

Male field crickets that provide reproductive benefits to females incur higher costs

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Abstract. 1. Females often select mates based on signals correlated with the quality of the direct benefits that males will provide to them. A male's quality as a mate and the structure of his mating signals may covary because both traits are energetically expensive for males to produce and because both traits are affected by short-term changes in nutritional condition.

2. In the variable field cricket, *Gryllus lineaticeps*, previous work has shown that females receive reproductive benefits from males that produce higher chirp rates and lifespan benefits from males that produce longer chirp durations, even when they only receive the sperm and seminal fluid contained in male spermatophores. Higher chirp rates are energetically expensive for males to produce, and chirp rate is strongly affected by diet quality, whereas longer chirp durations do not appear to be expensive for males to produce, and chirp duration does not appear to be affected by male diet quality. In this study two hypotheses were tested about the energetic costs of spermatophore production: (1) that spermatophores are expensive for males to produce and (2) that males providing greater direct benefits to females incur higher costs of spermatophore production.

3. Males that were provided with a lower quality diet took longer to produce a new spermatophore. This result suggests that spermatophores are costly for males to produce.

4. Males that produced higher chirp rates took longer to produce a new spermatophore. This result suggests that male chirp rate and female reproductive benefits may covary because both traits are energetically expensive for males to produce and thus are affected by male nutritional condition. There was no association, however, between male chirp duration and spermatophore production time.

Key words. Direct benefits, field cricket, *Gryllus lineaticeps*, mate choice, reliable signals.

Introduction

Females often select mates based on the quality of the direct benefits that males will provide, such as the quality of food items, territory quality or the quality of male parental care (Andersson, 1994; Jennions & Petrie, 1997). For some types of direct benefits, females can directly assess the magnitude of the benefit prior to mating with a

male. When females select mates based on male territory quality, for example, females can often directly evaluate a male's territory quality before allowing the male to mate (Howard, 1978; Alatalo *et al.*, 1986; Warner, 1987). For other types of direct benefits, such as better male care of offspring, females can directly assess the magnitude of the benefit only after mating has occurred. When females cannot directly assess benefit quality prior to mating, they may instead indirectly assess the quality of a mating benefit using male signals that are correlated with benefit quality. For example, female birds may use the amount of male courtship activity to assess the quality of the paternal care that males will provide (Searcy & Yasukawa, 1981; Petrie, 1983; Buchanan & Catchpole, 2000). Similarly, female fish

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may use either male courtship rate or the rate at which males fan a current batch of eggs to assess the quality of the care that males will subsequently provide for their eggs (Downhower & Brown, 1980, 1981; Knapp & Kovach, 1991; Pampoulie *et al.*, 2004).

The use of male signals to assess the quality of a direct benefit opens up the possibility of deception; males might gain from signalling that they will provide a high quality benefit even if they are unable to do so. For female choice based on signals of post-mating benefit quality, there thus need to be factors that disfavour the production of deceptive signals by males unable to provide high quality benefits (i.e. low quality males). The most important factor preventing deceptive signalling by low quality males is thought to be differential costs of signal production (Zahavi, 1975; Nur & Hasson, 1984; Grafen, 1990; Iwasa *et al.*, 1991). For example, if producing more attractive signals and providing higher quality mating benefits are both energetically costly, only males in good condition may be able to afford to express higher values of both traits. Male signals and the quality of the mating benefits provided by males may thus positively covary because each trait is expensive to express and because the expression of each trait depends on male nutritional condition. While numerous studies have examined the costs of signal production in male animals (reviewed by Kotiaho, 2001), few studies have tested whether males that pay more for signals also pay more to provide direct benefits to females.

In the variable field cricket, *Gryllus lineaticeps*, females prefer male calling songs with higher chirp rates and longer chirp durations (Wagner, 1996; Wagner & Reiser, 2000; Wagner *et al.*, 2001a). Higher chirp rates are energetically more expensive for males to produce (Hoback & Wagner, 1997), and males provided with a higher quality diet produce higher chirp rates (Wagner & Hoback, 1999). Male chirp rate is thus partially dependent on short-term fluctuations in male nutritional condition. Similar effects of diet on singing behaviour have been found in other orthopterans (e.g. Holzer *et al.*, 2003; Scheuber *et al.*, 2003a). In contrast, there is no evidence that longer chirp durations are more expensive to males to produce, and males provided with a higher quality diet do not produce longer chirp durations.

