

Female preference for multiple condition-dependent components of a sexually selected signal

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Theoretical models explain the evolution of multi-cue mate-choice decisions from a trade-off between benefits owing to improved assessment of potential mates and costs linked to the use of multiple signals. However, empirical support for these basic assumptions is lacking. In field crickets (*Gryllus campestris*) we experimentally investigated the female preference to variation in two key components of the male calling song: carrier frequency and chirp rate. Previous studies have revealed carrier frequency and chirp rate as reliable indicators of male quality that reflect past condition and current condition, respectively. In a two-way choice experiment, females significantly preferred test songs of lower carrier frequency and higher chirp rate, but prioritized the carrier frequency over the chirp rate. Hence, the static long-term indicator of mate quality was weighted more than the dynamic short-term one. Our results thus indicate that females integrate information from independent condition-dependent cues to discriminate between available males in mate-choice decisions.

Keywords: acoustic signalling; field cricket; multiple signals; female preference; sexual ornamentation; sexual selection

1. INTRODUCTION

Intersexual communication commonly involves multiple sexual signals, as shown by the increasing number of studies indicating that females integrate several male ornaments in mate-choice decisions (Candolin 2003). For instance, female red jungle fowl (*Gallus gallus*) use male tail length and comb features as criteria in mate choice (Zuk *et al.* 1992). Female guppies (*Poecilia reticulata*) base their mating decisions on male courtship display as well as on carotenoid-based pigment spots (Kodric-Brown & Nicoletto 2001). Female preference in the three-spined stickleback (*Gasterosteus aculeatus*) is positively related to the number of concordant male sexual traits (redness, courtship and body size) that presumably indicate high quality (Künzler & Bakker 2001). In the treefrog *Hyla ebraccata*, females show a directional preference for male calls of low carrier frequency and a stabilizing preference for intermediate pulse-repetition rates (Wollerman 1998). Consequently, the evolution of multi-cue mate-choice decisions is a key issue in sexual selection theory (Candolin 2003).

Sexual selection theory considers two main selecting forces to explain how females use multiple cues in mate-choice decisions: (i) the information content and reliability of different cues, and (ii) the costs involved in sampling potential mates and assessing their quality. Møller & Pomiankowski (1993) formulated several hypotheses on the information provided by different

signals. The ‘multiple messages’ hypothesis predicts that different signals indicate different aspects of male phenotypic or genetic quality, such as condition during different stages of the life cycle. Long-term signals might statically reflect past condition, such as during juvenile development, whereas short-term signals dynamically reflect current condition (Gerhardt 1991). Static indicators that integrate condition over a long time-period are further suggested to signal male genetic quality more reliably than dynamic signalling traits, which are more prone to short-term environmental variation and temporary cheating by inferior males (Sullivan 1994; Møller *et al.* 1998; Candolin 1999; Kokko *et al.* 1999).

Using a quantitative genetic approach, Pomiankowski & Iwasa (1993) and Iwasa & Pomiankowski (1994) investigated the evolution of female preference for multiple ‘Fisherian’ traits and multiple ‘indicator’ traits, respectively. Both models predict that female preference for multiple cues is likely to evolve only if joint costs of dual preference are not significantly higher than the cost of either preference. The relative importance of the two preferences thereby basically corresponds to the relative costliness of each preference (Iwasa & Pomiankowski 1994). A game-theoretical model by Johnstone (1996) predicts evolutionarily stable complex sexual displays despite high preference costs, provided that the costs to a male of investing in a given signal are strongly accelerating. Otherwise, the optimal female preference function concerns one signal only. Fawcett & Johnstone (2003) recently investigated optimal strategies of female mate choice as a function of the accuracy of male signals, how costly they are to assess, and the abundance of desirable mates. In particular, females are predicted to prioritize the more accurate cue over the less accurate one.

