Condition-dependent signaling affects male sexual attractiveness in field crickets, *Gryllus campestris*

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The condition dependence of sexually selected traits is an important assumption of sexual selection theory. Several laboratory studies have documented a positive relationship between food availability, body condition, and sexual display. However, these studies might not reflect the resource allocation between body maintenance, reserves, and the sexually selected trait under natural conditions. Further, the effect of condition-dependent signaling on female mate choice has hardly been investigated experimentally in the field. We therefore investigated the effect of food availability on body condition, calling behavior, and sexual attractiveness of male field crickets, *Gryllus campestris*, under field conditions. Food availability was manipulated for individual males by supplementing food in a confined area close to the burrow. Food-supplemented males showed a significant increase in body condition, whereas the opposite was found in the control males. Males receiving extra food called more frequently, whereas the calling-song characteristics were not affected by the treatment. Further, food-supplemented males attracted more females than did control males, and their higher attractiveness was partly explained by their superior calling rate. Our study thus indicates condition-dependent signaling as an important determinant of the sexual attractiveness of males to females under natural condition. *Key words:* body condition, calling behavior, condition dependence, field cricket, *Gryllus campestris*, sexual attractiveness, sexual selection, signaling. *[Behav Ecol 14: 353–359 (2003)]*

An important assumption in the theory of sexual selection is the condition dependence of sexually selected traits (Andersson, 1986; Andersson and Iwasa, 1996; Grafen, 1990; Zeh and Zeh, 1988). According to the "handicap" theory (Zahavi, 1975, 1977), honest signals have to be costly to produce or maintain, and only individuals in good condition can afford the expenditure for the extravagant mating displays. Empirical studies confirmed that the expression of an ornament or display is influenced not only by genetics but also by environmental factors such as food availability (Backwell et al., 1995; Emlen, 1997), risk of predation (Tuttle et al., 1982), risk of parasitism (Zuk et al., 1993), or parasitic infection (Houde and Torio, 1992; Milinski and Bakker, 1990). Provided that condition-dependent ornaments or displays contain reliable information about the phenotypic or genotypic quality of the male (see David et al., 2000; Rowe and Houle, 1996), females may obtain direct or indirect benefits from including the condition-dependence of male sexual signals in mate choice decisions (Andersson, 1994; Johnstone, 1995).

Most experimental studies investigating the condition dependence of sexually selected traits and their effect on female mate choice were performed in captivity or under controlled laboratory conditions (Andersson, 1994; Jennions and Petrie, 1997; Johnstone, 1995). However, these studies may not reveal how signaling males optimally allocate the dietary nutrients and energy between body maintenance, reserves, and the sexually selected trait in a natural habitat. Environmental variation in temperature, food availability, conspecific competition, and risk of predation or parasitism may affect the

trade-off between investment in sexual display and other life-history traits (McNamara et al., 1987). Further, environmental conditions affect the transmission and detection of acoustic signals (Endler, 1992; Forrest, 1994; Forrest and Raspet, 1994), and background noise and noise of conspecifics may mask the signal and make female phonotaxis more difficult (Gerhardt and Klump, 1988; Ronacher et al., 2001). Finally, it is unclear to what extent condition-dependent signals that affect mate choice under controlled laboratory situations are also relevant in the field. It is therefore important to assess the condition dependence of sexually selected traits and their effect on female mate choice directly in field experiments.

In addition, empirical studies are essential because the relationship between body condition and signal design might not reflect the condition dependence of a sexually selected trait. For instance, if signal design involves a life-history trade-off between present signaling effort and future reproductive output, then a disproportional allocation of resources to signaling relative to body reserves might be the evolutionary optimal strategy (Kokko, 1997). As a result, present body condition might be independent of signal intensity, if signalers invest all surplus energy above their basic metabolic requirements into sexual display, such as that found in the variable field cricket, *Gryllus lineatus* (Wagner and Hoback, 1999). In the extreme case, as shown in three-spined sticklebacks, *Gasteroteus aculeatus* (Candolin, 1999), males in poor body condition might even show a higher signaling effort than do males in better condition, if scant prospects for future reproduction favor a terminal investment in current sexual display. Therefore, nutritional condition, which involves the pool of resources through food availability or body reserves, must be manipulated experimentally to assess its effect on the expression of signaling traits.