During mating, a male field cricket transfers a spermatophore to a female that consists of a small ampulla containing sperm and seminal fluid. The spermatophore is attached externally to the female's genital pore, and it generally remains attached for between 30 and 90 min, after which the female removes and often consumes it (Loher & Dambach, 1989). Female *G. lineaticeps* appear to receive beneficial products in male seminal fluid (Wagner *et al.*, 2001b). In addition, females directly benefit from mating with males that produce higher chirp rates and longer chirp durations; females that were experimentally mated with males that produced higher chirp rates had greater lifetime fertility, while females that were mated with males that produced longer chirp durations had longer lifespans (Wagner & Harper, 2003). The fertility benefit

may result from females receiving more sperm from males that produce higher chirp rates, which allows females to fertilise a higher proportion of their eggs, or it may result from seminal fluid products that positively affect fertility. The lifespan benefit appears to result from females receiving more beneficial seminal fluid products from males that produce longer chirp durations. While the costs of variation in male singing behaviour have been examined (Wagner, 1996; Hoback & Wagner, 1997; Wagner & Hoback, 1999), it is not known whether males that provide greater benefits to females incur higher costs of spermatophore production.

The time it takes a male to replace a spermatophore after a given mating provides an indirect measure of the cost of spermatophore production (Simmons & Bailey, 1990; Wedell, 1993). For example, if spermatophores are costly to produce, males that receive a lower quality diet, and thus have less energy to invest in spermatophore production, should take longer to produce a new spermatophore than males provided with a higher quality diet (see Gwynne, 1990; Zia *et al.*, 2000). Diet quality can affect the time to produce a new spermatophore either because males experiencing a lower quality diet have a reduced ability to support spermatophore production at any given time or because these males conserve energy by increasing the time they take to produce a new spermatophore. In addition, if diet quality is held constant, males that produce costlier spermatophores should take longer to produce new spermatophores (Wedell, 1993). The cost of spermatophore production may affect the time to produce a new spermatophore either because males producing costlier spermatophores require longer to mobilise the energy required to produce their costlier spermatophores or because males producing costlier spermatophores conserve energy by increasing the time they take to produce a new spermatophore.

In the present study, the cost of spermatophore production for male *G. lineaticeps* and whether males that provide greater benefits to females incur higher costs of spermatophore production was examined. First, the effect of diet quality on spermatophore replacement time was tested. If spermatophores are costly for males to produce, males provided with a lower quality diet should take longer to produce a new spermatophore. Second, the relationship between male singing behaviour and spermatophore replacement time was examined. Males that produce calling songs containing higher chirp rates and longer chirp durations appear to transfer more beneficial seminal fluid products to females (Wagner & Harper, 2003). If the production of more beneficial ejaculates is more expensive than the production of less beneficial ejaculates, males that produce higher chirp rates and/or longer chirp durations should take longer to produce a new spermatophore.

Methods

Experimental subjects

The crickets that were used in experiments were the first- or second-generation offspring of field-inseminated females

that were collected from Tucker's Grove County Park, Santa Barbara, California. For the second-generation crickets, parental matings were arranged to minimise inbreeding and maximise genetic diversity in the laboratory stocks; only crickets that were the offspring of different field-collected females were mated, and offspring from all field-collected females were mated. Field-collected females or mated pairs were placed in a $16 \times 26 \times 17$ cm plastic family container provisioned with a paper towel substrate, paper or cardboard shelters, *ad libitum* cat chow, a water vial plugged with cotton, and a cup of moist vermiculite in which females could lay eggs. Offspring were raised in family containers until they neared their final moult, at which time they were transferred to $9 \times 16 \times 11$ cm individual containers where they completed their development. The individual containers were provisioned with a paper towel substrate, paper or cardboard shelters, and a water vial plugged with cotton. Because crickets were isolated prior to sexual maturation, all crickets used in the experiments were known to be virgins. In addition, the day of the final moult was recorded, thus all crickets were of known adult age. Females received *ad libitum* cat chow while males received *ad libitum* cat chow until placed on experimental diets (see below).

