

The effect of past condition on a multicomponent sexual signal[†]

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Sexual-selection theory predicts that multiple signals may reveal male condition at different stages of life, thus allowing females to make a more reliable assessment of male quality. While the effect of current condition on signal design is well established, few studies have experimentally investigated the effects of past condition. We therefore manipulated the nutritional condition of male nymph field crickets *Gryllus campestris* and assessed the enduring effects on multiple components of the adult calling song. Food-restricted males had longer nymphal development times and smaller adult body sizes than nymphs with *ad libitum* food access. Nymphal feeding conditions specifically affected the allometric relationship between body size and harp size, as food-restricted males developed comparatively small harps, leading to a calling song of higher carrier frequency than that produced by similar-sized control males. Other calling-song components, notably chirp rate and chirp intensity, were not affected by the nymphal food treatment, exposing carrier frequency as the key component indicating past condition. In a previous study we established chirp rate as the sole indicator of current condition. The combined results represent experimental evidence of a multicomponent sexual signal that provides distinct information on male condition during different stages of life.

Keywords: field cricket; sexual selection; multiple signals; honest signalling; condition dependence; past condition

1. INTRODUCTION

Female mate choice commonly involves the assessment of multiple male ornaments. Sexual-selection theory generally explains the advance of multiple signalling systems in terms of fitness benefits for females, resulting from either a reduction in mate-assessment costs or improved assessment of overall male quality (Møller & Pomiankowski 1993; Johnstone 1996; Candolin 2003). Indicator models for the evolution of sexual traits, i.e. honest advertisement or handicap models (Andersson 1994), may especially apply to the evolution of multiple secondary sexual characteristics. The expression of multiple ornaments might augment the overall cost of signalling, and thus allow a more reliable assessment of variation in resource availability, viability, physical condition and/or genetic quality between males than signalling systems based on a single trait (Johnstone 1996; Candolin 2003).

It has specifically been proposed that multiple ornaments predict male condition over different time-scales (Møller & Pomiankowski 1993). Short-term signals would respond rapidly to momentary variations in condition, while long-term signals would lastingly reflect past condition, for instance during the period of juvenile growth and development. Befitting 'good genes' models, long-term signals may be especially important in female mate choice, because such signals may more reliably reflect the genetic quality of males than would signals subject to short-term environmental variation (Hill *et al.* 1999; Kokko *et al.* 1999). Several empirical studies confirmed that variation in trait expression might reflect male con-

dition, as determined by current nutrition (Kodric-Brown 1989; Wagner & Hoback 1999) or degree of parasitism (Milinski & Bakker 1990; Møller *et al.* 1999). Alternatively, the expression of secondary sexual ornaments might vary with past condition, in particular with variation in the environmental conditions experienced during juvenile growth. Diet quality influences horn length in beetles (Emlen 1994), eye span in stalk-eyed flies (Knell *et al.* 1999; David *et al.* 2000) and wattle colour in pheasants (Ohlsson *et al.* 2002). In the striped ground cricket *Allonemobius fasciatus* variation in calling-song characteristics is related to rearing temperature (Olvido & Mousseau 1995). However, experimental support for the proposition that multiple male ornaments may specifically serve to reflect condition over different time-scales (Møller & Pomiankowski 1993) is lacking.

We recently proposed that the calling song of male field crickets *Gryllus campestris* is a multicomponent sexual signal, in which two key components, chirp rate and carrier frequency (pitch), reflect condition during different stages of life (Scheuber *et al.* 2003). The calling song is the main acoustic sexual display in crickets and female mate-choice decisions may involve both chirp rate (Wagner *et al.* 2001) and carrier frequency (Simmons & Ritchie 1996). First, among males, chirp rate and carrier frequency are uncorrelated calling-song components, as revealed by laboratory (Scheuber *et al.* 2003) and field data (Holzer *et al.* 2003). Second, manipulation of the current nutritional condition of adult males affects the chirp rate, but not the carrier frequency (Scheuber *et al.* 2003). A similar result was found in the variable field cricket, *G. lineaticeps* (Wagner & Hoback 1999). Third, carrier frequency, but not chirp rate, is negatively correlated with body size and particularly with the size of the harp, which is an important

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sound-producing structure in the modified forewings (Simmons 1995; Scheuber *et al.* 2003). Assuming that body size reflects juvenile growth condition, this suggests that carrier frequency is the main calling-song component indicating past condition. A larger harp generates a lower carrier frequency, which may therefore make males with superior past nutritional condition more attractive to females (cf. Simmons 1995).