The acoustic display of male crickets is a good example for a costly sexually selected trait. The calling song is used to attract females and is known to play an important role in intersexual and intrasexual selection (Zuk and Simmons,

1997). Costs for males while calling include the energetic expenditure (Prestwich and Walker, 1981; Wagner and Hoback, 1999), the reduction in foraging time, and the increase in the risk of predation (Bailey and Haythornthwaite, 1998) or parasitism (Cade, 1975). To enhance their attractiveness to females, males have the option to increase the calling rate, produce more costly song characteristics (Wagner and Hoback, 1999), or both. The acoustic display may serve not only to attract females but also to maintain spacing between neighboring males (Cade, 1981; Campbell, 1990; Campbell and Shipp, 1979). We experimentally investigated the effect of food availability on body condition, calling behavior, and sexual attractiveness of male field crickets, *Gryllus campestris,* under natural conditions. The nutritional condition of calling males was manipulated by supplementing one group of males with food, whereas the control males received no additional food. As an index for the sexual attractiveness of males, we used the number of females trapped near the male's burrow.

MATERIALS AND METHODS

Field cricket and study site

G. campestris overwinter as penultimate instar nymphs in burrows dug into the soil. Nymphs emerge early in spring and continue their development until adulthood. Soon after the imaginal molt, the males start calling on a small platform cleared of vegetation in front of their burrows to attract females for mating. The copulation activity peaks at noon and in the late afternoon. Males may switch burrows but occupy the same burrow on average for 7 days (Rost and Honegger, 1987). The reproductive season lasts for approximately 2 months in our study area, from the end of April until the start of July. Males and females mate multiply with the same, as well as with different, partners (Rost and Honegger, 1987).

The experiment took place between 10 May and 16 June 2000 in a cricket population situated in an uncut meadow, on a south-facing slope, near Hinterkappelen, Switzerland. All males in our study area had their imaginal molt in a 1-week period between 25 April and 1 May 2000. The males used at the end of the season were thus 5 to 6 weeks older than the males at the start of the season. All discovered burrows on the meadow were numbered with a flag. Crickets were captured and marked individually with a numbered opalith plate (Bienen-Meier, Switzerland) that was glued onto the pronotum.