Diet and spermatophore production

In order to examine the effect of diet quality on spermatophore replacement time, pairs of full-sibling brothers were selected and one member of each pair was randomly assigned to a high-nutrition diet and the other member to a reduced-nutrition diet. The members of a pair reached their final moult (to the adult stage) within 1 day of each other and they were started on the diet treatments a minimum of 7 days and a maximum of 10 days after their final moult. Full-sibling brothers were used to control for genetic effects on spermatophore characteristics. Variation in time since the final moult was minimised to control for age effects on spermatophore characteristics. Different pairs were selected from different full sibships in order to ensure that there was an adequate sampling of male genotypes, and thus that the results were representative of the study population. Each cricket was weighed immediately prior to the start of the diet treatment to the nearest 0.1 mg using a Sartorius BP61 scale. Males were then placed on experimental diets consisting of 14.3% casein, 40% bran, 28.6% baker's yeast, and 17.1% wheat germ. Males were fed 25 mg of the experimental diet per day, but the diet of males on the low-nutrition feeding regime was diluted with 50% non-nutritive cellulose (see Wagner & Hoback, 1999). Males were maintained on these experimental diets for 7 days.

After 7 days on the feeding regimes each male was weighed and placed in a $16 \times 26 \times 17$ cm container with a dry vermiculite substrate. Three randomly chosen virgin females that were 7 days past their final moult were then introduced into the container. The females used were from different full sibships than the males with which they

were paired and different full sibships from each other. Three virgin females were placed with each male to increase the probability that a receptive female would be available when a male was ready to transfer a spermatophore. The males and females were observed using a dim red light, and the time at which a male produced song and transferred a spermatophore to a female was recorded. After a female mated, the spermatophore was immediately removed, the wet mass of the spermatophore was determined, and the mated female was replaced with a virgin female so that there were always three virgin females present with the male. All males were observed continuously throughout the experiment. The mating trials were run until a male had transferred at least three spermatophores or until 6 h had passed.

After transferring a spermatophore to a female the male must produce a new spermatophore. A male does not sing again until it has produced and is ready to transfer another spermatophore. The time from the transfer of a spermatophore to a female until the male resumed singing was recorded (the spermatophore-singing interval). Because of the surplus of virgin females, males should benefit from transferring another spermatophore as soon as it is ready. The duration of the spermatophore-singing interval should therefore represent the time required for a male to produce a replacement spermatophore. In order to calculate the first spermatophore-singing interval for the males of a pair (full siblings of the same age placed on different diets), both males needed to transfer at least one spermatophore to a female and resume singing within the 6-h observation period. Data on the first spermatophore interval were available for 19 pairs of males. In 14 of these pairs both males transferred a second spermatophore. Of these 14 pairs, both males in 12 of the pairs resumed singing by the end of the 6-h observation period, allowing determination of the second spermatophore-singing interval.

The pairs of full-sibling males placed on different diets were tested at the same time, thus at the same temperature. Because of the paired design, and because all statistical comparisons were made within pairs, it was unnecessary to control for temperature effects on spermatophore-singing interval and on spermatophore mass.

Male phenotype and spermatophore production

In order to examine the relationship between male singing behaviour and spermatophore replacement time, males were placed on the high-nutrition diet described above upon their final moult. Male diet quality was thus held constant in this experiment. Between and 7 and 10 days after their final moult, the males were weighed to the nearest 0.1 mg using a Sartorius BP61 scale and male singing behaviour was measured. Male songs were recorded and analysed using a Cambridge Electronic Design micro1401 sound acquisition interface, Spike2 software and a Macintosh computer. Males were recorded in individual sound attenuating chambers equipped with a Sennheiser

ME 67 microphone with a K6 power module connected to the micro1401. Because the duration of singing activity varied among males, the segment of continuous calling song that was analysed ranged between 30 and 180 s. Songs were digitised at a sampling rate of 22 kHz, and they were analysed using a custom-designed script that automatically calculated chirp rate and average chirp duration. Chirp rate (chirps s^{-1}) was measured as the number of chirps a male produced over the sampling interval divided by the duration of the sampling interval. Chirp duration (ms) was measured as the average duration of all chirps produced during the sampling interval. Both of these song characters are affected by temperature (Hoback & Wagner, 1997; Wagner & Reiser, 2000). Because comparisons of male song phenotypes are potentially confounded by temperature variation among recording periods, all song characters were adjusted to 20.0 °C prior to statistical analysis based on the regression of each song character on temperature as follows: $CR_{adj} = CR_{obs} + 0.024 \times (20.0 - TEMP_{obs})$; $CD_{adj} = CD_{obs} - 0.003 \times (20 - TEMP_{obs})$, where CR is chirp rate and CD is chirp duration.

