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What's in a song? Female bushcrickets discriminate against the song of older males

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SUMMARY

The striking songs of insects such as bushcrickets have traditionally been interpreted as species recognition signals. If this is so, their information content should be relatively simple. Females should discriminate against atypical songs, but not between common differences between males. Alternatively, female preference may have evolved by sexual selection with variation between males providing reliable cues on which females discriminate among potential mates, or sensory biases may predispose females towards a particular form of song. We examined how the calling song of the bushcricket *Ephippiger ephippiger* varies in natural populations. Song structure changes over the course of a season, reflecting wear of the stridulatory apparatus. Males vary substantially in the rate at which they show ageing effects. Superimposed on this are consistent differences between males and temperature effects. This sexual signal therefore contains potentially reliable cues which females could use during mate choice. When presented with artificial songs that reproduce some of the song variants associated with older males, females show extremely strong preferences for unmanipulated song, typical of young males. These aspects of female preference will exert sexual selection on males, whether they originate for adaptive or arbitrary reasons.

1. INTRODUCTION

The evolutionary forces shaping female preference for male mating behaviours have long been the subject of research and debate (Cronin 1992). Darwin argued that elaborate male morphologies such as plumes must have evolved in the face of detrimental viability selection because females possessed preferences for these traits. Such preferences are now well documented, but the reasons why they have evolved are less well understood. Theories include adaptive models where females benefit by choosing males with better genotypes or by receiving immediate benefits such as nutritional donations or reduced probability of sexually transmitted disease, and non-adaptive models where females have arbitrary preferences caused by runaway evolutionary episodes or signal processing mechanisms (Kirkpatrick & Ryan 1992). Traits which seem less elaborate yet which are obligatory components of courtship, such as insect acoustic signals, are often thought to have evolved for species recognition rather than by sexual selection (Maynard-Smith 1991; Ewing 1989). Although sexual selection and species recognition are not mutually exclusive evolutionary forces (Ryan & Rand 1993), they do represent opposite ends of a potentially continuous distribution of female mating preferences and have contrasting predictions concerning the level of variability upon which females should base choices of mate. A sexual selection function predicts that females should discriminate among males within populations, whereas a species recognition function predicts that females should be relatively insensitive to such variation.

Here we report studies of the variability of calling song structure in a tettigoniid bushcricket (*Ephippiger ephippiger*). *E. ephippiger* has a typical tettigoniid mating system, with males calling and females showing phonotaxis (i.e. approaching behaviour) towards male song. Bushcricket calling song is typical of signals assumed to have been shaped more by species recognition than sexual selection (for reviews, see Ewing 1989; Bailey 1991). Some studies have shown that females distinguish between songs of conspecific males (see, for example, Latimer & Sippel 1987; Bailey 1985). This is often based on amplitude or spectral components that could indicate a nearby male and therefore result from a female minimizing her travelling distance, rather than the female using cues in the song to infer attributes of the signaller. A potential example of female discrimination which could represent choice among signallers would be if females show preferential phonotaxis towards low frequency song, often associated with a larger male. Such female discrimination has been predicted, but relevant experiments have found contradictory results which imply that females prefer higher frequency song (Latimer & Sippel 1987; Gwynne & Bailey 1988). This choice pattern is consistent with the 'prefer nearest male' interpretation of female choice. So, although the possibility of sexual selection operating on insect song has often been discussed, few examples relating preferences to particular structural song traits (rather than intensity or quantity of song) have been described.

Song is produced by elytral (wing) stridulation whereby a male drags a stridulatory file on one elytron across the other, causing reverberation (Bennet-Clark

