



Condition dependence of a multicomponent sexual signal in the field cricket *Gryllus campestris*

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In choosing a breeding partner, females in many animal species select between available males on the basis of several signalling traits. Some theoretical models of signalling evolution predict that multiple ornaments convey specific information on different aspects of male quality, such as current nutritional condition. We investigated the effect of nutrition on the calling song of male field crickets *Gryllus campestris*. This song is a multicomponent sexually selected signal. Adult males were kept on one of three feeding regimes, which resulted in significant differences in body condition between experimental groups. We found significant increases in calling rate and chirp rate and a significant decrease in interchirp duration with increasing food level. Other song characters, such as chirp duration, syllable number, chirp intensity and carrier frequency, were not affected by the food treatment. Furthermore, carrier frequency was correlated with harp area, which is an index of structural size in adult males. The calling song of the field cricket may thus serve as a multicomponent sexual signal, which contains discrete information on past growth and juvenile development as well as present nutritional condition.

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The evolution of multiple signalling traits is an unresolved topic in sexual selection. Although the use of multiple signals in sexual display has long been recognized (Darwin 1871), earlier theoretical models (Grafen 1990) and most empirical work (Andersson 1994) have so far considered only one signalling trait in mate choice. Recent models of animal communication have started to investigate the evolution and maintenance of multiple displays (Møller & Pomiankowski 1993; Iwasa & Pomiankowski 1994; Sullivan 1994; Johnstone 1995, 1996). These models generally presume a coevolution between multiple mating preferences in the choosing sex and multiple ornaments in the opposite sex. Empirical studies have shown that female mate choice (Andersson 1994) as well as male mate choice (Jones & Hunter 1993; Amundsen & Forsgren 2001) may select for ornamentation in males or females, respectively. Preference for multiple signals may evolve through a single preference or multiple mating preferences, each coevolving with a signal (Brooks & Couldridge 1999).

Considering species with female mate choice, female mating preferences for sexual display in males may be driven by three evolutionary mechanisms: direct benefits, indirect or genetic benefits, and sensory drive (Andersson

1994). In this context, several not mutually exclusive hypotheses have been proposed to explain the use of multiple signals (Møller & Pomiankowski 1993; Johnstone 1997). Multiple signals may indicate benefits of mate choice by revealing different aspects of the male's phenotypic and genetic quality (multiple messages hypothesis) or, alternatively, by signifying the overall quality of the signaller (back-up hypothesis or redundant signal hypothesis). Alternatively, multiple cues may be unreliable indicators of male quality (unreliable signals hypothesis), if preferences arise from pre-existing sensory biases (Ryan & Rand 1993) or through Fisherian runaway selection (Pomiankowski & Iwasa 1993). Some male display traits may further reflect past episodes of sexual selection and not affect current female mate choice (Holland & Rice 1998).

The multiple messages hypothesis has received some support from studies that investigated the use of multiple signals in female mate choice and the potential male quality signalled by each of the sexually selected traits. Female sedge warblers, *Acrocephalus schoenobaenus*, appear to select males by multiple cues that reflect different aspects of male and territory quality (Buchanan & Catchpole 1997). Female European bitterling, *Rhodeus sericeus*, appear to base their spawning decisions on multiple male signals, which are likely to indicate reproductive condition and genetic constitution (Candolin & Reynolds 2001).

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Multiple signals have further been proposed to indicate the condition of the signaller during different periods within its lifetime, such as the egg, juvenile and adult stages (Møller & Pomiankowski 1993). Long-term signals, which are determined over a long period of life, would reflect past condition, whereas short-term signals depend on current nutritional condition and are highly sensitive to short-term changes in the environment. Current nutritional condition concerns both dietary resources and body reserves. Signalling traits may, for instance, vary with nutritional intake only and not show a relation with body condition, if males allocate surplus energy solely to the signal (Wagner & Hoback 1999). Consequently, the condition dependence of an ornament can be investigated only by experimental manipulation of the past or current dietary intake of the male.