Experimental design

The nutritional condition of calling males was experimentally manipulated by food supplementation over a period of 6 days. We randomly selected experimental males among the calling males on the meadow. The overall sample size in the control group at the first day of the experiment was $n = 30$; in the group with food supplementation, $n = 34$; at day 6 of the experimental period, $n = 21$; respectively, $n = 31$. The decline in sample size is owing to failure of capture, escape, or death of the experimental males. The assignment of individuals to the control or the food-supplemented group was alternated according to body mass. We confined the crickets to a 32×32-cm area around the burrow with a 18-cm-high mosquito net cage. Four pit fall traps (7 cm diam, 9 cm depth) were placed around the cage to capture attracted females or males. The food tray was placed close to the entrance of each experimental burrow, protected with a plastic cover against rain. In the control group, the food tray was further covered with a small sieve that prevented the control males from feeding but allowed the food odor to pass. We thereby controlled for the potential bias of the food smell on the probability of trapping other crickets. Food-supplemented males were fed ad libitum with fish food (JBL, NovoBel aquarium fish food, Germany) that is successfully used in the breeding of *G. campestris* in our laboratory. To measure the food consumption, the remaining food was brought back to the laboratory, dried at 35°C for 12 h, and weighed.
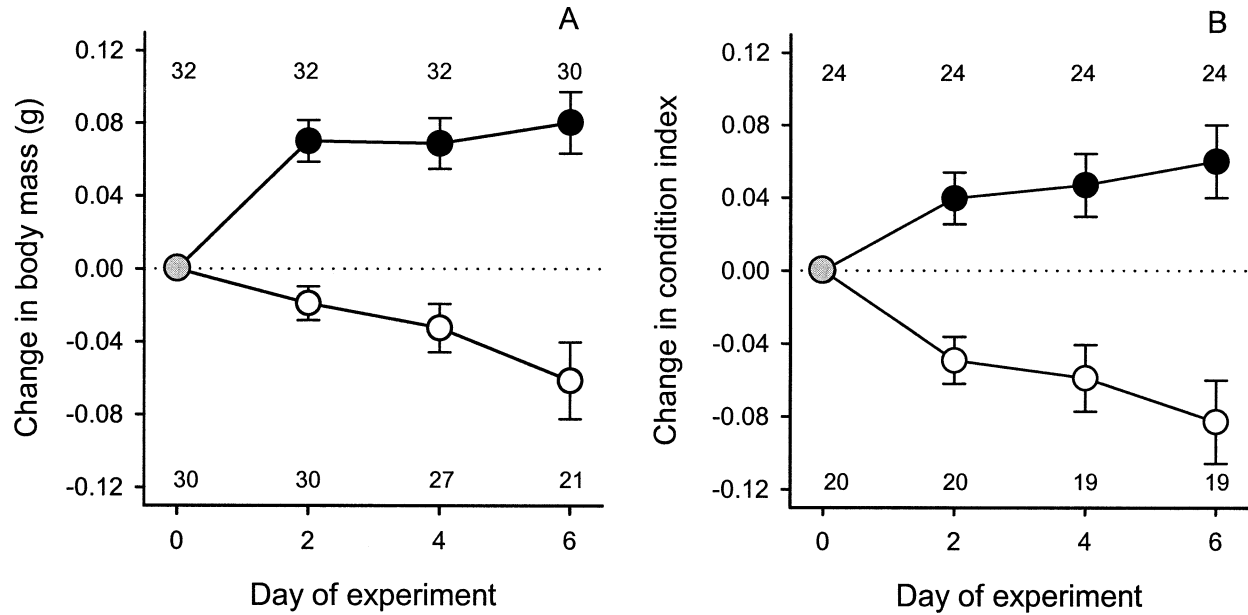
Measurements

Body mass was measured with an electronic balance (Sartorius PT150) to a nearest of 0.01 g at the start of the experiment and on the second, fourth, and sixth days. After the experimental period, males were caught and brought to the laboratory for morphological measurements. The left and right hind tibia, the pronotum area, and the harp area were measured according to the method of Simmons (1995) by using image analysis software (Image 1.61, National Institutes of Health, USA).

To quantify calling behavior, we observed the experimental males every hour between 1200 and 2100 h for 6 days and noted if they were silent or calling. We further recorded 3 min of the calling song on the second, fourth, and sixth days of the experiment to assess song characteristics. All recordings were performed by using a digital audio tape-recorder (Sony TCD-D100) and a stereo microphone (Sony ECM-MS957). The microphone was placed 15 cm above the calling platform. Recordings took place in the late afternoon and early evening between 1500 and 2100 h (mean recording time ± SE, 17:36 ± 1:29 h), which is the peak period of calling activity in *G. campestris* (Rost and Honegger, 1987). Calling song in crickets is influenced by temperature (Doherty, 1985; Martin et al., 2000). We therefore assessed the air temperature in the middle of the meadow. Air temperature during the field season between 1600 and 2000 h, when most of the recordings took place, was 20.5 ± 0.1°C (mean ± SE: range of mean daily temperature, 14.9°C–27.7°C).