Theoretically, variation in the carrier frequency of the calling song may reveal past condition through a change in the size of the harp area that is either proportional or disproportional to body size (cf. Emlen & Nijhout 2000). In insects, the development of the extremities takes place in the late larval stages, mediated by separate clusters of imaginal cells. Growth of legs and wings is therefore decoupled from growth of overall body size (Fairbairn 1990; Milan *et al.* 1996; Nijhout & Emlen 1998). The scaling relationship that relates trait expression to variation in body size commonly has a genetic basis, reflecting condition-sensitive mechanisms of trait expression that have been shaped by natural and sexual selection (Emlen & Nijhout 2000). Scaling might specifically reveal the selective forces acting on each trait as well as how these forces vary with body size (Emlen & Nijhout 2000). To understand the expression of past condition in the cricket calling song, it is therefore important to investigate the underlying allometric relationship between body size and harp size.

The present study experimentally tests the hypothesis that carrier frequency is the sole calling-song component indicating juvenile growth conditions. We therefore subjected males in the final stages of nymphal development to one of two food regimes. Wing development is completed during the last nymphal stages, thus nutritional condition during this phase may lastingly affect harp size and thereby carrier frequency following adult eclosion. By comparing full-sib males reared in a split-brood design, we further controlled for the effects of genetic variation on past condition, juvenile development and adult morphology. To determine the developmental mechanism by which the calling song reveals past nutritional condition we specifically investigated the allometric relationship between body size and harp size.

2. MATERIAL AND METHODS

The male field crickets *G. campestris* used in the present study were full-sib offspring produced by 20 virgin mating pairs, both adults in each pair originating from our laboratory stock population. Each family was reared in split broods, by randomly taking two groups of 30 newly hatched nymphs and placing them in separate plastic containers (length of 38 cm, width of 20 cm, height of 25 cm). The positions of the rearing containers of the same family were randomized over the available shelves within the climate chamber. Rearing containers contained sand substrate, egg cardboards for shelter, a water vial and a plastic tray with *ad libitum* food (i.e. fish chow, a 1 : 1 mixture of JBL Novovert and JBL Novogrand, JBL GmbH, Neuhausen, Germany). The temperature in the climate chamber was maintained at 26 °C, relative humidity at 65%, and a 14 L : 10 D photoperiod with lights on at 1000.

On average 93 (s.e. = 1.04) days after hatching, 240 fourth or fifth instar male nymphs were subjected to one of two food treat-

ments. The fourth and fifth instars are the penultimate and ultimate stages of nymphal development, and condition during this phase may lastingly affect wing development, harp size and thereby carrier frequency following adult eclosion. In these instars the absence of a budding ovipositor distinguishes male from female nymphs. From each family we randomly selected 12 male nymphs, six from each of the two split-brood containers. Experimental nymphs were housed individually in plastic jars (length of 13 cm, width of 9 cm, height of 18 cm) inside a second climate chamber under similar climate and light conditions to those experienced during the first period of nymphal development. The jars contained sand bedding, a cardboard shelter and two plastic cups, for water and food, respectively. Three individuals originating from each rearing container were assigned to the high-food treatment, and the remaining three nymphs were assigned to the low-food treatment, resulting in a total of six full-sibs per treatment group. Feeding regimes started immediately upon individual housing, with individuals in the high-food and low-food groups receiving on average 0.2 g or 0.015 g of food daily, respectively. Three times a week the food was refreshed, and mortality or moult into adulthood was recorded. For a subsample of individuals ($n = 40$) we measured food consumption by weighing the remaining food. Average daily food intakes were 0.059 g and 0.0126 g in the high-food and low-food groups, respectively. This difference was highly significant (Kruskal–Wallis test: $\chi^2 = 8.639$, $p = 0.003$), confirming that food availability was effectively *ad libitum* in the high-food group and restricted in the low-food group. Following adult eclosion food was available *ad libitum* to all individuals, thus restricting the direct manipulation of nutritional condition to the nymphal period only. Henceforth, to avoid confusion concerning the food regime during adulthood, we refer to the high-food and low-food treatments as the control and experimental groups, respectively.