1989). Song structure is therefore determined by the rate and pattern of wing movement and by the physical characteristics of the stridulatory apparatus. In *Ephippiger* the number of wing movements per chirp varies. This is known to influence female mating preference (Ritchie 1991, 1992*a*), but only between extremes found in allopatric song races (Ritchie 1992*b*). Other aspects of call structure include the duration of the wing movement and stridulatory peg strike rate. These are determined by the rate of wing movement and so will be temperature dependent. However, the speed of movement could perhaps provide a useful cue to females if it was also associated with male quality. Physical characteristics of the stridulatory file of tettigoniids are known to vary with age in some bushcrickets as pegs break off or wear down through use (Hartley & Stephen 1989; and personal observations), and there is evidence that peg strike information (both the number of pegs and peg strike rate) influences female preference in *Ephippiger* (Stiedl *et al.* 1991). Zuk (1987) found that females of two species of *Gryllus* discriminate between males of different ages, probably using cues from the males' calling song. Simmons & Zuk (1992) also found that mating success varied with age in *Gryllus bimaculatus* and a possible correlation between age and one parameter of calling song. We had noticed that males of *Ephippiger* reared in the laboratory break stridulatory pegs as they age, but animals probably live longer in the laboratory than in the field. The current work was done to assess: (i) does song structure modification occur in the field; (ii) are some modifications more reliably associated with male age under field conditions; and (iii) do common changes in song structure influence female preference and, if so, which modifications are most important to female choice? Answers to these questions will indicate the likelihood of sexual selection influencing the evolution of structural components of song pattern in *Ephippiger*.

2. MALE SONG

(a) Methods

We studied populations of *Ephippiger ephippiger* ('diurnus complex', see Oudman *et al.* 1990) from the eastern Pyrenees (Cerdagne-Capcir) during August 1994. Adults appear in late July or early August. The maximum adult lifespan must be around two months as the first frosts occur in late September at the high altitudes of these populations (*ca.* 1600 m). However, numbers seem to decline considerably before then. We concentrated on two sites. At the first (termed the 'indoor' population), 34 adult males were collected at the start of the season, maintained in small cages (three males per cage) for 33 days, and their song recorded onto reel to reel tape about every six days. The number of stridulatory peg strikes in the closing movement of the first three syllables and the duration of the stridulatory movement were measured. At the other site (an open meadow of habitat typical for *Ephippiger* termed the 'outdoor' population), 60 males were marked and recorded *in situ* over a period of 19 days.

Average number of recordings per male was 1.9 (range 1–6). Broken pegs, slips in the stridulatory movement, and worn pegs (indicated by 'fuzzy' peg strikes) were noted as present or absent for both populations, but wear could not be scored reliably from field recordings. Recordings were made using a UHER 4000 Report IC reel to reel tape recorder (tape speed 19 cm s⁻¹) and a Soundlab UD222 microphone. The manufacturer's specifications say this equipment has a flat frequency response to over 15 kHz, the main spectral component of *Ephippiger* song. Analysis was done by direct measurement of the waveform digitized into a Powerbook Macintosh computer at 22 kHz A/D conversion of tapes replayed at 1/8 recording speed.

Results were analysed in two ways. For each male, the average date from the start of the experiment on which a trait was scored as present or absent was calculated and compared by using non-parametric statistics. For the indoor population, the number of pegs and the duration of the major closing movement of each syllable satisfied parametric assumptions and were analysed using a generalized linear model (using the GLM procedure of 'Minitab') with individual and syllable number (1st, 2nd, or 3rd) as factors and male weight and temperature as covariates. All probabilities are two-tailed except for analysis of the field recordings in which one-tailed tests were used (we felt this was justified given the highly directional predictions arising from the other results).

(b) Results

Figure 1 shows examples of the modifications to song structure which were seen. Indicators associated with male age (slips in the stridulatory movement, broken pegs and worn pegs) were found in both populations. For the indoor population all were more likely to be found from recordings made later in the season (median day from the start of the experiment of recordings without slips = 10 days, $n = 165$, and with slips = 20 days, $n = 240$, Mann-Whitney $W = 25930$, $p < 0.0001$; without peg loss = 10 days, $n = 201$, with peg loss = 20 days, $n = 204$, $W = 35556$, $p < 0.0001$; without worn pegs = 18 days, $n = 366$, with worn pegs = 20 days, $n = 39$, $W = 71602$, $p = 0.0001$). Calculating these only from within an individual males' recordings reduced sample sizes but still produced significant results for slips (Wilcoxon $W = -199$, $n = 21$, $p < 0.001$; testing mean day of recordings without slips versus mean day of recordings with slips) and peg loss ($W = -50$, $n = 11$, $p = 0.01$). From the outdoor population peg loss was seen from later recordings (median time of recordings without peg loss = 5 days, $n = 67$, with peg loss = 8 days, $n = 48$, $W = 3418$, $p = 0.003$; within males $W = -70$, $n = 16$, $p = 0.035$). Slips were independent of day of recording.

