

SHORT COMMUNICATION

Nutritional condition influences investment by male katydids in nuptial food gifts

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Introduction

Nuptial food gifts in katydids come in the form of a spermatophylax, a gelatinous adjunct to the male's spermatophore that is consumed by the female after mating (Brown & Gwynne, 1997; Vahed, 1998). In some tettigoniid species, consumption of the spermatophylax leads to enhanced female reproductive output (Gwynne, 1984a, 1988; Simmons, 1990; Reinhold, 1999), whereas in others, females derive few, if any, nutritional benefits (Wedell & Arak, 1989; Vahed & Gilbert, 1997). Previous studies have revealed that when populations of certain species are subject to food stress, a sex-role reversal may occur in which females compete for choosy males (Gwynne, 1984b, 1993; Gwynne & Simmons, 1990). Such a reversal may occur because males' ability to produce food gifts under these circumstances is constrained, while the demand for food gifts by females is correspondingly increased. However, this argument is premised in part on the assumption that the nutritional quality of males' spermatophores is maintained across different nutritional regimes. If food-stressed males reduce the nutritional quality of their food gifts to maintain their potential rate of mating, the operational sex ratio under food stress may be similar to that under high food conditions, mitigating against sex-role reversal (see Gwynne, 1990).

Investment by male katydids in nuptial food gifts represents a trade-off between resources allocated to the spermatophylax and the time required to accrue those resources. Theoretically, males subject to food stress could respond in one of several ways: (1) maintain the quality of their food gifts, even if this necessitates longer intercopulatory intervals, (2) reduce the quality of their food gifts to achieve the same mating frequency as occurs under conditions of high food abundance, or (3) vary both investment in nuptial food gifts and intercopulatory interval. Studies of two Australian katydids and one European species suggest that males subject to food stress hold their investment in the spermatophylax constant. Gwynne (1990) found no difference in the average spermatophore

mass of male *Requena verticalis* maintained on either a low- or high-quality diet. Similarly, Simmons (1994) found no difference in the caloric content of the spermatophores of male *Kawanaphila nartee* maintained on a limited or *ad libitum* diet. Finally, Wedell (1993a) found no difference in either the mass or protein content of the spermatophylax of male wartbiters *Decticus verrucivorus* in relation to food quality; however, even under food stress, males were able to maintain their mating frequency, suggesting that the cost of producing a spermatophylax in this species is low. The extent to which the results of these studies can be generalised to other tettigoniids remains unknown.

In the present study, the effect of varying nutrition on male investment in the spermatophylax and remating ability was investigated in *Gampsocleis gratiosa* (Orthoptera: Tettigoniidae), a katydid species widely distributed in China. In *G. gratiosa*, the spermatophylax envelops a small sperm-containing ampulla whose contents are emptied through a narrow tube threaded into the female's genital chamber; both components of the spermatophore remain anchored outside the female's body after mating. Following spermatophore transfer, the female detaches the spermatophylax from the ampulla with her mandibles and consumes it.

Methods

Experimental individuals were collected from Yi County, Hebei Province, China (39°20'N, 115°30'E), held in individual cages, and maintained on an *ad libitum* diet consisting of powdered maize, apple, various green vegetables, and water for at least 7 days prior to the experiment. Cages were constructed by removing the tops and bottoms of empty 365-ml soda cans, and securing them to both ends of a cylinder constructed of aluminium-mesh screening (16 cm diameter × 30 cm height). Because the mating experience of field-collected katydids was unknown, all individuals were mated once 3 days prior to experimental trials to standardise mating condition. Males were weighed prior to matings. After the initial matings, males were held for 3 days under one of three

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nutritional regimes prior to mating trials: (1) high-protein diet (mixture of egg white and powdered maize); (2) low-protein diet (powdered maize and water); (3) no food (water only). All females were maintained on the low-protein diet.