We experimentally investigated the condition dependence of the calling song characteristics in male field crickets *Gryllus campestris*. The calling song is the main acoustic sexual display and serves to attract receptive females at a distance. The relation between components of the calling song, the phenotypic quality of the male, and female preference for certain song characteristics in several species of field crickets indicates its function as a multicomponent sexual signal (a signalling system that is based on one signalling trait that conveys different informative components; 'multiple signals' usually refers to the use of different signalling traits, e.g. Johnstone 1996). First, the calling song has a temporal structure that consists of different structural elements or song components, which are at least partly uncorrelated (e.g. Zuk et al. 1998). The temporal structure of the call may indicate the male's current nutritional condition (Wagner & Hoback 1999), and is at least partly heritable (Cade 1981; Hedrick 1988; Gray & Cade 2000). In addition, females can discriminate between males on the basis of temporal song characteristics, such as calling bout duration (Hedrick 1986) and chirp rate (Simmons 1988; Wagner 1996). Second, the calling song has a specific modulation or carrier frequency. The carrier frequency is an indicator of male size, since larger males have lower carrier frequencies (Simmons & Zuk 1992; Simmons 1995). Females prefer calling songs of low carrier frequency (Simmons & Ritchie 1996). Third, the acoustic display is energetically costly (Hoback & Wagner 1997). Further costs may arise from an enhanced risk of predation (Bailey & Haythornthwaite 1998) and parasitism (Zuk 1994). Thus, the calling rate and the loudness of the calling song may also indicate the general vigour of the male.

We allocated adult male crickets to one of three feeding regimes to investigate the effect of nutrition on body condition, calling rate and several calling song characteristics. The components of the calling song investigated included its temporal structure, carrier frequency and intensity. Finally, to identify long-term signals that may reflect growth and juvenile development, we investigated the correlation between structural body size and calling song characteristics.

METHODS

The field crickets used as subjects were descendants of a stock population collected at field sites near Bern, Switzerland. Male crickets were sired in the laboratory by mating virgin females with a single, nonsibling male. For each of the 20 mating pairs the hatching date of the first offspring was recorded. After 3–5 days a group of 30 full-sibling nymphs was randomly collected and placed in a plastic container (38 × 20 cm and 25 cm high) for rearing. The containers were provided with sand substrate, egg cardboard for shelter, a water vial and a plastic tray with ad libitum food (fish chow, a 1:1 mixture of JBL Novovort and JBL Novogrand, JBL GmbH/Neuhausen, Germany). Temperature in the climate chamber was maintained at 26°C and relative humidity at 65%. The light:dark period was 14:10 h with lights-on at 1000 hours. Upon adult eclosion of the first nymphs we checked the container daily, and removed freshly moulted adults. The males were placed singly in plastic jars (13 × 9 and 18 cm high) containing sand bedding, a cardboard shelter, a water vial and a plastic food cup. All males were kept in a second climate chamber under similar climate and light conditions as those experienced during the nymphal period.

We randomly assigned males from the same family to one of the three feeding regimes. The feeding regime started immediately upon adult eclosion (day 0) and lasted for 10 days. Individuals in the high-food group received 0.1 g/day, in the medium-food group 0.01 g/day, and in the low-food group 0.005 g/day. Food was refreshed daily and for 15 individuals of each treatment group we weighed the leftover fish chow to the nearest 0.0001 g to assess food consumption. Average daily food intake was 0.04 g, 0.009 g and 0.005 g for the high-food, medium-food and low-food group, respectively, and this difference was significant (Kruskal–Wallis test: $\chi^2_2=40.55$, $P<0.001$). Thus the experiment effectively manipulated food intake, which was ad libitum for males in the high-food treatment, and restricted for both the medium-food and low-food groups.

We weighed males on day 0 ($N=83$) and day 9 ($N=71$) to the nearest 0.01 g. The difference in sample size between measurement days is due to mortality ($N=12$). To obtain morphometric data we collected males at the end of the experimental period and froze them at -20°C . For a subsample of 30 males the whole intestinal tract was carefully removed and weighed to the nearest 0.0001 g to assess the extent to which body mass differences between groups were due to differences in intestinal food content. We further measured for all individuals pronotum area and harp area (following Simmons 1995; the harp is a triangular structure in the forewings, formed by the stridulatory file and the largest longitudinal vein) to the nearest 0.01 mm^2 using a digital imaging system and the public-domain NIH Image program (National Institutes of Health, U.S.A.; <http://rsb.info.nih.gov/nih-image/>). Pronotum size and harp size are indices of structural adult body size, as determined by growth and development during the nymphal period. Pronotum area and harp area were available for 68 males (71 survivors,