To exclude observer bias, the song analysis was performed blindly with respect to the food treatment. Tapes were checked by ear for a section of consistent calling, and 90 s of the acoustic signal was transferred to a Macintosh computer and analyzed with Canary (version 1.2.1; Charif et al., 1995). Before the analyses, we determined a minimal time period of calling song and the minimal number of calling song bouts needed to describe consistent differences in calling song characteristics between males. By using the recordings from 10 randomly chosen males, we assessed the repeatability (Lessells and Boag, 1987) of carrier frequency and average intensity (Simmons, 1988) by comparing a 30-sec interval at the start and the end of the 90-sec signal. In addition, the first six chirps and the last six chirps of the 90-sec signal were used to analyze the repeatability of chirp duration, the interchirp duration, and mean pulse duration per chirp (Simmons, 1988). All measurements were highly repeatable (repeatabilities: carrier frequency, 0.99; average intensity, 0.81; chirp rate, 0.97; chirp duration, 0.99; interchirp duration, 0.90; mean pulse duration, 0.76). In further data analysis, we therefore included the first 30 s and the first six chirps only. The mean chirp rate was assessed on basis of the first 30 chirps.

The pit fall traps were checked every hour between 1200 and 2100 h, and the number of females and males caught was noted for each experimental male. The crickets were marked and then released 1 m above the burrow of capture. We corrected for recaptures at the same male burrow before data analysis; thus, each individual was counted only once per experimental male. The capture data of females are based on 106 individuals: 87 were trapped at one experimental male burrow, 13 at two different burrows, and six at three different

Figure 1
The change in the mean body mass (± SE) (A) and in body condition (± SE) (B) during the six experimental days in the control males (open circles) and in the food-supplemented males (filled circles).

burrows. Retrapping data of individual females at different male burrows were included in the analysis, given that multiple mating is common (Rost and Honegger, 1987). Capture data of males concern 77 individuals; 61 males were trapped at the burrow of one experimental male only, whereas multiple recaptures include 11 at two different burrows, three at five different burrows, and one at seven different burrows.

Statistical analysis

We used the Kaplan-Meier product limit in JMP IN (version 3.2.1; Sall and Lehmann, 1996) for survival analysis. Escaped males were set as censored. The residuals from a regression of body mass on pronotum area were used to estimate body condition (Wagner and Hoback, 1999). Effects of treatment on body mass and condition were analyzed with repeated-measures ANOVA. Only complete records of males were included in the analysis (body mass: control, $n = 20$, food-supplemented, $n = 30$; condition: control, $n = 18$, food-supplemented, $n = 24$). Calling rate was analyzed by using logistic regression (GLMStat version 5.3.1; Beath, 2000), with the number of calling events as nominator and the number of observations as denominator. To account for overdispersion in the data (i.e., the scale parameter of models was larger than one), we used Pearson's χ^2 to adjust the scale parameter. From the resulting scaled deviances, the significance of predictor variables was then conservatively tested by using an F test instead of the χ^2 test (see Crawley, 1993).

We used the residuals of a linear regression of the song characteristics on temperature to standardize effects of temperature on chirp rate, chirp duration, and mean pulse duration (Walker, 1975). For interchirp duration and peak frequency, the residuals of a quadratic regression on temperature were used. Several song variables were intercorrelated: e.g., chirp rate with chirp duration ($r = -.77$), interchirp duration with chirp duration ($r = .64$), and chirp rate with interchirp duration ($r = -.85$). To summarize song characteristics into fewer axes that described independent uncorrelated
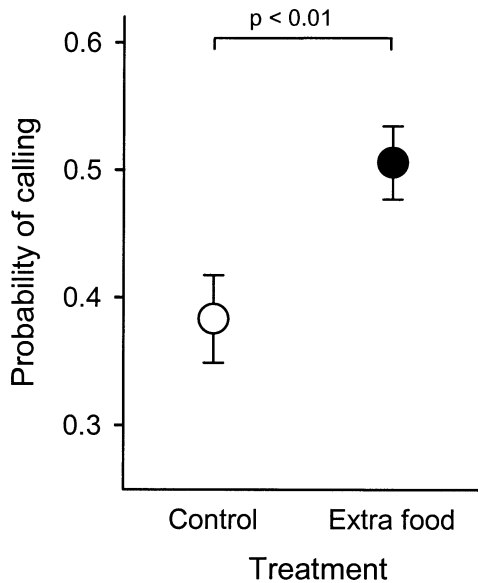
patterns of variation, we performed principal component analysis (Zuk et al., 1998).