Within 2 days of measuring a male's singing behaviour, the first spermatophore-singing interval for each male was measured. Each male was weighed, the room temperature was recorded, and then the male was placed in a $16 \times 26 \times 17$ cm container with three virgin females. The females used were from different full sibships than the males with which they were paired and different full sibships than each other. The first spermatophore-singing interval for each male was measured as described for the previous experiment. A trial was stopped when a male resumed singing after having transferred an initial spermatophore.

Results

Diet and spermatophore production

There was not a significant difference in the initial masses of the full-sibling males placed on the two feeding regimes (high nutrition: $\bar{x} \pm SE = 0.518 \pm 0.020$ g; reduced nutrition: $\bar{x} \pm SE = 0.514 \pm 0.020$ g; paired $t_{18} = 0.14$, $P = 0.888$). After 7 days on the feeding regimes, males provided with a high-nutrition diet did not show a significant change in mass ($\bar{x} \pm SE = -0.005 \pm 0.007$ g; paired $t_{18} = 0.71$, $P = 0.487$) whereas males provided with a reduced-nutrition diet showed a significant reduction in mass ($\bar{x} \pm SE = -0.017 \pm 0.006$ g; paired $t_{18} = 2.75$, $P = 0.013$).

There was a significant difference between males in the two diet treatments in the first spermatophore-singing interval; males on the high nutrition diet were ready to transfer a second spermatophore to females approximately 37% faster after transferring a first spermatophore than their brothers on the low nutrition diet (Fig. 1a; paired $t_{18} = 2.73$, $P = 0.014$). Similarly, there was a significant difference between males in the two diet treatments in the

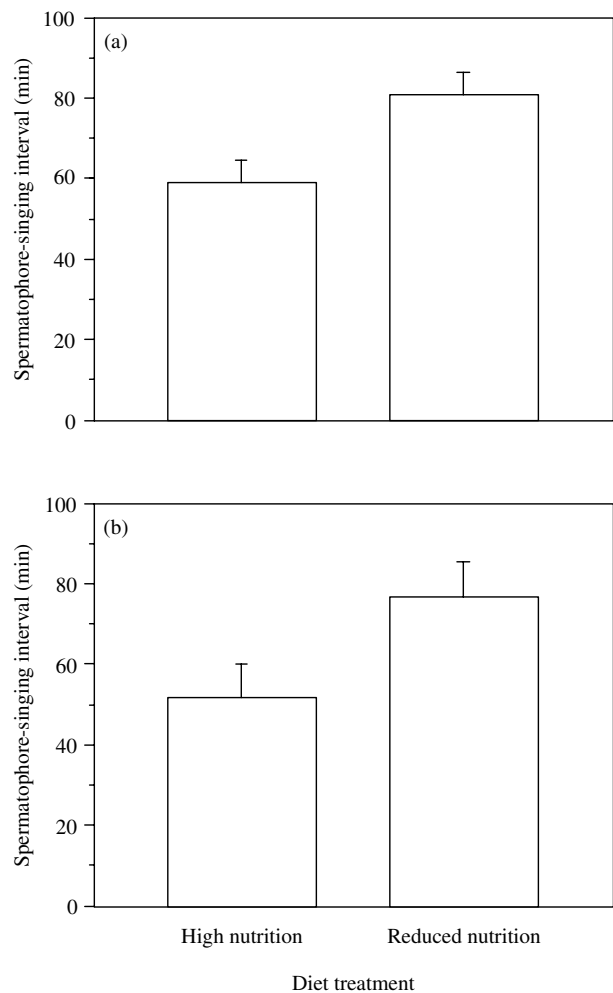


Fig. 1. The effect of diet on (a) the first spermatophore-singing interval (the time it took a male to resume singing after transferring his first spermatophore) and (b) the second spermatophore-singing interval (the time it took a male to resume singing after transferring his second spermatophore). Males do not sing until they are ready to transfer a spermatophore to a female. Bars show means + standard errors.

second spermatophore-singing interval; males on the high nutrition diet were ready to transfer a third spermatophore to females approximately 47% faster after transferring a second spermatophore than their brothers on the low nutrition diet (Fig. 1b; paired $t_{11} = 2.29$, $P = 0.043$).