three samples lost). Initial body mass (assessed on day 0, ANOVA: $F_{2,80}=0.59$, $P=0.56$), pronotum area (Kruskal–Wallis test: $\chi^2_2=0.78$, $P=0.68$) and harp area (ANOVA: $F_{2,65}=0.70$, $P=0.50$) did not vary significantly between groups. A similar result was found when including only individuals that survived until the end of the experiment. This comparison confirms the random distribution of males with respect to body mass and body size over groups. We used the change in body mass as an index for the effect of the food treatment on nutritional condition.

On day 9 we obtained a quantitative and qualitative measure of the male's calling song activity by audio recording between the first and third hour of the dark phase. This is the period of highest calling activity in *G. campestris* under natural conditions (Rost & Honegger 1987). Throughout the experiment about 200 adult males resided in the climate chamber, which provided a continual background chorus. Calling activity was assessed on the basis of a 45-min recording made with a cassette recorder (Sony TCM-38V) and a microphone (Sony ECM-T140) that was positioned on the top of the male's cage. We scored factual calling song for every minute during the first 42 min of the recording to obtain an index of overall calling rate for 69 males. To analyse the structure of the calling song (song quality), we further obtained from 65 males a digital recording of the calling song using a digital tape recorder (Sony TCD-D100) and a second microphone (Sony ECM-16). Each individual was recorded for at least 60 min between the first and fourth hour of the dark period. Some males ($N=12$) did not call during this period and these were recorded again between 1600 and 1800 hours. For the analysis we digitized a 30-s sequence taken 15 min after the start of the recording. If a male was silent during this period we digitized the sequence that occurred 1 min after the start of calling. To analyse calling song we used Canary software (Charif et al. 1995). We measured chirp rate (chirps/s), chirp duration (ms), interchirp duration (ms), syllable number (syllables/chirp), chirp intensity (fW/m²) and carrier frequency (kHz) using standard criteria (e.g. Hedrick & Weber 1998; Wagner & Hoback 1999; Fig. 1).

Several calling song components were highly correlated. For example, chirp rate is a function of chirp duration and interchirp duration. To divide the song variables into fewer patterns we performed a principal components analysis (Tabachnick & Fidell 1983). However, for clarity we also present the effect of food treatment on separate calling song components. For statistics we used JMP IN (Sall & Lehmann 1996) software. To correct for the multiple testing in the analysis of the six song characters we adjusted the significance level to $\alpha=0.0083$ using the Bonferroni method (Sokal & Rohlf 1995).

RESULTS

We first analysed the effect of food treatment on survival of males to day 9, the day we recorded the calls. The overall survival in the high-, medium- and low-food groups was 0.96 ($N=25$), 0.78 ($N=32$) and 0.85 ($N=26$),