The sum of females trapped over the six treatment days was used as a measure for the sexual attractiveness of the male to females. The data were analyzed by using Poisson regression (GLMStat; Beath, 2000). To account for overdispersion, the scale parameter was estimated using Pearson's χ^2, and significance of predictor variables was assessed with an F test (Crawley, 1993). Some males died or escaped before the end of the experimental period. To control for variation in the number of days that the male was present in the experimental set-up, we included this time period as a covariate. The same procedure was used to investigate the number of males trapped. Means (± SE) are given, unless indicated otherwise.

RESULTS

The control males remained on average for 5.4 ± 0.2 days and the food-supplemented males for 5.8 ± 0.2 days in the experimental set-up. The survival probability did not differ between the two groups (log-rank test: $\chi^2 = 1.96$, df = 1, $p = .16$). The mean daily food consumption by food-supplemented males was 0.15 ± 0.01 g. Food-supplemented ($n = 25$) and control males ($n = 20$) showed similar pronotum area ($F_{1,43} = 0.01$, $p = .97$), tibia length ($F_{1,43} = 0.08$, $p = .87$), and harp area ($F_{1,43} = 0.18$, $p = .68$).

The mean body mass of the males at the start of the experiment was 1.20 ± 0.04 g, and there was no difference in body mass between the two treatment groups ($F_{1,60} = 0.78$, $p = .38$). Further, variation in initial body mass among males was independent of season ($F_{1,60} = 0.15$, $p = .70$). The change in body mass over the six experimental days was significantly different between the two treatment groups (repeated-measures ANOVA, interaction time * treatment: $F_{3,46} = 10.20$, $p < .001$). The food-supplemented males increased their body mass, whereas the control males showed a decline (Figure 1A). Analysis of the effect of treatment on body condition gave a similar result (repeated-measures ANOVA, interaction time * treatment: $F_{3,38} = 8.31$, $p < .001$) (Figure 1B).

Figure 2
The mean calling rate ($\pm$ SE) in the control males (open circle) and in the food-supplemented males (filled circle) during the six experimental days.

Over the experimental period, the average probability of calling for the food-supplemented males was 0.51 ± 0.03 and 0.38 ± 0.03 for the controls (Figure 2). Males provided with food called significantly more often than did control males (logistic regression, scale parameter $= 3.44$, $F_{1,62} = 9.32$, $p < .01$).

Because the largest increase in body mass occurred during the first 2 days of the experiment (Figure 1), we used the data from the second day of the experiment for principal component analysis (PCA) on song characteristics. The PCA yielded three factors with eigen values greater than 1.0, accounting for 77.9% of the total variation in the song variables (Table 1). The first component was primarily explained by chirp measurements (i.e., increasing pulses per chirp, pulse duration, and chirp duration and decreasing chirp rate). The second component is associated to the energy content of the calling song (i.e., increasing average intensity and decreasing interchirp duration). The third component portrays carrier frequency. ANOVA revealed no significant effect of treatment on any of the three principal components (PC 1: $F_{1,55} = 0.05$, $p = .83$; PC 2: $F_{1,55} = 2.80$, $p = .20$; PC 3: $F_{1,55} = 0.13$, $p = .72$). A comparable result was found when analyzing calling-song data collected on the fourth or sixth day of the experiment.