There was no significant difference between males in the two diet treatments in either first spermatophore mass (Fig. 2a; paired $t_{18} = 0.533$, $P = 0.601$) or second spermatophore mass (Fig. 2b; paired $t_{13} = 0.534$, $P = 0.603$). In addition, there were no significant correlations between spermatophore interval and spermatophore mass for males on either the high nutrition diet (interval 1 and mass 1: $r_{19} = -0.34$, $P = 0.156$; interval 1 and mass 2: $r_{17} = 0.04$, $P = 0.890$; interval 2 and mass 1: $r_{15} = -0.40$, $P = 0.144$; interval 2 and mass 2: $r_{15} = 0.08$, $P = 0.784$) or

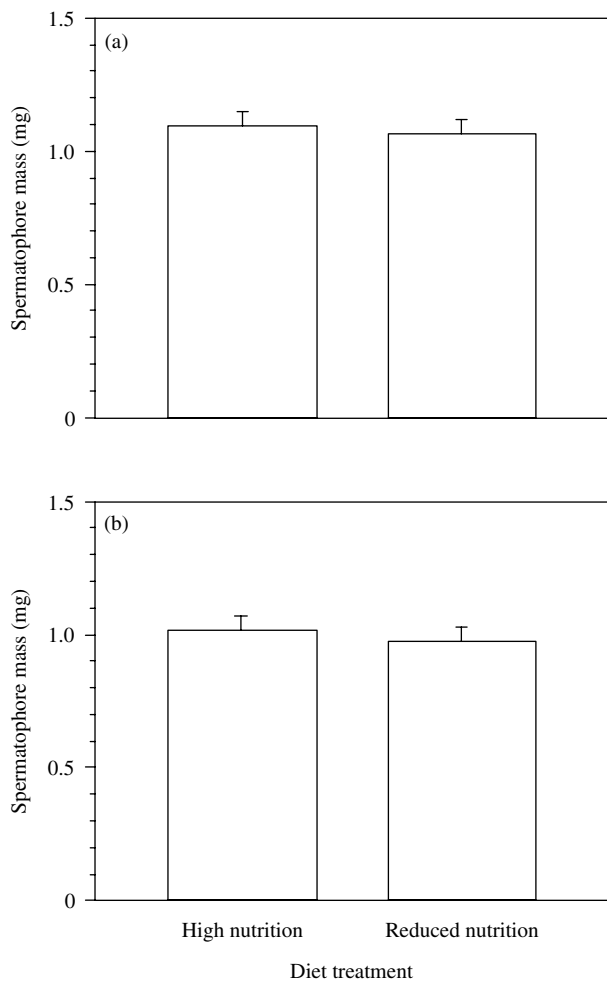


Fig. 2. The effect of diet on (a) first spermatophore wet mass and (b) second spermatophore wet mass. Bars show means + standard errors.

the low nutrition diet (interval 1 and mass 1: $r_{19} = 0.28$, $P = 0.255$; interval 1 and mass 2: $r_{16} = -0.25$, $P = 0.367$; interval 2 and mass 1: $r_{13} = 0.07$, $P = 0.833$; interval 2 and mass 2: $r_{11} = -0.36$, $P = 0.292$).

Male phenotype and spermatophore production

There was a significant positive correlation between male chirp rate and the spermatophore-singing interval ($r_{61} = 0.32$, $P = 0.011$); males that produced lower chirp rates were ready to transfer a second spermatophore to a female faster than were males that produced higher chirp rates. There was no significant correlation between male chirp duration and the spermatophore-singing interval ($r_{61} = -0.20$, $P = 0.111$). Because male chirp rate and chirp duration were negatively correlated ($r_{61} = -0.29$, $P = 0.019$; see also Wagner & Harper, 2003), multiple regression was used to examine the independent effects of

chirp rate and chirp duration on the spermatophore-singing interval. Testing temperature was included in the analysis as the spermatophore interval was positively correlated with temperature ($r_{63} = 0.31$, $P = 0.014$). Chirp rate had a significant independent effect on the spermatophore interval (Table 1); males that produced lower chirp rates were ready to transfer a second spermatophore to a female faster than males that produced higher chirp rates (Fig. 3a). There was no significant independent effect of chirp duration on the spermatophore interval (Table 1, Fig. 3b).

Discussion

Diet quality had a small effect on the mass of male *G. lineaticeps*; males that were provided with a lower quality diet lost mass while males that were provided with a higher quality diet did not lose mass. In a previous study that examined the effect of diet quality on male singing behaviour, diet quality had no effect on male mass but had large effects on male singing behaviour (Wagner & Hoback, 1999). Males of this species appear to defend their mass when nutritionally stressed by reducing the amount of energy invested in the costly singing activity.