Males were paired individually with females during mating trials. Following copulation, the spermatophore was removed from the female and each component of the spermatophore was weighed separately to the nearest 0.1 mg. The spermatophylax and ampulla were then dried in a drying oven at 49 °C for 48 h, and re-weighed. Males were weighed after mating. Immediately following copulations, mated females were replaced with fresh females and the frequency of rematings was scored.

Mating trials were staged outdoors in the shade over a period of several days [ambient temperature 29.3 ± 2.3 (SD) °C]. Observation periods lasted 14.2–16.5 h, and if a male did not remate within this time, the trial was terminated and the male was scored as having not remated. No food or water was provided to experimental individuals during mating trials.

Results and discussion

There was no difference in the body mass of males assigned to different treatments prior to being placed on their respective dietary regimes ($P > 0.05$). There was a significant effect of diet on the mass of the spermatophylax synthesised by males (Table 1). Tukey *post hoc* pairwise comparisons revealed that high-protein males produced significantly larger spermatophylaxes than low-protein and food-deprived males, but there was no difference in spermatophylax mass between low-protein and food-deprived males. Similarly, high-protein males were of higher body mass and produced larger ampullae than either low-protein or food-deprived males, but there was no difference between low-protein or food-deprived males in either of these parameters. Nuptial food gifts of starved males tended to have a higher water content than those of other males, but this trend was not significant ($F = 2.70$, $P = 0.079$). Across all males, there was a significant positive correlation between the mass of the ampulla and the mass of the spermatophylax ($n = 44$, $r = 0.92$, $P < 0.001$; Fig. 1). Nutritionally stressed males were significantly less likely to

remate than were males held on the high-protein diet (likelihood ratio χ^2 , $L = 20.4$, $P < 0.001$; Fig. 2).

There was a significant decrease in the mass of the spermatophylax produced by nutritionally stressed males. There was also the suggestion that males deprived of food increased the water content of their spermatophylaxes. Hence, it appears that under conditions of low food abundance, males are willing to sacrifice the nutritional quality of their food gifts. Although variation in diet has been implicated as an important cause of variation in the nutritional quality of the spermatophylax across katydid species (Wedell, 1994; but see Gwynne, 1995), this is the first study to document an effect of diet on variation in spermatophylax quality within a species. A decrease in the nutritional quality of food gifts of males subject to food stress may, in turn, lower their value to females and thereby constrain the potential for sex-role reversal. This may explain at least partially why certain katydid species show evidence of sex-role reversal (Gwynne, 1981, 1984b, 1985; Gwynne & Simmons, 1990; Ritchie *et al.*, 1998), whereas others do not (Morris, 1971; Gwynne, 1982; Feaver, 1983).

Gwynne (1985) suggested that a tactic of manufacturing smaller spermatophylaxes would be unlikely to evolve because it would lead to greater female interference with sperm transfer. The basis for this argument is that females typically remove and eat the sperm ampulla following their consumption of the spermatophylax and, because smaller spermatophylaxes require less time to consume, their production often leads to premature removal of the ampulla and reduced sperm transfer (review in Vahed, 1998). This argument assumes, however, that males hold the size of their ejaculates constant irrespective of the size of their nuptial food gifts. But in the study reported here, there was a significant positive correlation between the mass of the spermatophylax and mass of the ampulla across all treatments, suggesting that males adjust the size of their ejaculates in accordance with the size of the food gifts they are able to produce, thereby avoiding any waste of sperm (see also Wedell, 1993b; Heller & Reinhold, 1994; Vahed & Gilbert, 1996). The reduced fertilisation rate of males producing smaller food gifts and transferring smaller ejaculates may be more than offset by an increased mating frequency relative to males failing to make such facultative adjustments (see Calos & Sakaluk, 1998).

Table 1. Body mass and mass of spermatophore components of male *Gampsocleis gratiosa* held under different nutritional regimes. All P -values based on one-way ANOVA. Means with different letters are significantly different based on Tukey *post hoc* pairwise comparisons.