Over the experimental period, the control and food-supplemented males attracted on average 0.17 ± 0.05 and 0.45 ± 0.08 females per day, respectively (Figure 3A). The difference between the treatment groups was significant (Poisson regression: scale parameter $= 1.62$, $F_{1,61} = 9.43$, $p < .01$). The effect of treatment on the number of females attracted was partly explained by the difference in calling rate among the treatment groups ($F_{1,61} = 4.56$, $p = .04$), whereas variation in the three independent clusters of song characteristics was not significant (Poisson regression, PC 1: $F_{1,54} = 0.25$, $p = .62$; PC 2: $F_{1,54} = 2.23$, $p = .14$; PC 3: $F_{1,54} = 0.24$, $p = .62$). The mean daily number of males attracted was 0.20 ± 0.047 and 0.26 ± 0.057 for the control and food-supplemented males, respectively, and independent of treatment (Poisson regression: scale parameter $= 2.02$, $F_{1,61} = 0.30$, $p = .60$) (Figure 3B).

Table 1

Principal component analysis of calling-song characteristics measured on 57 males at the second day of the experiment
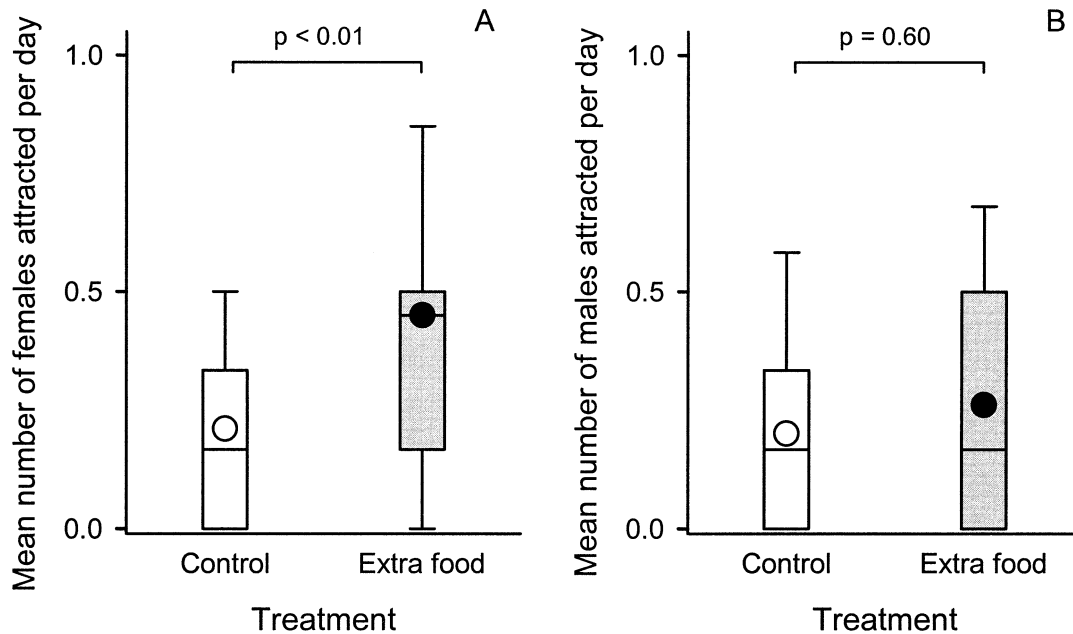
Variable	Component 1	Component 2	Component 3
Pulses per chirp	0.71	—	—
Pulse duration (ms)	0.62	—	—
Chirp duration (ms)	0.96	—	—
Interchirp duration (ms)	—	−0.64	—
Chirp rate (chirp/s)	−0.79	—	—
Average intensity (fW/m^2)	—	0.72	—
Carrier frequency (Hz)	—	—	0.81
Eigen values	2.7	1.7	1.0
Cumulative variance explained (%)	39.2	63.6	77.9

The Pearson correlation coefficient between components and the original variable is given. Variables accounting for less than 33% of the variance of an original variable are denoted by dash.