Quantitative analysis of the indoor population shows that both the number of stridulatory pegs and duration of the stridulatory movement are influenced by temperature and age, and there are also consistent differences among individuals (see table 1). After allowing for temperature effects and differences between individuals, both the number of pegs per syllable

Table 1. Song modifications seen in field recordings

(Analysis of variance of quantitative data from indoor population. Regression coefficients are for covariates).

source of variance	DF	MS	coeff (SD)	F	p
Number of Pegs					
Individual	30	120.90		9.52	< 0.001
Weight (g)	1	7.45	1.182 (1.54)	0.59	NS
Temperature (°C)	1	96.57	-0.367 (0.13)	7.60	0.006
Syllable	2	45.77		3.6	0.028
Age	1	193.21	-0.118 (0.03)	15.26	< 0.001
Syllable*Age	2	5.83		0.46	NS
Individual*Age	30	40.57		3.20	< 0.001
Error	337	12.70			
Syllable Length					
Individual	30	36382		8.44	< 0.001
Weight (g)	1	320	7.750 (28.44)	0.07	NS
Temperature (°C)	1	1175035	-40.486 (2.45)	272.46	< 0.001
Syllable	2	29672		6.88	0.001
Age	1	18453	-1.156 (0.56)	4.28	0.039
Syllable*Age	2	328		0.08	NS
Individual*Age	30	23973		5.56	< 0.001
Error	337	4313			

and syllable length were less in older males, reflecting the increased likelihood of broken pegs and slips in the stridulatory movement. Effects were greatest for the first syllable. Interestingly, the rate or extent with which males showed age effects varied substantially between individuals (see table 1).

Age effects in song patterns would provide reliable and informative cues to females if older males produce a less valuable spermatophore, suffer from sperm depletion, or produce lower quality sperm. Peg strike rates and syllable lengths are associated with temperature and also vary consistently between individuals (allowing for age effects). If these covary with male quality, females could also derive information from these parameters. However, temperature variation would confound these cues.

3. FEMALE PREFERENCE

(a) Methods

Figure 2 shows details of the synthetic songs produced, which were modified to mimic the age effects seen in the field. The songs synthesized were a basic unmodified song plus: (i) BREAKPEG (see figure 2*a*) in which a single peg strike was removed from the middle of the closing wing movement, by replacing the 19th peg strike with silence; (ii) OPENSLIP (see figure 2*b*) in which the first three quarters of the opening wing movement was removed; (iii) SLIP1 (figure 2*c*) in which the first seven pegs of the closing wing movement were removed. The gap between the opening and closing syllable was maintained at around 10 ms; (iv) SLIP2 (figure 2*d*) in which both a mid-syllable slip and subsequent decrease in peg strike rate were incorporated; (v) FUZZY1 (figure 2*f*) in which the normal peg strike (figure 2*e*) was replaced with one simulating mild peg wear; and (vi) FUZZY2 (figure 2*g*) in which more extensive wear was simulated (note that this is still not an extreme example of the wear seen in natural recordings).

Song synthesis was done using the 'SIGNAL' software system (Engineering Design) with a sampling rate of 250 kHz and was based on a synthetic opening syllable and a single real stridulatory peg impact, recorded using a Beyer MCE 6.1 microphone (flat to over 20 kHz) in a sound attenuated room. The major syllable of the basic (unmanipulated) song was made by copying the single peg strike repeatedly into a file at a location specified by the experimenter (in 250 kHz sampling units) to produce a closing syllable 34 peg strikes long. The basic song model was based on a natural recording showing typical peg strike number, rate and pattern. The amplitude envelope used for the syllable shape was the average of six envelopes extracted from different recordings. The manipulations for the above song models were all made to the basic song model, so songs were otherwise identical. Worn pegs were simulated by increasing the width of the amplitude envelope of the individual peg strike. The sound wave used was from the real peg impact used for the basic model, equalized in amplitude and repeated to the necessary duration. Exactly the same strike pattern was used as in the basic song model. The frequency content of all songs was identical at source and realistic (as it was derived from a real peg strike) and all songs had four syllables per chirp, which is typical for these populations. A monosyllabic song was also synthesized, to be used in control experiments. Monosyllabic song is found in allopatric races of this species and females are known to discriminate against it (Ritchie 1991).