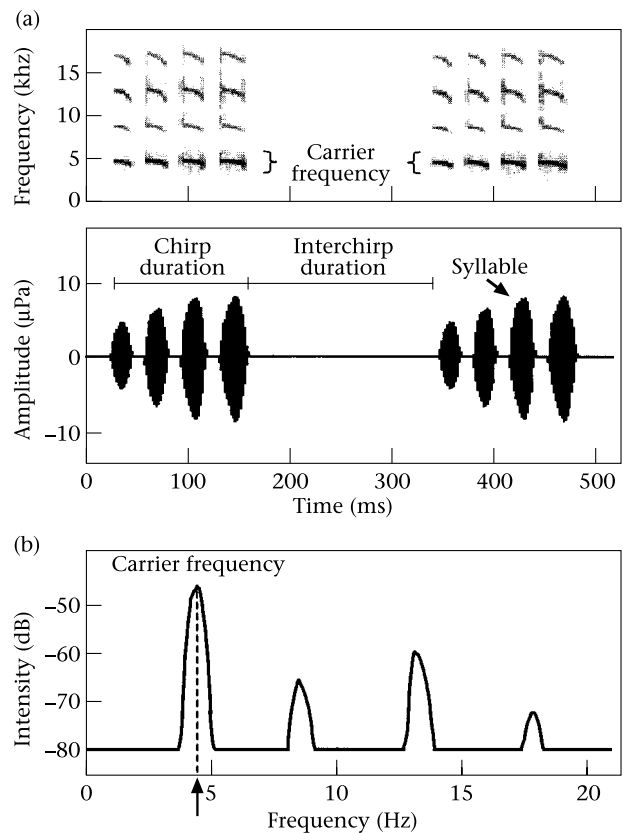


Figure 1. (a) Spectrogram and waveform of a typical calling song sequence of *Gryllus campestris*, indicating the major calling song components. (b) Frequency spectrum of the calling song. The four successive peaks represent the basal tone and three overtones. The frequency of the basal tone conveys the peak energy and is referred to as the carrier frequency (arrow).

respectively. This variation was independent of treatment (Kruskal–Wallis test: $\chi^2_2=4.25$, $P=0.12$).

The change in body mass between days 0 and 9 was significantly affected by food treatment (ANOVA: $F_{2,68}=38.35$, $P<0.0001$; Fig. 2). A post hoc Tukey–Kramer comparison between groups revealed that the increase in body mass in the high-food group was larger than in the medium-food ($MSD_{1,2}=2.48$, $P<0.05$) and low-food groups ($MSD_{1,3}=2.50$, $P<0.05$), while the difference between the two latter groups was not significant ($MSD_{2,3}=2.36$, NS). Intestinal tract weights did not vary between groups (ANOVA: $F_{2,27}=1.11$, $P=0.35$); thus differences in body mass between groups were not due to differences in intestinal content.

Calling rate varied significantly with food treatment (Kruskal–Wallis test: $\chi^2_2=10.91$, $P=0.004$). Males in the high-food group called on average twice as often as the males in the low-food group (Fig. 3a).

Feeding regime had a significant effect on interchirp duration (Kruskal–Wallis test: $\chi^2_2=13.30$, $P=0.0013$) and thereby on chirp rate (ANOVA: $F_{2,61}=5.15$, $P=0.0083$; Fig. 3b). Chirp rate was highest in the high-food group, and interchirp duration was highest in the low-food group. Chirp duration, syllable number, chirp intensity and carrier frequency were not affected by the food treatment (Table 1).

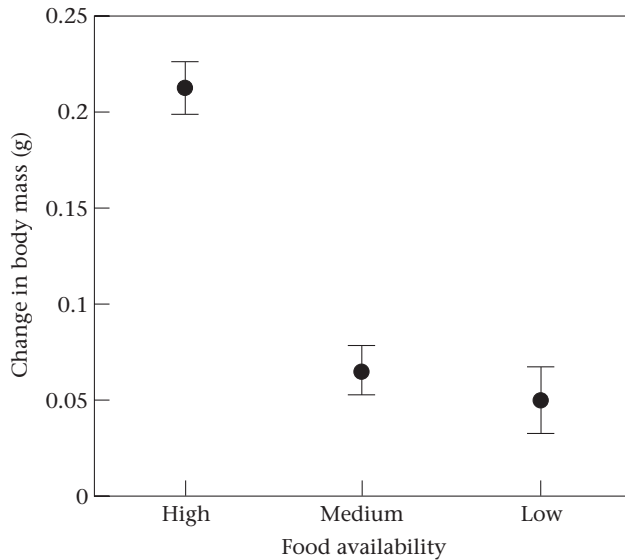


Figure 2. Effect of food treatment on change in body mass ($\bar{x} \pm SE$) over the experimental period.