Upon individual housing, nymphal body mass was measured to the nearest 0.001 g. Further, the length and width of the pronotum were assessed to the nearest 0.02 mm using a digital imaging system and the public domain NIH Image program (National Institutes of Health, USA, <http://rsb.info.nih.gov/nih-image/>). We used pronotum area, calculated as the product of pronotum length and width, as an index of structural body size. Body condition was determined as the residual of the regression of body mass on body size. In field crickets mass residuals give an appropriate index of body condition, reflecting energetic fat reserves under controlled feeding conditions (Gray & Eckhardt 2001). Initial body size and body condition at the start of the food treatment varied significantly between families (both $p < 0.001$), but not between treatment groups ($p = 0.18$ and $p = 0.45$, respectively). Adult body mass was measured on the first day and the eighth day following adult eclosion. After recording the calling song (days 8 and 9, see below) we used the digital imaging system to take final measurements of pronotum size, tibia length and harp size (according to Simmons 1995; Scheuber *et al.* 2003).

On day 8 after adult eclosion we obtained a quantitative measure of calling behaviour by assessing calling rate over a period of 24 h. Daily calling rate was recorded using a sound sensor (DCP Microsense Sound Level Sensor), which was placed in the lid of the housing container and connected to a data logger (Lego Mindstorms RCX 1.0 programmable brick). Every 5 min the data logger scored the sound intensity (dB) inside the housing container. The background sound intensity caused by the continuous chorus provided by other males reached peak values

of 60 dB, while calls of resident males never dropped below 70 dB. Therefore, to discriminate the calling activity of individual males from the background chorus reliably we scored only peaks above a threshold level of 65 dB. Daily calling rate was quantified as the proportion of time spent calling over a 24 h period.

On day 9 we further audio recorded the calling song between 1300 and 1700 (i.e. within the first 5 h of the dark phase) to obtain a qualitative measure of calling behaviour. Recordings were made with a microphone (Sony ECM-16), which was located in the lid of the housing container and connected to a digital tape recorder (Sony TCD-D100). For data analysis we digitized a 30 s sequence taken at least 2 min after the start of calling activity. Using CANARY software (Charif *et al.* 1995) we evaluated chirp rate (number of chirps per second), syllable number (number of syllables per chirp), chirp duration (ms), interchirp duration (ms), chirp intensity (fW m^{-2}) and carrier frequency (kHz) according to standard criteria (Scheuber *et al.* 2003).

Data analyses were performed with the JMP statistical package (Sall *et al.* 2001). Nymph survival until adult eclosion and the probability of calling activity were analysed with logistic regression using log-likelihood ratio tests, testing the significance of prediction variables chi-square, given that the scale parameters of the models were close to one (McCullagh & Nelder 1989). Calling-rate data were arcsin-transformed to obtain a normal distribution. To analyse the experimental variation in morphological traits and calling-song characteristics we used a mixed-model analysis of variance (ANOVA) approach (Sokal & Rohlf 1995), with food treatment as a fixed effect and family as a random effect. We thus controlled for trait variation between families, but sample sizes per sib-group across treatments were too small to obtain reliable heritability estimates or to investigate genetic variation in conditional expression. In the analyses of adult body mass, body size and body condition, we further controlled for variation in initial body mass, initial pronotum size and initial body condition, respectively.

3. RESULTS

Nymph survival over the food-treatment period (i.e. until adult eclosion) varied significantly between families ($\chi^2_{19} = 65.90$, $p < 0.0001$), independent of variation in initial body condition ($\chi^2_1 = 2.20$, $p = 0.14$). Mean nymph survivals were 0.58 and 0.53 for the control and experimental groups, respectively, and independent of food treatment ($\chi^2_1 = 1.40$, $p = 0.24$). For the 132 individuals attaining adult eclosion, the mean development time over the food-treatment period was 40.3 (s.e. = 2.4) days for controls ($n = 69$) and 45.9 (s.e. = 2.3) days for food-restricted nymphs ($n = 63$). By controlling for significant variation between families ($F_{19,105} = 2.05$, $p = 0.011$), we found that food-restricted nymphs took significantly longer to reach adult eclosion than did controls ($F_{1,105} = 7.66$, $p = 0.007$).