The synthetic songs were recorded onto a 2-track 'TEAC' reel to reel tape recorder (X-2000M, tape speed 38.1 cm s⁻¹) and replayed through 'Ultrasound Advice' ultrasonic amplifiers (S55) and speakers (S56) in an anechoic room. Because some of the modifications to song models were rather subtle, we checked the quality of them following replaying off tape with this equipment. The replayed songs were sampled into the PC via a Brüel & Kjær 1/2' condenser microphone (type 4133) and preamplifier (type 2615). Figure 3

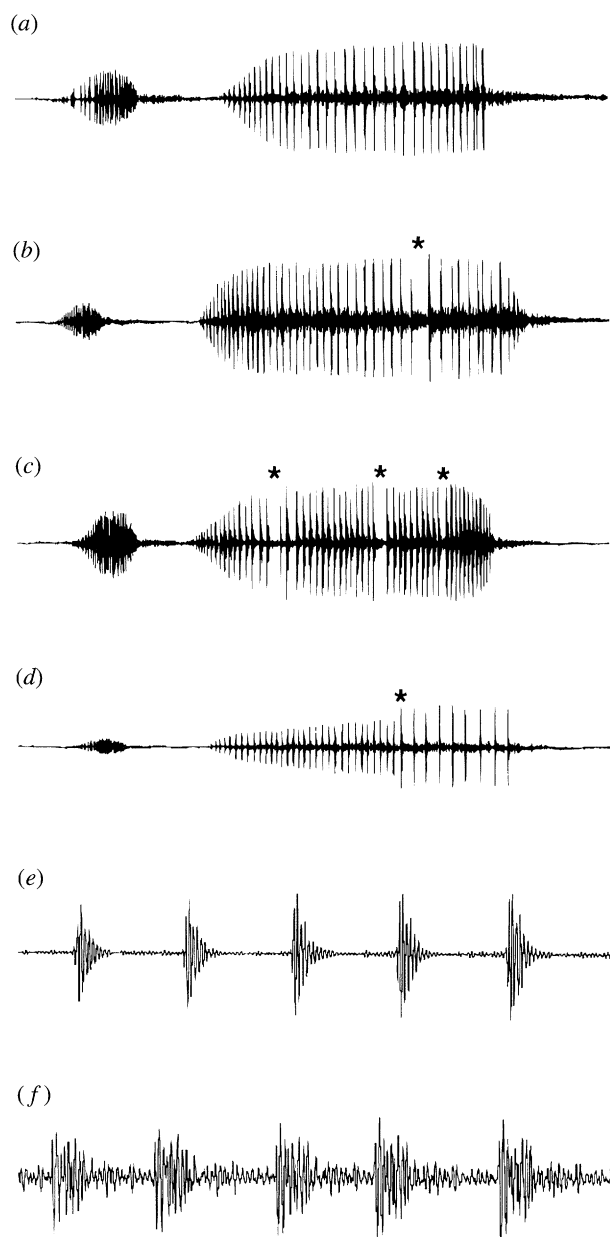


Figure 1. (a) One syllable of a chirp of *Ephippiger* song. Each consists of a rapid opening and longer closing wing movement, the latter including clearly visible stridulatory peg impacts. (b) One syllable of a male with a single broken stridulatory peg. (c), (d) Males with extensive song pattern modification (this can occur partly because of damage inflicted during mating attempts). The location of the change in song structure is indicated in (a)–(d) by an asterisk. (e), (f) The appearance of peg strikes of younger (e) and older (f) males is compared. The spreading of peg strikes in older males (to produce ‘fuzziness’ in the song) is caused by worn stridulatory pegs. Typically, the length of a closing syllable is around 60 ms, and peg strike intervals around 1.7 ms.

compares the amplitude information of the original BREAKPEG song model with that detected around the choice junction of the phonotaxis apparatus. The manipulation is reproduced clearly. Similar results were obtained with the other models. When preparing for playback, one song would be adjusted to equal sound pressure level (SPL, around 90 dB at source, 60 dB at the choice junction) through both speakers by adjusting the separate speaker amplifiers. Then the