If spermatophores are costly for males to produce, males could respond to a reduction in available energy by increasing the time they take to produce a spermatophore, by decreasing the size of the spermatophore they produce, or by both increasing spermatophore production time and decreasing spermatophore size (Zia *et al.*, 2000). Males provided with a higher quality diet produced a new spermatophore 37% faster than males provided with a lower quality diet. This result provides indirect evidence that spermatophores are costly for males to produce. Similar results have been found in other studies of arthropods (Gwynne, 1990; Proctor, 1992; Zia *et al.*, 2000). In contrast, there was no effect of diet quality on spermatophore mass. It thus appears that males take longer to produce a spermatophore when they experience a poor quality diet but maintain spermatophore size relatively constantly, at least across the range of diets tested. Differences in spermatophore mass, however, can be a poor predictor of differences in chemical composition (Marshall & McNeil, 1989). It is possible that male *G. lineaticeps* experiencing a lower quality diet produced less costly spermatophores, and spermatophores that were less beneficial to females, without a concomitant change in spermatophore mass. Some orthopterans are known to produce less valuable spermatophores when provided with a lower quality diet (Zia *et al.*, 2000).

At least two hypotheses can explain the effect of diet quality on spermatophore replacement time: (1) males in poor nutritional condition may not have had sufficient usable energy to rapidly replace spermatophores; or (2) males in poor nutritional condition may have had to extend the time they took to replace their spermatophores in order to conserve energy. It is not possible to discriminate between these hypotheses with the available data. It is also possible that males in poor nutritional condition had

Table 1. Multiple regression of male chirp rate, chirp duration, and testing temperature on the spermatophore interval ($F_{3,59} = 4.16$, $P < 0.010$).

Variable	Coefficient	SE	<i>t</i>	<i>P</i>
Chirp rate	8.29	3.73	2.23	0.030
Chirp duration	-40.09	148.20	0.27	0.788
Temperature	3.50	1.44	2.43	0.018

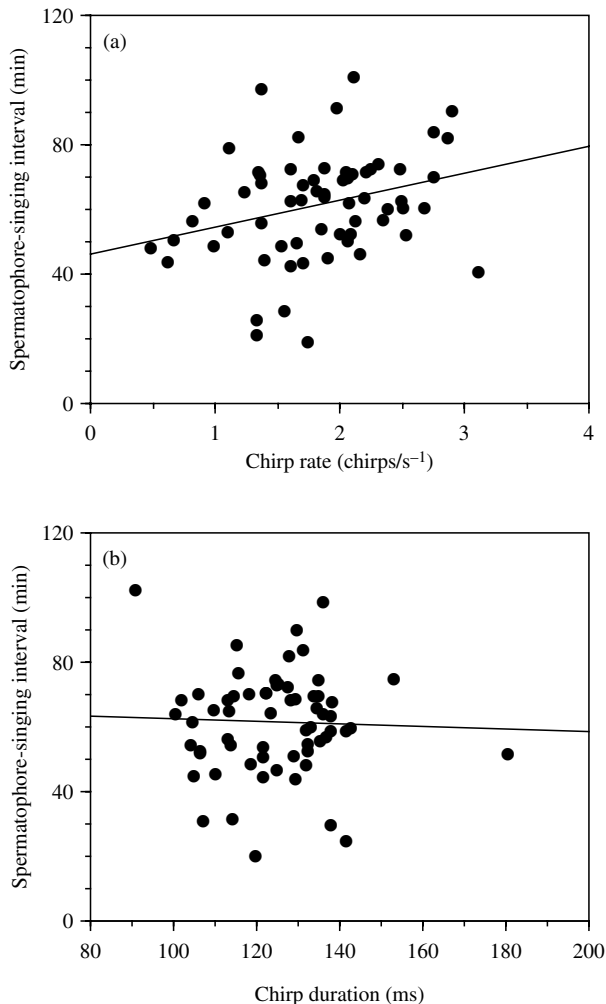


Fig. 3. The relationship between male calling song and spermatophore replacement time. (a) Partial regression of chirp rate on the spermatophore-singing interval. (b) Partial regression of chirp duration on the spermatophore-singing interval.

spermatophores ready to transfer before they resumed singing but chose to wait to provide them to females. If so, the spermatophore-singing interval would not provide an accurate measure of the time it took a male to produce a replacement spermatophore. This hypothesis, however, would also suggest that spermatophores are costly to produce and that males conserved energy by rationing their

spermatophores. This explanation seems unlikely as males were provided with a surplus of virgin females and should have benefited from mating with one of these females as soon as a new spermatophore was ready to transfer.