At adult eclosion, control nymphs showed a significantly higher body mass, larger pronotum size, higher body condition and a larger harp size than food-restricted nymphs. The variation in growth parameters was independent of family (table 1). Harp size was positively related to pronotum size ($F_{1,111} = 37.95$, $p < 0.0001$), but experimental males had smaller harps than similar-sized control males ($F_{1,111} = 35.97$, $p < 0.0001$). The slope of

the relationship did not differ between food treatments (interaction pronotum \times treatment: $F_{1,110} = 1.54$, $p = 0.22$; figure 1).

Over the first 8 days following adult eclosion, under conditions of *ad libitum* food availability, experimental males gained more body mass than control males (0.072 g (s.e. = 0.014 g) and 0.036 g (s.e. = 0.013 g), respectively). However, the post-treatment changes in adult body mass ($F_{1,83} = 1.95$, $p = 0.17$) and in body condition ($F_{1,78} = 0.50$, $p = 0.48$) were not significantly different between treatment groups.

Among eclosed adults that survived until day 8 ($n = 129$), 47 males did not show any calling activity over the 24 h period. The probability of calling activity was independent of treatment ($\chi^2_1 = 0.24$, $p = 0.62$) and family ($\chi^2_{19} = 28.40$, $p = 0.08$). Among the 82 males showing calling activity, the daily calling rate of control males was slightly higher than that of experimental males, but the effect of the nymphal food treatment was not significant. In addition, there was no effect of family (table 2). Nymphal food treatment had a significant effect on carrier frequency, but not on other calling-song characteristics. The carrier frequency of the calling song of experimental males was on average higher than that of control males (table 2). In addition, carrier frequency and syllable number varied significantly between families (table 2). Carrier frequency was not correlated with chirp rate (Pearson's correlation coefficient $r = 0.146$, $n = 82$, $p = 0.19$) or other calling-song characteristics.

We finally investigated whether the effect of food treatment on harp size explained the treatment-related variation in carrier frequency. Carrier frequency was negatively related to harp size ($F_{1,57} = 21.97$, $p < 0.0001$; figure 2), while harp size did not explain the variation in carrier frequency between families ($F_{17,57} = 1.90$, $p = 0.04$). When accounting for the effect of harp size, the effect of food treatment on carrier frequency was no longer significant ($F_{1,56} = 0.03$, $p = 0.86$; figure 2). Thus, experimentally induced variation in harp size fully explained the effect of the food treatment on carrier frequency.

4. DISCUSSION

Our present study clearly demonstrates that the calling song of field crickets *G. campestris* contains specific information about the past condition of the male. Under conditions of *ad libitum* food male nymphs had shorter development times and achieved a larger adult size than did nymphs kept under a restricted feeding schedule. Males reared under superior nymphal feeding conditions produced calls of lower carrier frequency than males with restricted food access, while other calling-song characteristics as well as the daily rate of calling were not affected. The effect of past nutritional condition on carrier frequency was fully explained by variation in the area of the sound-producing harp between males reared on different feeding regimes. Moreover, males of superior past condition had relatively larger harps than males of inferior past condition. In addition, we found a significant effect of family on carrier frequency.

Carrier frequency is under directional sexual selection in field crickets *G. campestris*, because females markedly prefer playbacks of low carrier frequency to those of

Table 1. Statistical evaluation of mean \pm s.e. variation in morphological traits.

variable	control	experimental	food treatment	family
body mass at eclosion (g)	1.14 \pm 0.02	0.96 \pm 0.02	$F_{1,97} = 77.67^{***}$	$F_{19,97} = 0.67$
adult pronotum size (mm ²)	30.98 \pm 0.30	28.81 \pm 0.27	$F_{1,93} = 39.38^{***}$	$F_{19,93} = 0.85$
body condition at eclosion ^a	0.04 \pm 0.02	-0.04 \pm 0.02	$F_{1,86} = 11.37^{**}$	$F_{19,86} = 0.77$
harp size (mm ²)	16.99 \pm 0.14	15.24 \pm 0.14	$F_{1,92} = 84.20^{***}$	$F_{19,92} = 0.25$

^a Expected mean square method.

