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*Proc. R. Soc. Lond. B* 1996 **263**, 1305-1311

doi: 10.1098/rspb.1996.0191

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# Symmetry in the songs of crickets

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## SUMMARY

Acoustic signals produced by males are often subject to sexual selection. The mechanism of song production in crickets is well documented. Cricket songs are said to be characterised by almost pure tones of constant frequency. However, contrary to previous work, we show that cricket songs exhibit frequency modulation to varying degrees, dependent on the degree of asymmetry in the sound resonators or harps. Recent studies of sexually selected traits suggest that size and symmetry may reflect male quality. The harps of crickets exhibit directional asymmetry to a degree that is directly related to the degree of fluctuating asymmetry in a measure of body size. We show that females prefer pure tones of low carrier frequency, characteristic of large symmetrical harps. Directional asymmetry may thus convey reliable information regarding male quality encoded in the male's song.

## 1. INTRODUCTION

Acoustic signals produced by males are the secondary sexual traits most often subject to sexual selection (Andersson 1994). Variation in song parameters convey information concerning species identity and/or phenotypic qualities of the signaller, and females use these cues in long-range mate discrimination (for examples, see Gerhardt 1982; McGregor & Krebs 1982; Butlin *et al.* 1985; Ryan 1985; Ritchie *et al.* 1995).

Recent studies of sexually selected traits suggest that size and symmetry may convey reliable information of male quality (Møller & Hoglund 1991; Møller 1992*b*; Møller 1993*c*; Møller & Pomiankowski 1993). Fluctuating asymmetries, random deviations from perfect bilateral symmetry (Palmer & Strobeck 1986), are more likely to occur in individuals that are unable to withstand genetic and/or environmental stress. High degrees of symmetry are associated with high overall fitness (Mitton & Grant 1984; Harvey & Walsh 1993; Møller 1993*a*; Naugler & Leech 1994; Ueno 1994). Because secondary sexual traits are subject to strong directional selection, they tend to exhibit higher levels of fluctuating asymmetry than other morphological traits (Møller & Hoglund 1991; Møller 1992*b*; Tomkins & Simmons 1995) and females appear to use this information when discriminating amongst males (for examples, see Møller 1992*a*; Møller 1993*b*; Swaddle & Cuthill 1994).

Male field crickets (Orthoptera: Gryllidae) produce an acoustic signal that serves to attract females and repel rival males (Zuk 1987; Simmons 1988). The sound producing structures are found on the modified forewings, or tegmina, of the male and represent a secondary sexual character. Within each tegmen is a triangular area known as the harp (Ragge 1955; Bennet-Clark 1989). The harps act as mechanical

resonators that are excited when the plectrum of the left tegmen impacts against the file of the right tegmen. The system appears analogous to the workings of a clock (Elliott & Koch 1985; Koch *et al.* 1988); the harp acts as a pendulum and the file and plectrum as an escapement mechanism. The resonant frequency of the harp determines the tooth impact rate which is coincident with the carrier frequency of the song. The carrier frequency is said to be an almost pure tone of constant frequency (Pierce 1948; Koch *et al.* 1988).

Studies of natural populations of field crickets have demonstrated non-random pairing with respect to a variety of putative fitness traits in males; paired males are frequently larger, older, have lighter gut parasite loads, and lower degrees of fluctuating asymmetry than their calling neighbours (Zuk 1987; Zuk 1988; Simmons & Zuk 1992; Simmons 1995; Zuk & Simmons 1996). Yet it has proved extremely difficult to identify parameters in male songs that convey information concerning these traits. Most studies have focused on the temporal properties of male songs which often convey critical information concerning species identity (Shuvalov & Popov 1973; Pollack & Hoy 1981; Stout *et al.* 1983; Huber *et al.* 1989), but little within species variation that can be attributed to phenotypic variation among males (Simmons & Zuk 1992; Souroukis *et al.* 1992; Webb & Roff 1992; Ciceran *et al.* 1994; Zuk & Simmons 1996). In contrast, the spectral properties of cricket songs have rarely been studied. The resonant frequency of the harp is determined by its mass such that larger harps are predicted to generate lower frequency sound (Pierce 1948; Nocke 1971; Michelsen & Nocke 1974). Indeed, in at least two cricket species, call frequency is a reliable indicator of male size (Simmons & Zuk 1992; Simmons 1995). As both left and right harps are involved in generating sound (Michelsen & Nocke 1974) we might expect deviations from perfect bilateral

symmetry in the harps to affect the spectral properties of a male's song. Here we examine size and deviations from bilateral symmetry in the harps of male *Gryllus campestris* L. We determine the affect of harp morphology on the spectral properties of male songs and their consequences for female choice.