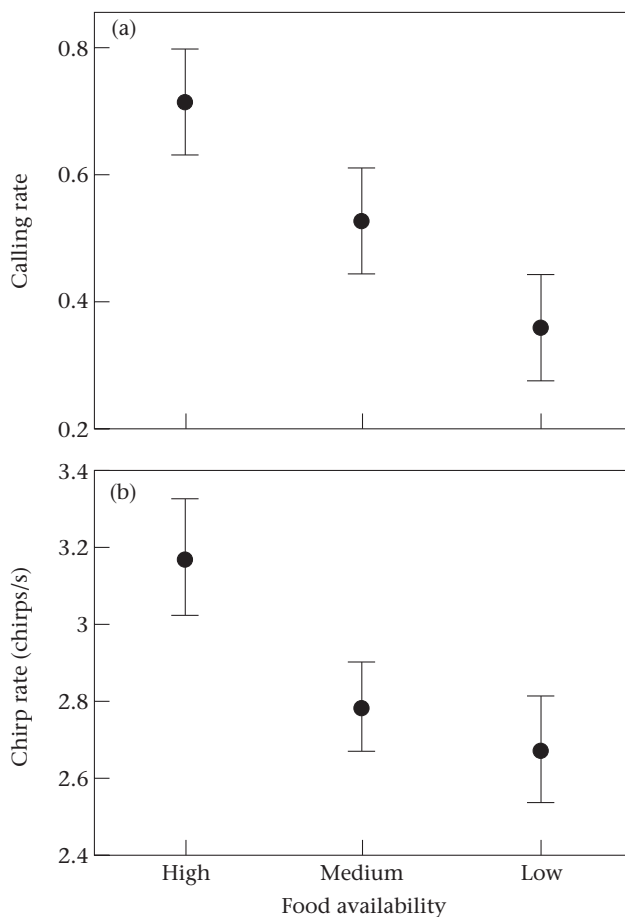


Figure 3. Effect of food treatment on (a) calling rate, i.e. proportion of time calling ($\bar{x} \pm SE$) and (b) chirp rate ($\bar{x} \pm SE$).

We also investigated the relation between calling song activity, components of the calling song and the structural size of the male, as indicated by pronotum and harp

size. Pronotum area and harp area were highly correlated (Spearman correlation coefficient: $r_s=0.47$, $N=68$, $P<0.0001$). Carrier frequency was negatively correlated with harp area (Pearson correlation coefficient: $r_{60}=-0.35$, $P=0.005$). All other song characters were independent of harp area and body size (all $P>0.3$).

The principal components analysis (PCA) yielded three factors with eigenvalues greater than 0.9, accounting for 82.3% of the total variation in the song characteristics. The first component is mainly explained by the calling activity, that is, increasing calling rate was associated with increasing chirp rate, but decreasing interchirp duration (Table 2). The second component incorporates chirp characteristics, that is increasing chirp duration and increasing syllable number, and the third component represents the carrier frequency (Table 2). Treatment had a significant effect on PC1 (Kruskal–Wallis test: $\chi^2_2=9.93$, $P=0.006$), but not on PC2 (ANOVA: $F_{2,60}=0.81$, $P=0.45$) and PC3 (ANOVA: $F_{2,60}=0.53$, $P=0.59$; Fig. 4). This finding outlines the results of the analyses on separate calling characteristics, which indicate significant treatment effects on calling rate, chirp rate and interchirp duration (Table 1).

DISCUSSION

Our results show that the calling song of male *G. campestris* should be regarded as a multicomponent sexual signal. Three clusters of correlated song characters best described the calling song. One of these clusters was influenced by experimental variation in food availability, but the other two clusters were not affected by this variation. One of the latter two clusters correlated with structural body size, which is an intrinsic aspect of male phenotypic quality that may reflect genetic make-up, past environmental conditions for growth and development, or both.

Acoustic display is usually associated with considerable energetic costs (Ryan 1988; Prestwich 1994; Reinhold et al. 1998). The average metabolic rate of signalling field cricket males is nearly three times that of noncalling males (Hoback & Wagner 1997). Among calling males, energy expenditure is further positively related to certain calling song components, such as chirp rate (Hoback & Wagner 1997). *Gryllus campestris* males enhanced their overall calling rate and chirp rate, that is, the energetically costly elements of the calling song, with increasing food availability. This suggests that these calling song characteristics reliably reflect current nutritional condition. Similar nutritional effects on the incidence of costly calling behaviour were found in the variable field cricket *G. lineaticeps* (Wagner & Hoback 1999), and bush crickets (*Requena verticalis*: Simmons et al. 1992; *Ephippiger ephippiger*: Ritchie et al. 1998). Other studies also generally conclude that males provided with a high-quality diet invest more in costly signalling traits (e.g. Backwell et al. 1995; Johnstone 1995; Kotiaho 2000; but see Candolin 1999). Females frequently prefer energetically costly elements of male display in field crickets (Hedrick 1988; Wagner 1996; Hoback & Wagner 1997; Holzer et al., in press) and other animal species (Wells & Taigen 1989;