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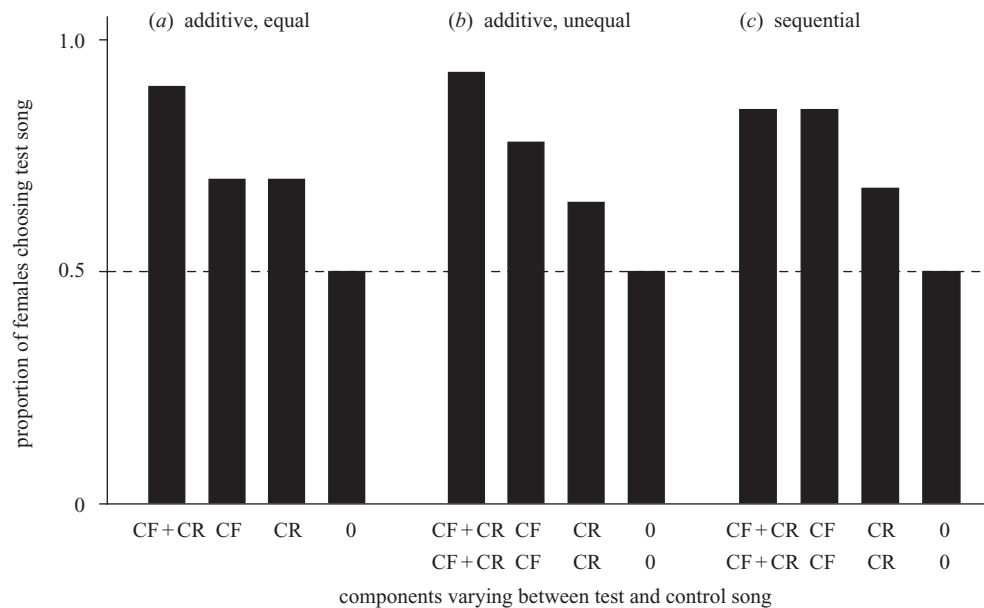


Figure 1. Predicted choice patterns of female preference for a test song in a two-way choice experiment, as a function of the relative importance of two cues on female choice decisions. (a) Additional, equal: $CF = CR$. (b) Additional, unequal: $CF > CR$ and $CR > CF$. (c) Sequential: $CF|CR$ and $CR|CF$. The dashed line depicts the baseline of female preference when test and control song are identical (control). In all other situations the test song reflects a male of superior quality in the signalling component(s) varying between test and control song. For further explanation see § 2.

Our understanding of the evolution of multi-cue mate choice is currently hampered by a lack of experimental data on female preference in sexual signalling systems that encompass genuine multiple traits of known information content. We therefore investigated the choice of female field crickets (*Gryllus campestris*) in relation to variation in multiple condition-dependent components of the male calling song. Male field crickets produce an elaborate calling song to attract receptive females. We previously showed that the calling song is a true multi-component sexual signal that indicates condition during different stages of life (Scheuber *et al.* 2003b). One calling-song component, the chirp rate (CR), dynamically reflects the male's current condition in both *G. campestris* (Scheuber *et al.* 2003a) and *G. lineaticeps* (Wagner & Hoback 1999). A second component, the carrier frequency (CF), is static and indicates a male's juvenile growth as well as his current body size (Scheuber *et al.* 2003b). Moreover, CF and CR are phenotypically uncorrelated song characteristics (Holzer *et al.* 2003; Scheuber *et al.* 2003a). Female choice tests varying individual calling-song components demonstrated a preference for calls of low CF in *G. campestris* (Simmons & Ritchie 1996), whereas high CRs are favoured in other cricket species (Wagner 1996; Hoback & Wagner 1997). In a two-way choice experiment, we investigated the relative importance of CF and CR in female mate-choice decisions.

Assuming that CF and CR are both under directional sexual selection (Simmons & Ritchie 1996; Wagner 1996), we consider three main hypotheses for the relative importance of the two calling song components (figure 1). First, the two components are independently and evenly weighted in mate assessment, resulting in an additive effect on female mate preference (additive, equal: $CF = CR$; figure 1a). Second, the components are independently assessed, but one of the components has a stronger impact on

female preference than the other (additive, unequal: $CF > CR$ or $CR > CF$; figure 1b). Third, assessment is sequential, such that one component has complete primacy, whereas the secondary component is considered only when the prioritized component is similar among competing calls (sequential: $CR|CF$, CF prioritized over CR, or $CF|CR$, CR prioritized over CF; figure 1c). The aim of this study was to distinguish experimentally between these hypotheses by offering females a choice between two artificial calls varying in CF, CR or both.