## 2. PATTERNS OF ASYMMETRY

### (a) Methods

Animals were collected from single cohorts of singing males located in uncut meadows in Loire, France (1993), Mount Subasio, Italy (1994), and Andechs, Germany (1994). We measured the area of the harps, a sexually selected trait, as well as the length of the hind tibia, a naturally selected trait. Pronotum width was taken as an independent measure of male size. All measurements were made using an eye-piece graticule in a binocular microscope and were repeated after an interval of one month. The harp is formed by a loop in vein Cu1 and vein Cu2 (the file) (Ragge 1955; Bennet-Clark 1989) and approximates a right angled triangle; its area was thus calculated as half the base times its height (Simmons 1995). Harp area was calculated as the mean of the left and right harps. Asymmetries were calculated as left minus right measures of harp area and hind tibia length.

### (b) Results

Repeatabilities of the signed values of harp and tibia asymmetry were significant; the variance between males was significantly greater than the variance between measures of the same male (harp asymmetry  $F_{(28,29)} = 2.76$ ,  $p = 0.004$ ; tibia asymmetry  $F_{(10,11)} = 9.20$ ,  $p < 0.001$ ). Both harp and tibia asymmetries were normally distributed (Filliben correlations: harp 0.991,  $p > 0.1$ ,  $n = 116$ ; tibia 0.978,  $p > 0.1$ ,  $n = 105$ ). The mean signed asymmetry in tibia length did not deviate from zero (mean  $\pm$  s.e.,  $-0.01 \pm 0.01$ ,  $t = 1.211$ , d.f. 104, NS) indicating that the tibia exhibited fluctuating asymmetry (Palmer & Strobeck 1986). However, the mean signed asymmetry of harps was negative ( $-0.11 \pm 0.04$ ,  $t = 3.050$ , d.f. 116,  $p = 0.003$ ) indicating that, on average, left harps tended to be smaller than right harps. Absolute values of asymmetry were used to test for interrelations between variables. There was significant variation between populations in both the size and asymmetry of the traits measured (see table 1). Correlations between trait size and asymmetry, thought to be indicative of honest signalling,

Table 2. Spearman rank correlations between size and asymmetry of morphological traits after controlling for population differences

(Sample sizes in parenthesis; all values remained significant at the table-wide level of 0.05 using the sequential Bonferroni method.)

	harp area	tibia asymmetry	harp asymmetry
pronotum width	0.748 <sup>c</sup> (116)	-0.240 <sup>b</sup> (105)	-0.118 (116)
harp area	-	-0.169 (99)	-0.112 (116)
tibia asymmetry	-	-	0.264 <sup>b</sup> (99)

<sup>a</sup>  $p < 0.05$ .

<sup>b</sup>  $p < 0.01$ .

<sup>c</sup>  $p < 0.001$ .

can be confounded by between-population differences (Swaddle *et al.* 1994; Simmons *et al.* 1995). We therefore calculated standard scores, as the trait value minus the mean trait value for the population from which the datum was drawn, and used these to assess interrelations between morphological variables (see table 2). There was a positive relation between male size (pronotum width) and mean harp area and a negative relation between male size and the degree of fluctuating asymmetry in the hind tibia. Fluctuating asymmetry in hind tibia was positively correlated with the degree of directional asymmetry in the harps.

## 3. SPECTRAL PROPERTIES OF MALE SONG

### (a) Methods

Songs were recorded in the field, from the same populations that were sampled for morphometric analyses, using a Sony Professional Walkman and condenser microphone. The microphone was placed 5 cm from a male's burrow and recording started after the male had been singing continuously for a period of 2 min. A 1 min sample of the male's song was recorded. Songs were analysed using 'SoundEdit' software on an Apple Macintosh computer. Sampling rate was set at 11 kHz. The low frequencies of *Gryllus* song make this software satisfactory for frequency analysis and reproduction. The song consists of a series of chirps, each containing three to five pulses (see inset to figure 1*b*). One pulse is produced by a single closure of the tegmina (Kochet *et al.* 1988). The dominant frequency,

Table 1. Morphological characteristics of male *Gryllus campestris* from different populations

population	pronotum width/mm	mean harp area/mm <sup>2</sup>	harp asymmetry/mm <sup>2</sup>	hind tibia asymmetry/mm	<i>n</i>
France	7.86 $\pm$ 0.06	14.84 $\pm$ 0.19	0.313 $\pm$ 0.032	0.056 $\pm$ 0.009	60
Italy	7.72 $\pm$ 0.07	15.49 $\pm$ 0.18	0.288 $\pm$ 0.045	0.080 $\pm$ 0.012	39
Germany	7.15 $\pm$ 0.06	14.16 $\pm$ 0.34	0.357 $\pm$ 0.063	0.150 $\pm$ 0.031	26
$\chi^2$ H	35.93 <sup>b</sup>	12.44 <sup>b</sup>	1.38	9.05 <sup>a</sup>	

<sup>a</sup> Kruskal-Wallis ANOVA,  $p < 0.01$ .