	High protein ($n = 14$)	Low protein ($n = 15$)	No food ($n = 15$)	P
Body mass (g)	4.84 ± 0.12^a	3.86 ± 0.13^b	3.67 ± 0.15^b	<0.001
Wet spermatophylax (g)	0.39 ± 0.02^a	0.27 ± 0.01^b	0.27 ± 0.02^b	<0.001
Wet ampulla (g)	0.12 ± 0.005^a	0.09 ± 0.005^b	0.09 ± 0.005^b	<0.001
Water content of spermatophylax (%)	87.0 ± 0.47^a	86.9 ± 0.90^a	88.8 ± 0.48^a	0.079
Dry spermatophylax (g)	0.050 ± 0.003^a	0.036 ± 0.003^b	0.030 ± 0.003^b	<0.001
Dry ampulla (g)	0.026 ± 0.001^a	0.018 ± 0.001^b	0.017 ± 0.001^b	<0.001

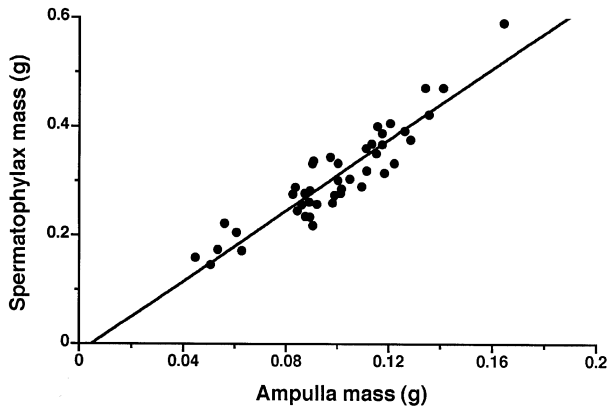


Fig. 1. Correlation between the mass of the spermatophylax and mass of the sperm ampulla produced by male *Gampsocleis gratiosa* pooled across all treatments ($n=44$, $r=0.92$, $P<0.001$). The line shown is derived from a least-squares regression (spermatophylax mass = $3.26 \times$ ampulla mass $- 0.015$).

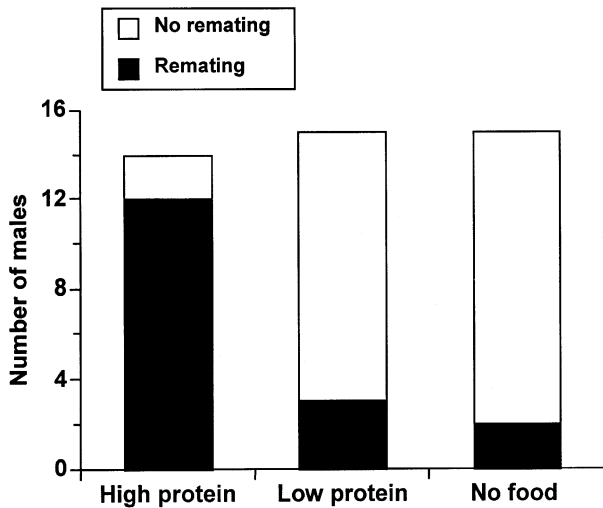


Fig. 2. The proportion of male *Gampsocleis gratiosa* that remated within 14.2–16.5 h. A significantly higher proportion of males maintained on the high-protein diet remated compared with males held on the low-protein and no-food treatments (likelihood ratio χ^2 , $L=20.4$, $P<0.001$).

Despite synthesising smaller food gifts, food-stressed males were far less likely to remate than males held under the high-protein regime. The reduction in spermatophylax mass does not therefore appear to be sufficient to ameliorate constraints imposed by food deprivation on male mating frequency. Thus, the number of sexually active males would be expected to decrease with decreasing food abundance, while the number of sexually receptive females would either remain the same or increase. This result supports previous studies showing an increase in the operational sex ratio under conditions of high food stress (Gwynne, 1990, 1993; Gwynne & Simmons, 1990; Simmons, 1992, 1994).

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