Table 1. Mean±SE of the song characters in the three food treatment groups

Variable	Food availability			Test statistic	P
	High	Medium	Low		
Chirp rate (chirps/s)	3.17±0.13	2.78±0.12	2.56±0.13	$F_{2,61}=5.15$	0.008*
Interchirp duration (ms)	220.18±19.68	252.63±18.41	294.36±20.69	$\chi^2_2=13.3$	0.001*
Chirp duration (ms)	111.76±3.47	110.60±3.25	109.33±3.65	$\chi^2_2=0.16$	0.92
Syllable number (syllables/chirp)	3.65±0.12	3.55±0.11	3.49±0.12	$\chi^2_2=0.57$	0.75
Chirp intensity (fW/m ²)	6.53±1.09	3.68±0.61	3.65±0.92	$\chi^2_2=4.78$	0.09
Carrier frequency (kHz)	4.74±0.05	4.74±0.05	4.72±0.05	$\chi^2_2=0.04$	0.98

*Significant at the $\alpha=0.0083$ level (Bonferroni corrected).

Table 2. Principal components analysis on calling song characters

Variable	PC1	PC2	PC3
Calling rate	0.746	—	—
Chirp rate	0.866	—	—
Interchirp duration	-0.890	—	—
Chirp duration	—	0.796	—
Syllable number	—	0.731	—
Chirp intensity	—	—	—
Carrier frequency	—	—	0.692
Eigenvalue:	3.29	1.53	0.95
%	46.93	68.79	82.33

Values indicate the factor loadings, i.e. the correlation coefficients between the components and the included song variables. Loadings below 0.65 are represented by a dash.

Watson & Lighton 1994; Reinhold et al. 1998), which may suggest that food-limited males are energetically constrained. Alternatively, males in poor nutritional condition may be selected to refrain from producing a more attractive sexual signal, when condition-dependent trade-offs with other life history traits reduce the marginal fitness returns per unit of signalling effort for low-quality signallers (Grafen 1990; Getty 1998). Costs associated with elaborate signalling may involve an enhanced risk of predation or parasitism (Ryan et al. 1982; Wagner 1996; Zuk & Kolluru 1998; Rosenthal et al. 2001), and signallers in poor condition may concurrently have inferior predator avoidance traits, parasite resistance or immunocompetence (Getty 2002).

Under field conditions *G. campestris* are food limited, since food-supplemented males use additional energy to enhance both body reserves and calling rate (Holzer et al., in press). Our study indicates the existence of a condition-dependent trade-off between the investment in signalling and storage in body reserves. This essentially concerns a trade-off between current reproductive effort, here represented by calling behaviour, and future reproductive output, which is usually positively linked to body condition (Williams 1966; Lessells 1991). With increasing food availability experimental males progressively showed more energetically expensive calling behaviour, but only males of the high-food group showed more weight gain than the males of the low-food group; males

in the medium-food group showed similar weight gain. Below a certain nutritional threshold, males apparently invest any excess energy above their basic maintenance requirements in energetically costly calling behaviour to increase their attractiveness to females. Above this threshold, additional energy is stored in body reserves, which may improve survival or later mate attraction in periods of poor weather conditions or food shortage (Rost & Honegger 1987). Male bush crickets *R. verticalis* also increased their body mass and calling effort when given extra nutrients (Simmons et al. 1992). Wagner & Hoback (1999) found no effect of nutrition on body mass gain in variable field crickets. Because of the high rate of parasitism by acoustically orienting parasitoid flies, males in this species might be selected to invest excess energy in current calling behaviour, rather than storing it for future use.

Food manipulation had no effect on the other two clusters of song components, which reflected chirp duration and syllable number or carrier frequency, respectively. Several studies in crickets suggest that phenotypic variation in these components of the calling song partly reflect heritable variation (Hedrick 1988; Webb & Roff 1992; Roff et al. 1999; Gray & Cade 2000), which may be linked to heritable variation in immune function (Ryder & Siva-Jothy 2000, 2001).

