: when females are deprived of water, both longevity and fecundity are decreased relative to those of females provided with water *ad libitum*. Water-deprived females provided with spermatophylaxes increase their fecundity relative to females unable to secure spermatophylaxes, but still experience the same reduced longevity; this result suggests that females use the resources contained in food gifts for reproduction instead of for their own survival.

For reasons unknown, the generation from which experimental females were drawn did have a significant effect on nymph production. The number of experimental containers varied with generation, and only one generation of females were experimental subjects at any one time. The varying numbers of experimental containers per generation and the concomitant increase in humidity with an increase in the number of containers inside the

incubator may have resulted in differences in nymph production.

There has been considerable debate over the extent to which resources donated by males actually contribute to the donating male's offspring (reviewed in Vahed 1998). Parker & Simmons' (1989) models suggest that selection favours the immediate use of resources contained in nuptial gifts because a male's certainty of paternity is likely to decline over time owing to successive matings by the female. Indeed, several studies suggest that incorporation of male-donated nutrients can occur rapidly and within the refractory period of females (for a review see Parker & Simmons 1989). In this regard, water would appear to be the ideal nuptial gift as one might expect it to be incorporated into eggs fairly rapidly. Because females do not use the resources contained in spermatophylaxes toward somatic maintenance, it is certainly conceivable that the water contained in spermatophylaxes benefits the donating male's progeny, although further study is needed to test this hypothesis.

The present study and others have demonstrated that male donations may serve as prezygotic male investment and yet not benefit females in a strictly nutritional sense. For example, Mullins & Keil (1980) revealed that female cockroaches secure an important source of nitrogen from urates that bind to the spermatophores donated by males. Male provision of defensive chemicals, which serve to protect eggs against predation, has been documented in beetles, butterflies, and moths (Eisner & Meinwald 1995). Parker & Simmons (1989) expanded Trivers' (1972) classic definition of parental investment to include 'any increase in the reproductive output of a given female [that produces that male's offspring]'. Under this definition, male provision of water to females via spermatophylax consumption could be considered prezygotic paternal investment. Although it is generally believed that the spermatophylax evolved as a device serving to ensure transfer of a male's sperm (Wickler 1985; Quinn & Sakaluk 1986; Simmons & Parker 1989), this does not preclude the possibility that gifts are maintained as a result of fitness benefits realized by females through their consumption. However, the hydration benefits to spermatophylax consumption in female *G. sigillatus* may be wholly incidental if males simply lack the ability to manufacture a viable spermatophore that is devoid of water (see Quinn & Sakaluk 1986; Will & Sakaluk 1994).

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