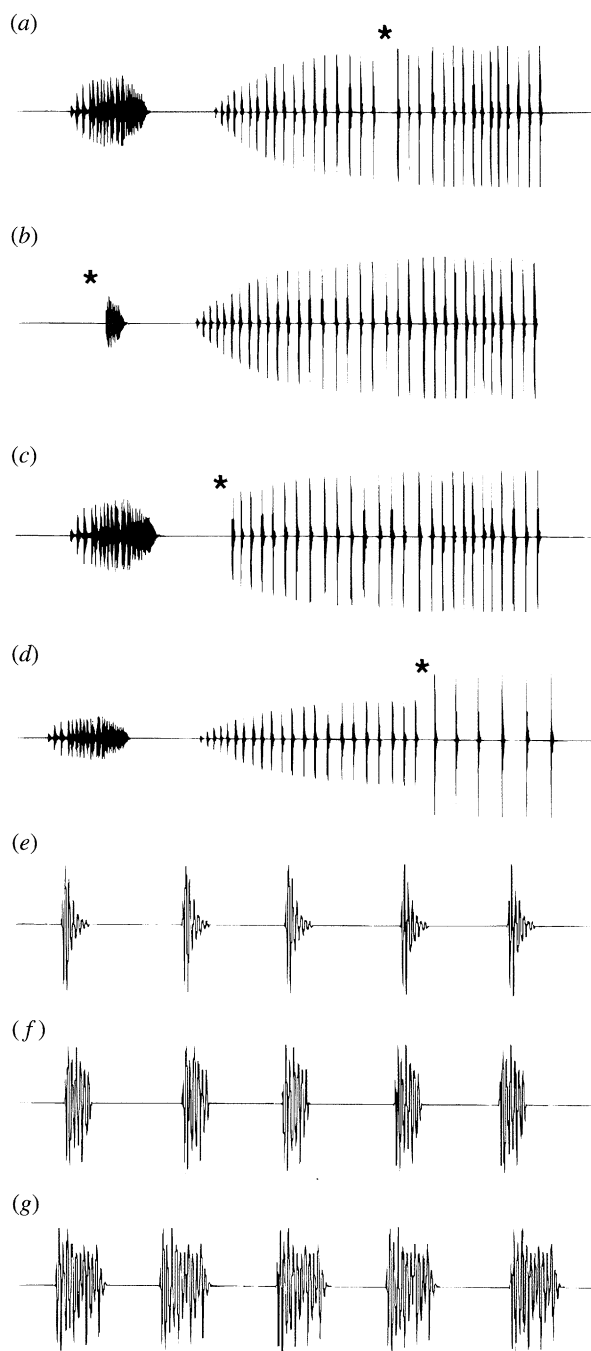


Figure 2. Syllables of artificial song designed to mimic age effects observed in the field. The songs shown are (a) BREAKPEG, (b) OPENS LIP, (c) SLIP1, (d) SLIP2, (e) detail of normal peg strike (f) detail of peg strikes from FUZZY1, (g) detail of peg strikes from FUZZY2. See text for further explanation.

other song was adjusted using the independent channel output controls of the TEAC to give a similar SPL. During this, SPL was measured using a ‘Realistic’ sound level meter (33–2050 on ‘fast’ setting). This meter is flat to only around 7 kHz (–10 dB at 15 kHz), but because the songs had the same spectral structure inaccuracies should have been consistent across songs. We assumed that we would be replaying song with larger deletions (e.g. OPENS LIP) slightly louder than the unmodified song, to compensate for the reduced song duration. This SPL equalization procedure was repeated before each playback. After the

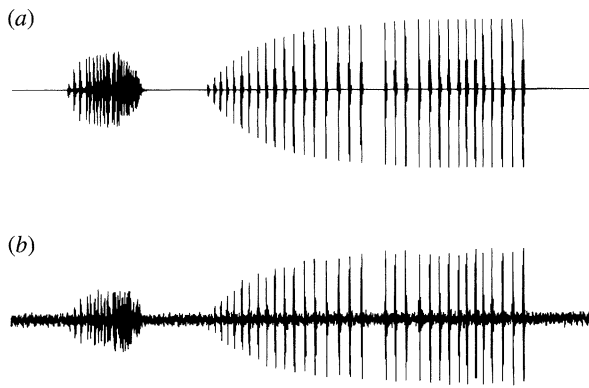


Figure 3. The BREAKPEG song model (a) as synthesized, (b) as presented to the females following recording and replaying with our equipment.

experiment this procedure was repeated twice and volumes measured using the Brüel & Kjær microphone and a type 2608 measuring amplifier (on 'fast' setting and linear weighting mode). Discrepancies in SPL between the two songs were small (mean 0.9, maximum 2 dB). *Ephippiger* female's preferences based on syllable number are robust to considerably larger changes in SPL (Ritchie 1991).