As in other studies on crickets (Simmons & Zuk 1992; Simmons 1995) and anurans (e.g. Ryan 1980; Robertson 1986; Wagner & Sullivan 1995), we found a negative correlation between structural body size and carrier frequency, the main explanatory parameter for the third cluster in the calling song variation. Apart from genetic variation, adult body size in insects may reflect environmental factors such as temperature (Olvido & Mousseau 1995) or food availability (David et al. 2000) during larval development. In the striped ground cricket, *Allonemobius fasciatus*, temperature-dependent nymph development also affects carrier frequency of the calling song of adult males (Olvido & Mousseau 1995). Thus, carrier frequency appears to be an honest indicator of past condition.

In conclusion, our results support the multiple messages hypothesis (Møller & Pomiankowski 1993), as the calling song of *G. campestris* clearly contains specific information about current condition (short-term signal), and other signalling components may indicate past

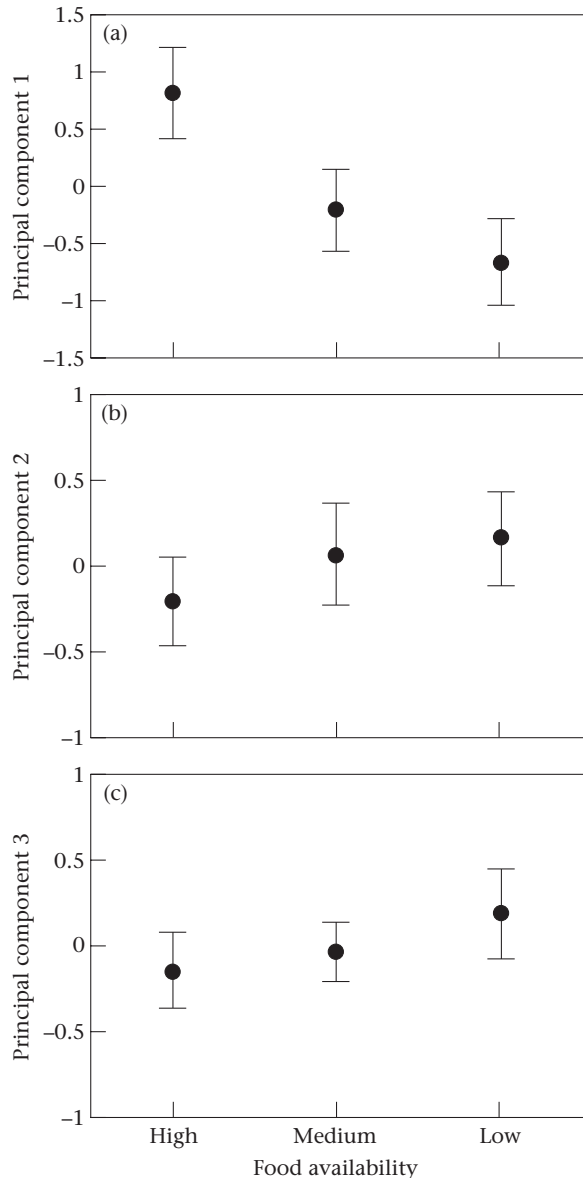


Figure 4. Effect of food treatment on the principal components ($X \pm SE$).

condition (long-term signal). Studies on orthopterans (reviewed by Andersson 1994) and crickets (Hedrick 1986; Simmons & Ritchie 1996; Wagner 1996; Bateman et al. 2001) have shown that females incorporate short-term or long-term signal components in mate choice. However, the relative importance of these components in determining female preference is poorly understood. Future work should reveal what benefits females may gain from choosing mates on the basis of condition-dependent sexual display. Because female *G. campestris* receive no apparent direct benefits from their mates, naturally occurring phenotypic variation in long-term or short-term condition should reflect heritable genomic quality, to allow females that choose males on the basis of condition-dependent calling characteristics to acquire 'good genes' for their offspring (Andersson 1994; Johnstone 1995; Kotiaho et al. 2001).

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