2. MATERIAL AND METHODS

Experimental individuals were offspring of field-mated *G. campestris* females, which were collected in June 2002 on a study site near Bern, Switzerland. In the laboratory the females were individually housed in plastic jars to oviposit. The climate chamber was kept at 26 °C and in a 14 L : 10 D regime, with lights on at 22.00. Hatched nymphs were randomly split into groups of 20 individuals and reared in plastic containers. Rearing containers were equipped with sand litter, a water vial and part of a cardboard egg carton for shelter. Nymphs were fed *ad libitum* on fish chow, a 1 : 1 mixture of JBL Novovort and JBL Novogrand (JBL GmbH, Neuhausen, Germany). Rearing containers were checked three times a week for individuals that had completed their final moult. Newly moulted females were individually marked on the pronotum with numbered tags (Opalith-plates, Bienen Meier, Künten, Switzerland) and transferred to group cages (38 × 20 cm and 25 cm high; maximum of 10 females per cage) until the mate-choice test. Group cages were provided with sand substrate, egg carton for shelter, a water vial and a plastic tray with *ad libitum* food.

The preference experiment was run in a climate chamber at 26 °C and under red fluorescent light conditions. Tests took place between 08.00 and 19.00, i.e. mainly during the perceived artificial dark period, which corresponds to the time of most intensive male calling activity under natural conditions (Rost & Honegger

1987). Female preference was tested in a 1 m² arena, which was embedded with a layer of synthetic grass (AstroPlay). The arena was tilted to a slope of 10° from the horizontal to mimic the topography of the natural habitat. To avoid disturbance and observer bias, the initiation of test trials as well as data collection were completely automated and controlled from outside the climate chamber. The centre of the lowered side of the arena was the starting point for test females, which were initially retained for 10 min under a small cup to accustom them to the test situation. Subsequently, the cup was automatically lifted by an electromotor, allowing females free range of the arena. The elevated side of the arena served as the choice area, where two test calls were broadcast separately from two loud speakers located 5 cm from the opposite corners. Experimental songs were processed on an Apple Macintosh computer and amplified to a standard loudness of 80 dB at 10 cm in front of the loudspeaker. This sound intensity relates to the level of maximal orientation performance in *G. campestris* females (Schmitz 1985). Below each speaker we placed an artificial burrow with a light barrier, which automatically registered entry of the female using a datalogger (LEGO RCX 1.0 programmable brick). When a female entered one of the burrows she was considered to have chosen the song associated with that burrow, and the test was ended.

The relative female preference for CF and CR and the associated time-costs of multi-cue assessment were investigated in a two-way choice experiment using artificially created calling songs. We implemented a 2 × 2 factorial design, in which the factorial levels of each calling-song component differed considerably, while staying well within the natural range of variation. For that purpose we used a sample of 50 field-collected calling songs and took, for each component, a lower and upper value that was close to the 10% and 90% quartiles of the distribution. This gave us 4 kHz (low CF: LCF) and 5 kHz (high CF: HCF) for CF, and 2 chirps per s (low CR: LCR) and 4 chirps per s (high CR: HCR) for CR, respectively. Combining these levels, we obtained four different test songs: HCF/LCR, HCF/HCR, LCF/LCR and LCF/HCR. The female preference for each of the test songs was assessed against a simultaneously broadcast control song, which was HCF/LCR. The control song was thus indicative of a male in poor past condition (high CF) and poor current condition (low CR). Consequently, we predicted a positive female preference for the test songs HCF/HCR, LCF/LCR and LCF/HCR, since each of these test calls represented males with a superior past and/or present condition to the control. Trials with the test song HCF/LCR represented a no-cue situation, which yielded a baseline level for comparing the female preference and choice duration in other test trials. Thus, the two one-cue situations, using the test songs LCF/LCR and HCF/HCR, monitored the sole effects of CF (CF group) and CR (CR group), respectively. The combined effect (and relative importance) of the two components is revealed in the female preference and choice duration of the two-cue situation (CF + CR group), using the test song LCF/HCR, compared with the no-cue and one-cue situations (figure 1).

D-SOUNDPRO v. 3.5.1: i3 (Software Engineering, Rome, Italy) and CANARY v. 1.2.4 (Charif *et al.* 1995) software were used to create the artificial test songs. The songs were constructed from a pulse of intermediate CF (4.5 kHz, pulse length: 34.5 ms) that was modulated 0.5 kHz up (HCF) or down (LCF). We then synthesized for each CF a single chirp of four identical pulses, with the first pulse conveying half the amplitude of the succeeding ones, thus mimicking the most common chirp pattern in *G. campestris*. We varied CR by producing calling songs of 10 s that contained either 10 (LCR) or 20 (HCR) chirps. To prevent a fixed phase

relationship between played-back calls, which might suggest precedence in a chorus and affect female mate choice (Murphy & Gerhardt 2002), we randomly varied the interchirp durations ($n = 40$ for HCR; $n = 20$ for LCR) using sets of six interchirp lengths with chirp-rate-specific means, but equal standard deviations. During test trials the synthetic 10 s calls were broadcast continuously using automatic replay in SOUNDEFFECTS v.0.9.2 software. The playback of the four different test songs was randomly distributed over the testing period (ANOVA: $F_{3,156} = 0.060$, $p = 0.98$) and speaker location (log-likelihood ratio test: $\chi^2_3 = 0.40$, $p = 0.94$).