** $p < 0.01$; *** $p < 0.001$.

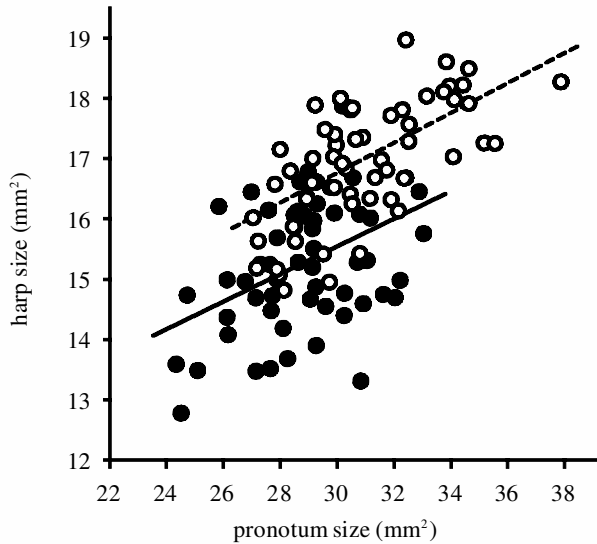


Figure 1. Allometric relationship between body size and trait size in relation to past nutritional condition. The food-restricted treatment group is indicated by the solid symbols and the solid regression line; the control group is indicated by the open symbols and the dashed regression line.

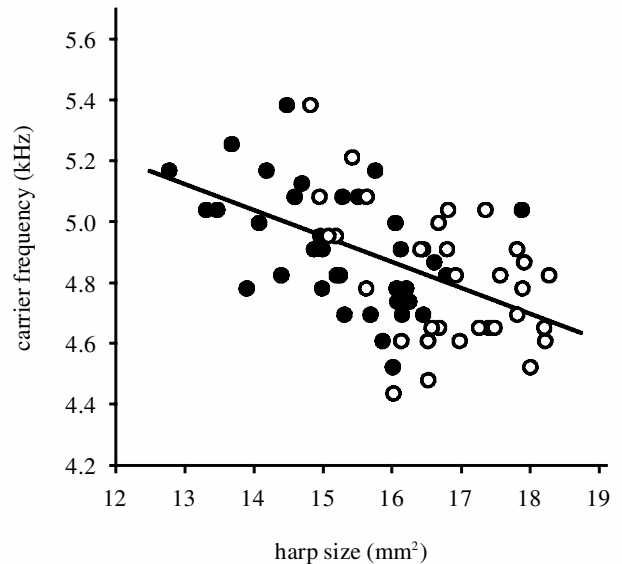


Figure 2. Regression of carrier frequency on harp size. Solid and open symbols indicate the food-restricted group and the control group, respectively.

Table 2. Means \pm s.e. and test statistics for daily calling rate and calling-song characters.

variable	control	experimental	food treatment	family
daily calling rate	0.22 \pm 0.02	0.17 \pm 0.02	$F_{1,64} = 2.94$	$F_{16,64} = 0.36$
carrier frequency (kHz)	4.81 \pm 0.03	4.92 \pm 0.03	$F_{1,62} = 5.96^*$	$F_{18,62} = 2.13^*$
chirp rate ^a (chirps s ⁻¹)	3.28 \pm 0.10	3.15 \pm 0.08	$F_{1,62} = 0.09$	$F_{18,62} = 0.84$
syllable number (syllables/chirp)	3.71 \pm 0.08	3.61 \pm 0.08	$F_{1,62} = 1.43$	$F_{18,62} = 2.03^*$
chirp duration (ms)	105.69 \pm 2.70	100.34 \pm 2.40	$F_{1,62} = 2.22$	$F_{18,62} = 1.18$
interchirp duration ^a (ms)	203.55 \pm 9.08	225.65 \pm 9.08	$F_{1,62} = 1.01$	$F_{18,62} = 0.71$
chirp intensity (fW m ⁻²)	11.00 \pm 1.30	9.10 \pm 1.05	$F_{1,62} = 1.55$	$F_{18,62} = 0.38$

^a Expected mean square method.