DISCUSSION

Over the experimental period control, males showed a decline in body condition, whereas the opposite was found among food-supplemented males. Because we found no difference in initial body mass over the season, this suggests that the temporal change in body mass among either treatment group is not caused by aging. More likely, the artificial restriction of the foraging area caused a deprivation of natural foods to all experimental males. This caused a decline in body condition among control males, whereas food supplemented males were able to compensate and effectively improve their body condition above the natural level. Our experimental set-up thus effectively created a food-deprived and a food-supplemented group, which allowed us to investigate the role of nutritional condition on energy allocation patterns, signal design, and sexual selection under field conditions.

Food-supplemented males used the surplus energy to enhance both acoustic display and body reserves. We found a similar effect of food availability in a laboratory study using *G. campestris* (Scheuber et al., 2003). This allocation pattern basically reflects the current reproductive effort relative to the future reproductive potential, because energy reserves may serve to increase longevity and future investment in mate attraction. Theoretically, the optimal pattern of allocation depends on the fitness returns per unit of investment in current and future reproduction, and the resulting trade-off may vary among species with the specific aspects of life history (Lessells, 1991; Williams, 1966). Similar to *G. campestris*, bush crickets, *Requena verticalis* (Simmons et al., 1992), stored part of the excess energy in body reserves, whereas the variable field cricket, *G. lineaticeps* (Wagner and Hoback, 1999), showed no weight gain and invested in more costly calling behavior only. Wagner and Hoback (1999) suggested that *G. lineaticeps* might be selected to refrain from storing energy, because of the high risk of parasitism by acoustically orienting parasitoid flies, which severely reduces the prospective future reproductive output of the male. In *G. campestris* the accumulation of body reserves may be favored by the frequent, yet temporally unpredictable, occurrence of cold and rainy weather. During such periods, males cease feeding and often remain in their burrow (Rost and Honegger, 1987; Brinkhof MWG, personal communication). Large body reserves may improve survival under conditions of food deprivation (Burpee and Sakaluk, 1993). Further, heavier males are more likely to win fights with other males over

Figure 3
Mean number of females and males trapped per day at the burrow of control (open circles) and food-supplemented males (filled circles). The box plot with error bars indicates the median and the 10th, 25th, 75th, and 90th percentiles for each of the treatment groups.

burrows and attending females (Simmons, 1986). In addition, high body reserves may improve fertilization success and paternity under sperm competition. Female *G. campestris* generally mate multiply, with the same partner and with different males (Rost and Honegger, 1987). In katydids, males in good condition produced more spermatophores and were able to maintain the quality of the spermatophore when mating repeatedly (Gwynne, 1990). *G. bimaculatus* males that were able to mate several times with the same female increased their reproductive success (Simmons, 1987).

Males may signal a good nutritional condition by enhancing their calling rate, the display of more costly song elements, or both. In the variable field cricket, calling increased the male's metabolic rate on average nearly three times above noncalling metabolic rates, and the cost of calling was further positively correlated with chirp rate (Hoback and Wagner, 1997). In the present study, nutritional condition enhanced calling rate, but we found no additional effect on any component of the calling song, including chirp rate. In contrasts, male *G. campestris* taken from the same study population, but reared and kept under laboratory conditions, elevated their calling rate and also displayed more costly calling-song components with increasing food availability (Scheuber et al., 2003). One possible explanation for this discrepancy is that environmentally induced variation in body temperature strongly affected calling-song characteristics (Doherty, 1985; Martin et al., 2000), thereby obscuring the effects of nutritional condition in the field study. Although we statistically removed variance in calling-song components associated to ambient temperature, this might not have accounted for variation in operative body temperature among calling males. Moreover, if female body temperature is a better predictor for male body temperature than is ambient temperature, calling-song characteristics may still have contained information on the male's nutritional condition to females, because female phonotaxis with respect to calling-song characteristics may be temperature compensated (Doherty, 1985).