On the test day, females were aged on average 14.6 (± 0.30 s.e.) days from adult eclosion. One hour prior to the trial, females were weighed to the nearest 0.01 g and then kept singly in a plastic sand-bedded box. After the trial we measured pronotum size as an index of overall body size 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/niimage/>). Females were randomly assigned to one of the four test-song combinations, balancing with respect to body mass (ANOVA: $F_{3,156} = 0.531$, $p = 0.66$) and age (Kruskal–Wallis: $\chi^2_3 = 3.68$, $p = 0.30$). At the start of the experiment, the test individual was placed under the plastic cup in the arena and left for 10 min to habituate to the test situation. Next, the song broadcast was started and 1 min later the female was automatically released and data-logging initiated. Individuals were left in the arena for up to 60 min and 64% of all tested females entered one of the burrows within this time-period ($n = 40$ in each treatment group). The proportion of individuals unsuccessfully tested was independent of body mass ($\chi^2_1 = 0.27$, $p = 0.60$), body size ($\chi^2_1 = 2.53$, $p = 0.11$) and treatment group ($\chi^2_3 = 6.84$, $p = 0.08$).

Statistics were performed using JMP IN Software v.4.0.3 (Sall *et al.* 2001). To control for temporal variation in female motivation and locomotion activity (Rost & Honegger 1987), we included daytime and daytime squared as covariates in all analyses. Body size was also included because female phenotype may affect mate-choice decisions (Jennions & Petrie 1997). The relative importance of CF and CR on female preference was analysed with nominal logistic regression, expressing rejection or choice of a test call as a binomial variable (i.e. values of 0 and 1, respectively) and testing the significance of predicted variables with a χ^2 -test. To test the five ordered hypotheses directionally (figure 1), we subsequently extended this analysis using the ordered heterogeneity test (Rice & Gaines 1994). Bonferroni correction (Sokal & Rohlf 1995) was applied to account for multiple testing, thus reducing the significance level to $\alpha' = 0.01$.

3. RESULTS

Females showed an overall preference for the calling songs of lower CF and higher CR (figure 2). The choice pattern significantly fitted the ‘sequential CR|CF’ hypothesis (figure 1; ordered heterogeneity test (Rice & Gaines 1994), based on log-likelihood ratio test: $\chi^2_3 = 6.15$, $p_{\text{dir}} = 0.009$). Thus, females included both calling-song components in their choice, but prioritized the CF over the CR (figure 2). Daytime ($\chi^2_1 = 0.001$, $p = 0.97$), daytime squared ($\chi^2_1 = 0.016$, $p = 0.90$) and body size ($\chi^2_1 = 1.64$, $p = 0.20$) did not affect the female preference. We further found weak statistical support for the ‘additional, unequal CF > CR’ hypothesis ($p_{\text{dir}} = 0.015$). All alternative hypotheses (see figure 1) lacked statistical support (‘additional, equal CF = CR’: $p_{\text{dir}} = 0.036$; ‘additional,

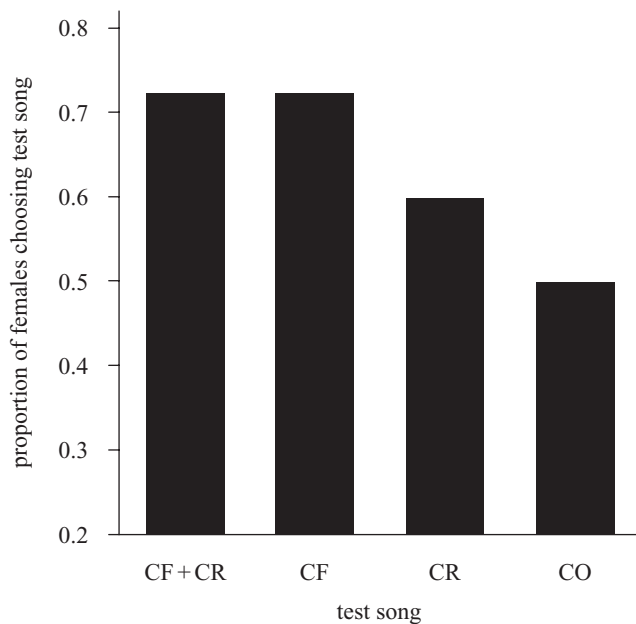


Figure 2. Female choice pattern in relation to the number and type of signalling components varying between alternative calls. In the CF + CR group and the CF group, 72.5% of the females chose the test song. In the CR group 60% of the females preferred the test song.