* $p < 0.05$.

higher-pitched calls in dual-choice experiments (Simmons & Ritchie 1996). Because carrier frequency is negatively related to body size (Simmons 1995), the preference for a low carrier frequency might be indicative of female choice for larger males. This is supported by field data, which showed an increase in pairing success with male body size (Simmons 1995). Female preference for call characteristics that are related to larger male size is common in orthopterans (e.g. Brown *et al.* 1996; Gray 1997) and in other taxa (e.g. anurans) and may be related to various direct benefits, such as food supply, oviposition

sites or fertilization success (reviewed by Andersson 1994; Zuk & Simmons 1997). Our present study specifically indicates that the female preference for low carrier frequency (Simmons & Ritchie 1996) arises because carrier frequency is an indicator of the past condition of the male. Some theoretical models suggest that secondary sexual characters that show condition-dependent expression may be especially likely to reflect heritable variation in fitness (Rowe & Houle 1996). In house crickets and field crickets, the existence of heritable variation in past condition (and the ability to acquire resources) is indicated by quantitat-

ive genetic studies that revealed heritable components of development time and body size under laboratory (Simmons 1987; Simons & Roff 1994; Ryder & Siva-Jothy 2001) and semi-natural (Simons & Roff 1994) conditions. However, it is unclear in these cricket species whether calling-song characteristics related to past condition show genetic variation in conditional expression, as predicted by conditional capture models (Rowe & Houle 1996), and empirically shown for ornament expression in stalk-eyed flies (David *et al.* 2000) and dung beetles (Kotiaho *et al.* 2001). Although we found a significant effect of family on carrier frequency, our sample sizes per family and across food treatments were too small to investigate its heritability and genetic variance in conditional expression.

Emlen & Nijhout (2000) recently proposed that the shapes of sexual-trait scaling relationships reflect condition-sensitive mechanisms of trait expression that reflect underlying developmental mechanisms, selection pressures on each trait and selection pressures in relation to body size. In horned beetles *Onthophagus acuminatus*, males reared on a low-quality diet had longer horn lengths at any given body size than sibling males reared on a high-quality diet. This condition-dependent scaling was explained by body-size related variation in male mating strategy (Emlen 1997). Male stalk-eyed flies *Cyrtodiopsis dalmanni* reared under high larval density had relatively smaller eye spans than those reared under low-density conditions, suggesting that poor larval conditions restrain the trait exaggeration favoured by female mate choice (David *et al.* 1998). Correspondingly we found in field crickets that nymphal nutritional condition shapes the allometric relationship by affecting body size and horn size disproportionately, such that differences in past condition are augmented in the corresponding signalling trait, i.e. carrier frequency. Consequently, carrier frequency contains additional body-size-independent information on past condition, which may increase the reliability of carrier frequency as an indicator of male quality and explain its importance in female mate choice (Simmons & Ritchie 1996).

By manipulating food availability during adulthood only, we recently demonstrated that the current condition of male *G. campestris* is indicated by variation in daily calling rate and in chirp rate, while other calling-song components including carrier frequency were not affected (Scheuber *et al.* 2003). Because the present study revealed the carrier frequency as the sole signalling component indicating past condition, the combined results of the two studies indicate that the calling song of this field cricket is a multicomponent sexual signal that specifically indicates condition during different stages of life. This proposition is supported by field data (Holzer *et al.* 2003) and laboratory data (Scheuber *et al.* 2003), which reveal carrier frequency and chirp rate to be uncorrelated calling-song characteristics. This also suggests that, although size asymmetry is an important factor determining resource-holding potential in field crickets (Alexander 1961; Hofmann & Schildberger 2001), variation in past condition does not affect variation in current condition. Summarizing, calling-song characteristics of field crickets do not merely contain redundant information on overall male quality, as predicted by the redundant signals hypothesis (Møller & Pomiankowski 1993; Johnstone 1996; Candolin

2003). By contrast, our combined studies give, to the best of our knowledge, the first support to the multiple messages hypothesis with respect to male condition during different periods of his life cycle (Møller & Pomiankowski 1993; Johnstone 1996; Candolin 2003). An important task for future work is to investigate the relative importance of the long-term signal (carrier frequency) and the short-term signal (chirp rate) in female mate choice.

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