Our finding that the number of females attracted was positively related to calling rate, although there was no relationship with any of the calling song characteristics, may also suggest that males in good nutritional condition optimally used the surplus energy to enhance the efficiency of their signaling under natural conditions. Selection favors signals with the highest efficiency in transmission, detection, and reception (Endler, 1992), and the number of sexual partners that respond to the sexual advertisement is directly related to the effectiveness of the signal (Alexander et al., 1997). Investment in energetically costly song characteristics is only favored by selection, if females are able to distinguish between single song characteristics of different males, and if the additional costs to assess these differences are low (Iwasa and Pomiankowski, 1994; Schluter and Price, 1993). In frogs, natural background sound may reduce a female's ability to discriminate between male calls on the basis of song components (Gerhardt and Klump, 1988; Wollerman and Haven Wiley, 2002). A similar mechanism might explain why cricket females in the present study may not have included calling-song characteristics in mate choice, because males usually call from aggregations amid a considerable background chorus. Finally, it is also possible that food-supplemented males enhanced their efficiency by calling with a greater overall continuity or on different times of the day than did control males. Males in good condition tended to lengthen their daily signaling period, both by starting earlier in the afternoon and finishing later in the evening (Brinkhof MWG, personal communication). Unfortunately, the costs and benefits of temporal variation in calling behavior are still poorly understood (Zuk and Simmons, 1997).

Food-supplemented males called more frequently and effectively attracted more females than did control males, although the number of males trapped was similar in both groups. Effect of food odor on male or female attraction can be excluded, considering that food was placed close to all experimental burrows. In crickets, the acoustic display may serve as a signal to neighboring males to maintain spacing (Cade, 1981; Campbell, 1990; Campbell and Shipp, 1979). We have no data to assess whether condition-dependent signaling affected spacing behavior, which would have required

a comparison of the spatial social environment of focal males before and after the start of the food-supplementation experiment.

We assume that the larger number of females attracted by males in good nutritional condition compared with males in poor condition reflects variation in female mating preference. Evolution of female preferences for condition-dependent male traits may be explained by direct and indirect selection on female mating preferences (Kirkpatrick and Ryan, 1991). Direct selection of female mating preference arises when the preferences affect the survival or fecundity of the female. Males in good condition might produce larger spermatophores (Gwynne, 1990) or more sperm, which may enhance fertilization success and reduce the need for the female to remate with another male (Blay and Yuval, 1997; Taylor and Yuval, 1999). Further, males in good condition might have less parasitic infections and reduce the risk for females to obtain parasitic infections during copulation (Borgia and Collis, 1989). Transmission of parasitic nematodes during copulation has, for instance, been shown in the decorated cricket *Gryllodes sigillatus* (Luong et al., 2000).

Indirect selection of female mating preferences assumes a genetic correlation between the preference for a sexually selected trait and the genotypic quality of the male. The benefit of choosing a male in prime condition might be increased offspring fitness as suggested by "good genes" models, if variation in condition indicates heritable variation in genetic quality (Andersson, 1994; Kirkpatrick and Ryan, 1991). Some theoretical models suggest that characters that show condition-dependent expression may be especially likely to reflect heritable fitness differences (Rowe and Houle, 1996). In stalk-eyed flies, the condition-dependent signal (eye span) reflected male quality, and environmental stress magnified the differences between male genotypes (David et al., 2000). Genetic variation of a condition-dependent trait was also shown in the dung beetle, *Onthophagus taurus* (Kotiaho et al., 2001). Finally, genetic variation in condition may indicate heritable variation in immunocompetence or parasite resistance. In the house crickets, *Achaeta domesticus*, body size, hemocyte load, and encapsulation ability were heritable and positively genetically correlated among offspring (Ryder and Siva-Jothy, 2001). Hemocyte load was further positively correlated with a syllable number (Ryder and Siva-Jothy, 2000), which is an important, male size-related calling-song characteristic in female mate choice (Gray, 1997). It remains to be shown in *G. campestris* whether variation in condition-dependent male signaling under natural conditions indicates heritable variation in genetic quality.

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