Synthetic song was presented to females in pairs, one of the modified songs alongside unmodified song. The positive control pair was unmodified song played alongside the monosyllabic song. The negative control pair was the least preferred polysyllabic song (FUZZY2) played alongside monosyllabic song. Songs were played in alternation through two loudspeakers and females walked up a T-shaped apparatus, turning towards one of the songs (Ritchie 1991). A trial consisted of playing each song pair to a female four times, switching the song between speakers for each presentation. Four choices of one song therefore required three consecutive changes of direction. In total, 33 females (laboratory reared in acoustic isolation) were given one trial to each song pair in random order. All readily completed all trials and make an equal contribution to the total level of choice indicated.

(b) Results

Figure 4 illustrates the degree of discrimination between the unmanipulated and artificially aged songs. In the positive control (unmanipulated normal song versus allopatric song), females showed a preference of over 90% in favour of normal song. Females also showed discrimination against some traits associated with older males. They did not discriminate against a slip in the opening syllable or against 'SLIP2', which involved both a mid-closing syllable slip and a change in peg strike rate. 'SLIP1', which was missing the first seven peg strikes of the closing syllable, was discriminated against on around 70% of choices. However, the strongest discrimination was against song with a single missing peg in the middle of the closing syllable (discriminated against on around 75% of choices) and song simulating worn pegs (discriminated against on over 80% of choices). The most

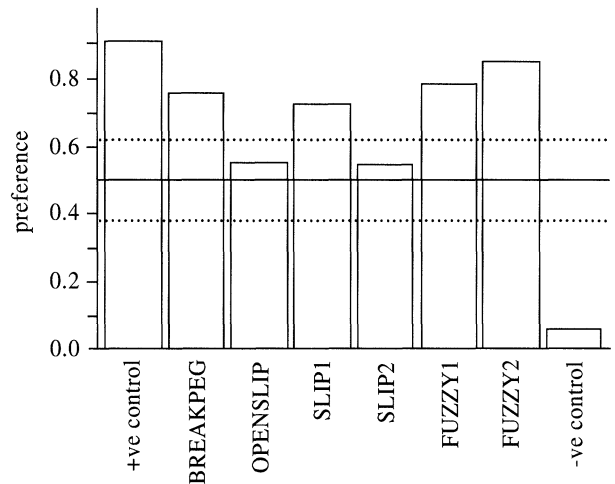


Figure 4. Female preference, as indicated by the total proportion of approaches to unmodified synthetic song during phonotaxis experiments. The solid line is 50% (no discrimination), the dotted lines correspond to a likelihood ratio with a probability of 0.6% (Bonferroni adjusted from 5%), were there no discrimination. See figure 2 for song designations.

discriminated against 'older' song was strongly preferred (over 90% of choices) when presented paired with allopatric song: an important control because it demonstrates that our synthetic 'older' song could be recognized and favoured i.e. it was not simply aberrant.

4. DISCUSSION

Most studies of the communication system of acoustic insects have taken place in the context of the system as a mechanism for the transmission of information concerning species identity and localization (for summaries, see Ewing 1989; Huber *et al.* 1989; Bailey 1991). Studies of acoustic communication in the context of sexual selection are more common with birds or anurans (for examples, see Searcy & Andersson 1986; Gerhardt 1994). Nevertheless it is not clear which force is usually most important in the evolution of insect communication systems, or even if they are mutually exclusive (Ryan & Rand 1993). From an operational point of view, systems which act as species recognition systems will be less sensitive to variation within a natural population than systems which primarily exert sexual selection upon the communicators.