Not only do the results suggest that spermatophores costly for male *G. lineaticeps* to produce, but they also suggest that males that provide some types of mating benefits to females incur greater costs of spermatophore production. Females receive lifetime fecundity and fertility benefits from mating with males that produce higher chirp rates, and these benefits appear to result from products transferred in male ejaculates (Wagner & Harper, 2003). Because males that produced higher chirp rates took longer to produce a new spermatophore, indirect evidence suggests that males that provide greater reproductive benefits to females incur higher energetic costs of ejaculate production. Females receive lifespan benefits from mating with males that produce longer chirp durations, and these benefits also appear to result from products transferred in male ejaculates (Wagner & Harper, 2003). Because males that produced longer chirp durations did not take longer to produce a new spermatophore, there is no evidence that males that provide greater lifespan benefits to females incur higher energetic costs of ejaculate production.

While a number of studies have shown female choice based on signals correlated with the quality of a direct benefit (reviewed by Andersson, 1994; Jennions & Petrie, 1997), few studies have examined the factors that may affect the reliability of signals of direct benefits (reviewed by Kotiaho, 2001). Previous studies of *G. lineaticeps* have shown that higher chirp rates are energetically more expensive for males to produce (Hoback & Wagner, 1997) and that males provided with a higher quality diet produce higher chirp rates (Wagner & Hoback, 1999). The results presented here further suggest that males that produce higher chirp rates may incur higher energetic costs of spermatophore production. Male chirp rate may thus provide reliable information about the quality of the reproductive benefits provided to females; because higher chirp rates and greater reproductive benefits are energetically expensive for males to produce, only males in good nutritional condition may be able to afford to express both traits. Additional work will be necessary, however, to test whether males provided with a higher quality diet do in fact provide greater reproductive benefits than males provided with a lower quality diet. Male nutritional condition is known to affect male sperm count in a variety of animals (Gage & Cook, 1994; Blay & Yuval, 1997; Birkhead *et al.*, 1998) and the value of male spermatophores in some orthopterans (Zia *et al.*, 2000).

In contrast to higher chirp rates, longer chirp durations do not appear to be more expensive for male *G. lineaticeps* to produce (Hoback & Wagner, 1997), and there is no evidence that chirp duration varies with diet quality (Wagner & Hoback, 1999). Furthermore, the results presented here do not support the hypothesis that males that produce longer chirp durations incur higher energetic costs of spermatophore production. It thus seems unlikely that

male chirp duration and the quality of the lifespan benefits provided to females covary because both traits are dependent on male nutritional condition. While longer chirp durations and greater lifespan benefits do not appear to be energetically costly for males to produce, these results do not imply that there are no costs. It is possible, for example, that the costs are paid in a different currency, such as reduced lifespan. Much of the literature on the evolution of reliable signalling has focused on condition-dependent signals (e.g. Kotiaho, 2001; Houle & Kondrashov, 2002; Lorch *et al.*, 2003). In fact, a large number of studies have used the lack of short-term nutritional effects on signal structure to suggest that a given signal does not provide reliable information about mating benefits. But as the results presented here suggest, reliable signalling (i.e. a correlation between a male signal and a female mating benefit) can exist without the signal and the benefit signalled being dependent on short-term changes in male nutritional condition. Juvenile conditions are known to affect adult male singing behaviour in orthopterans (Olvido & Mousseau, 1995; Scheuber *et al.*, 2003b), and juvenile conditions may likewise affect the quality of the direct benefits that males can provide to females. Additional work will be necessary to determine why male chirp duration in *G. lineaticeps* covaries with the lifespan benefits that males provide to females.

In conclusion, indirect evidence suggests that spermatophore production is costly in *G. lineaticeps* and that males that provide greater reproductive benefits to females incur higher costs of spermatophore production. Because the production of higher chirp rates is also more expensive, male chirp rate and female reproductive benefits may covary because both traits are dependent upon male nutritional condition. Deceptive signalling of reproductive benefits may therefore be constrained because the signal that is correlated with benefit quality is affected by some of the same physiological mechanisms as is the benefit itself.

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