<sup>b</sup> Kruskal-Wallis ANOVA,  $p < 0.001$ .

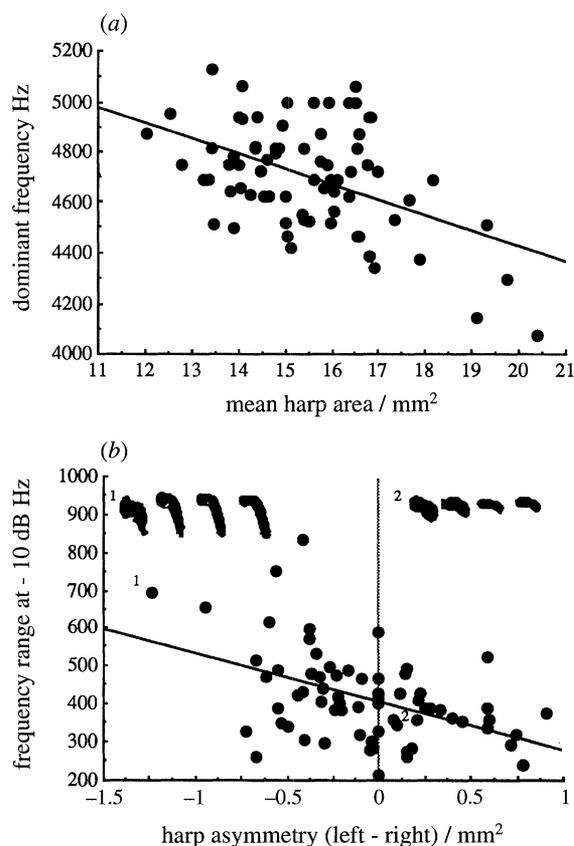


Figure 1. The relation between harp morphology and frequency characteristics of the songs of male *Gryllus campestris*. (a) Dominant frequency decreased with increasing mean harp area ( $F_{(1,71)} = 20.30$ ,  $r^2 = 0.22$ ,  $p < 0.001$ ; dominant frequency =  $-61.15$  harp area + 5651). (b) The degree of frequency modulation increased as the area of the right harp increased, relative to the area of the left harp ( $F_{(1,67)} = 17.52$ ,  $r^2 = 0.21$ ,  $p < 0.001$ ; frequency range =  $-127.89$  harp asymmetry + 407.12). Inset are sonograms (kHz by ms plots) of a single chirp of a male that had relatively asymmetrical harps and high frequency modulation (1) and of a male that had relatively symmetrical harps and low frequency modulation (2). The datum from each of these males is marked on the scatterplot.

defined as the frequency with maximum intensity, was determined from FFT spectrograms (frequency by dB plots) of five randomly chosen pulses from each male, and the frequency range measured at  $-10$  dB down from the dominant frequency.

#### (b) Results

The dominant frequency of male song was negatively related to mean harp area (figure 1a). However, sonograms of cricket songs clearly show that they exhibit frequency modulation to varying degrees (figure 1b). Within each pulse of sound there appeared to be an initial portion with a sustained frequency, followed by a period during which the frequency fell.

To examine the role of both left and right harps in song production, we recorded the songs of males before and after removing one of their harps (see figure 2). The male's songs were recorded in the laboratory using a Uher 4000 Report IC recorder and digitised into a PC using 'Signal' sound analysis software at 40 kHz.