Previous studies of *Ephippiger* have shown that variation between populations in male calling song is matched by changes in female preference (Ritchie 1991, 1992a), but that female preferences for the trait involved (syllable number) seemed relatively insensitive to variation within a population (Ritchie 1992b). Here we examined other structural changes in the song of *Ephippiger*. Both peg strike rate and syllable length varied with temperature, between males and with male age. The latter effect was at least in part the result of the presence of slips in the stridulatory movement and broken stridulatory pegs. In addition, the sound pulses produced by individual peg strikes showed evidence of wear in older males, being broader and less sharp in

appearance (see also Hartley & Stephen 1989). It seems likely that the less strong effects seen in males recorded directly in the field were the result of a shorter study period, although maintaining males in cages could perhaps accelerate ageing effects by increasing singing activity.

The synthetic songs reproduced different song modifications associated with male age. We found that females showed extremely strong discrimination (almost as great as that between allopatric song races) against some of these changes. Most interestingly, the extent of discrimination was not closely matched to the extent of song modification. Strongest discrimination was against song simulating worn pegs, and the effect simulated was relatively slight. When slips and broken pegs were simulated, females discriminated most strongly against a single broken peg in the middle of the stridulatory movement. In retrospect, this pattern of discrimination might follow the reliability of these traits in reflecting age. Natural song shows considerable variation in peg strike rate at the beginning and end of syllables, and variation in syllable length is very strongly associated with temperature. The pattern of discrimination could therefore result from selection favouring females who discriminate against older males most reliably.

Female discrimination against older males could be adaptive if females obtain benefits from mating with younger males. Detrimental traits associated with older males could include less valuable spermatophores, sperm depletion or reduction in sperm quality. It is not known if any of these effects occur, though *Ephippiger* does have a very large spermatophore that can represent over 30% of male body weight and which females readily consume. This substantial spermatophore means there is more scope for female preference to be influenced by immediate benefits than in other mating systems such as leks. Wedell (1993, 1994) has suggested that some bushcricket spermatophores could have a low protein content and in effect be partly a 'sham' offering of little nutritious quality, whereas others have a substantial effect on female fecundity. It seems possible that even spermatophores low in protein could contain rare resources (perhaps just water) which are valuable to females. Studies of some tettigoniids have shown that sex-role reversal can occur in species with large spermatophores, especially under conditions of high nutritive stress (Gwynne & Simmons 1990). Clearly this is one important area in which follow up work can clarify the significance of our findings. Note also that the possibility of a resource-based mating system in *Ephippiger* might explain the contrast between our findings and those of Zuk (1987), who found that *Gryllus* females preferred older males. Zuk (1987) argued that choice in *Gryllus* was likely to be for genetic benefits with older males being more likely to have a genotype associated with high viability. A possible adaptive explanation for the preference against worn pegs not involving age is that this structural change mimics the effect of environmental reverberation on song structure, and so be associated with more distant males, who are either more energetically expensive or dangerous to approach.

Alternatively, the discrimination against older males' song may not be adaptive. The changes in song structure might simply impair pattern recognition. For example, if females possess neurons tuned to typical peg strike rates, song containing broken pegs could present a less stimulating signal (even after SPL equalization). We do not think this is likely, however, because we were expecting that such preferences would result in females: (i) discriminating more strongly against SLIP2 (with extensive peg strike modification) than BREAKPEG (with a single broken peg); and (ii) preferring song containing worn pegs, as this contains a much greater 'duty cycle' (i.e. coherent signal per millisecond). In fact, females showed the opposite preferences to those predictions. As stated before, the pattern we found could reflect preference for the most reliable cues. Nevertheless, there is obviously insufficient information at this stage to allow firm conclusions regarding any adaptive significance of the preferences we have demonstrated.

We conclude that the calling song of *Ephippiger* contains many cues that are potentially informative to females when choosing amongst males of her population, and females have extremely strong preferences among commonly occurring cues. These aspects of song preference are not compatible with a species recognition function. Even if the female preferences we have described have not arisen to function in a sexual selection context, they have the effect of exerting sexual selection on males. Sexual selection will therefore be having a major role in the evolution of these characteristic (but not stereotyped) 'species specific' male mating signals. We also found that males vary in the rate with which they develop 'aged' song. Males who show aged traits most quickly will be at a selective disadvantage. It would be very interesting to know if this is counterbalanced by having a higher initial mating success.

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