unequal CR > CF': $p_{\text{dir}} = 0.14$; 'sequential CF|CR': $p_{\text{dir}} = 0.19$; note that $\alpha' = 0.01$, Bonferroni corrected).

4. DISCUSSION

In recent years there has been growing interest in multiple cues in sexual selection and animal communication, and growing recognition of their widespread occurrence (Candolin 2003). However, much of this discussion has been of a theoretical nature (Johnstone 1996; Fawcett & Johnstone 2003). The present experimental study reveals that intersexual communication in *G. campestris* concerns two condition-dependent components of the male calling song. Experimental females showed an overall directional preference for calls of higher CR, indicative of a superior current condition (Scheuber *et al.* 2003a) and lower CF, signifying a prime past condition (Scheuber *et al.* 2003b). The latter result confirms the findings of Simmons & Ritchie (1996). Moreover, as assumed by theory (Kokko *et al.* 1999; Fawcett & Johnstone 2003), the mating preference involves a two-stage process, in which females prioritize the long-term (or static) signal (i.e. CF) over the short-term (or dynamic) signal (i.e. CR) in discriminating between competing male calls. Although several studies indicate the use of multiple cues in mate choice (Zuk *et al.* 1992; Hill *et al.* 1999; Kodric-Brown & Nicoletto 2001; Künzler & Bakker 2001; see also table 2 in Candolin (2003)), our study provides, to our knowledge, the first test of hypotheses for how females integrate information from independent male signals.

To date we can only speculate why female field crickets demonstrate a preference based on two male traits, and why the trait associated with juvenile condition has precedence over the trait indicating current adult condition. It is possible that the conditional expression of CF and CR partly captures and thereby indicates genetic variation in

male quality (Rowe & Houle 1996; Kotiaho *et al.* 2001). Thus, the associated female preference may be driven by indirect genetic benefits (Zuk & Simmons 1997), especially if long-term condition-dependent signals provide more reliable information about male genetic quality (Sullivan 1994; Møller *et al.* 1998; Candolin 1999; Kokko *et al.* 1999). Alternatively, the mating preference is based on direct benefits, such as a superior food supply or a reduced predation risk that the female may enjoy while residing for up to 3 days at the male's burrow (Rost & Honegger 1987; M. W. G. Brinkoff, personal communication).

Our findings are of general interest to the study of how animals collect and process multi-cue information in different contexts so as to maximize their fitness. Communication often involves complex displays that contain components in one or more sensory modalities. However, most studies on the evolution of complex displays have considered components in isolation instead of investigating their combined effect (Rowe 1999). Begging displays used by nestling birds to solicit food from their parents consist of multiple components, including posturing, gaping and calling (Kilner & Johnstone 1997). Different components of the display may signal short-term or long-term nutritional need (Price *et al.* 1996; Lotem 1998; Wright *et al.* 2002). Recent work further indicates that the complex display may provide parents with more detailed information about nestling hunger (Kilner *et al.* 1999), whereas distinct display components affect parental food allocation differently (Glassey & Forbes 2002). The use of multiple signals may also involve species recognition, as suggested in female swordtail fish (*Xiphohorus pygmaeus*), which employ visual and chemical cues to avoid mating with heterospecifics (Hankison & Morris 2003). Finally, parasitoid hymenopterans take advantage of multiple cues when searching for hosts, and the synergistic use of mechanosensory, olfactory and visual cues increases the precision of host location (Wäckers & Lewis 1994; Fischer *et al.* 2001). To summarize, these studies suggest that use of multiple cues allows individuals to obtain more reliable information about key parameters to fitness, such as food, the quality and needs of offspring and the quality of potential mates (Scheuber *et al.* 2003a,b). Moreover, individuals may appropriately adjust their behavioural decisions in response to these cues, as demonstrated here by the multi-cue mating preference of female field crickets.

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