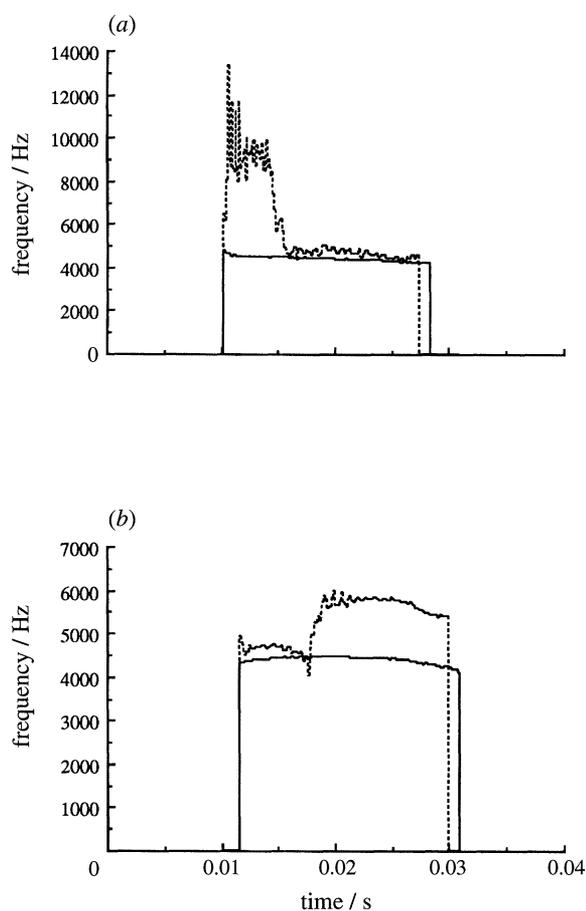


Figure 2. The change in frequency across a single pulse produced by a male before (solid line) and after (dashed line), (a) the left harp and (b) the right harp had been removed by amputating the tegmen distal to the file.

Frequencies were detected by instantaneous zero-crossing analysis. Removal of the left harp led to disruptions in the frequency content of the leading portion of the sound pulse (figure 2a) while removal of the right harp led to disruptions in the frequency of the later portion of the sound pulse (figure 2b). Thus, the relative importance of the two harps in generating sound changes over the course of a pulse; the dominant frequency of the song appeared to be influenced primarily by the initial sustained portion generated by the left harp, with the song decreasing in frequency when a larger right harp took over from the left. Indeed, the greater the difference in area between left and right harps, the greater the degree of frequency modulation observed (figure 1b). Further analysis of the data in figure 1b showed that frequency modulation resulted when the right harp area was greater than the left (negative harp asymmetries;  $F_{(1,35)} = 8.55$ ,  $p = 0.006$ ), but not when the left harp area was greater than the right (positive harp asymmetries;  $F_{(1,22)} = 0.95$ ,  $p = 0.34$ ).

## 4. FEMALE PREFERENCES

### (a) Methods

We produced synthetic songs that varied with respect to their frequency characteristics and used

these song models in simultaneous choice trials to examine female preferences. All song models were synthesised using 'Signal' at a digital to analogue rate of 40 kHz. A single pulse envelope was produced based on the typical shape seen in field recordings. Each chirp contained four pulses (the first at half amplitude). Pulses were repeated every 30 ms and chirps were repeated every 266 ms. These temporal parameters conformed to the observed species mean values. The chirp envelope was applied to pure tones of a specified frequency ranging from 4.25 kHz to 5.0 kHz. Song models thus simulated males that had symmetrical harps of differing sizes. This frequency range covers that seen in the songs of males recorded in the field. Frequency modulated song models were produced as above but the pulse used contained a pure tone for the first half of the pulse (initial frequency), then the frequency was dropped over the second half at a rate set to produce the desired level of frequency modulation. Frequency modulated song models had identical initial frequencies set at either 4.25 kHz or 5.0 kHz. Thus, the song models were representative of males that had identical sized left harps (body size) and increasing size of right harps (directional asymmetry). Using left harp area to control for male size is realistic, since both left and right harp areas are equally strongly related to pronotum width (left harp  $r = 0.669$ , d.f. 118,  $p < 0.001$ ; right harp  $r = 0.670$ , d.f. 114,  $p < 0.001$ ). Song models were recorded onto one track of a 1-min 'endless' TDK cassette tape at a set amplitude.

A Sony walkman was connected to each of the left and right channels of an amplifier and one song model broadcast from each walkman, via a high pass filter, through tweeter horns (Radio Shack 40-1228A) positioned at opposite ends of an arena. The arena measured 100 cm in length and 25 cm in width and was lined with fan-folded dark green garden netting for cover during phonotaxis. A small shelter was placed equidistant from the two speakers and covered with a glass beaker. Before testing the sound intensity of each song to be simultaneously broadcast was set at a mean intensity of 70 dB (72 dB peak) at the release point using a 'Realistic' sound level meter. This intensity is typical of normal song 50 cm from a males burrow. A female was placed under the glass beaker and left to settle; females invariably entered and remained within the shelter. After 2 min the beaker was removed and the broadcasts started. A positive response was recognized when the female left the shelter, moved the length of the arena and entered the speaker. Females that did not respond within 10 min of broadcast were removed and tested again the following day. If they failed to respond a second time they were not used in that particular trial. The songs broadcast from each speaker were switched between trials to control for possible end biases. All trials were run under ambient light conditions between 12h00 and 18h00, the peak activity period for phonotactic females (Rost & Honegger 1987). A total of 40 females were available for trials and each female was used only once per trial or song pair. The number of females that failed to respond in any one trial ranged from two to six. Females were collected as adults in May 1995 from

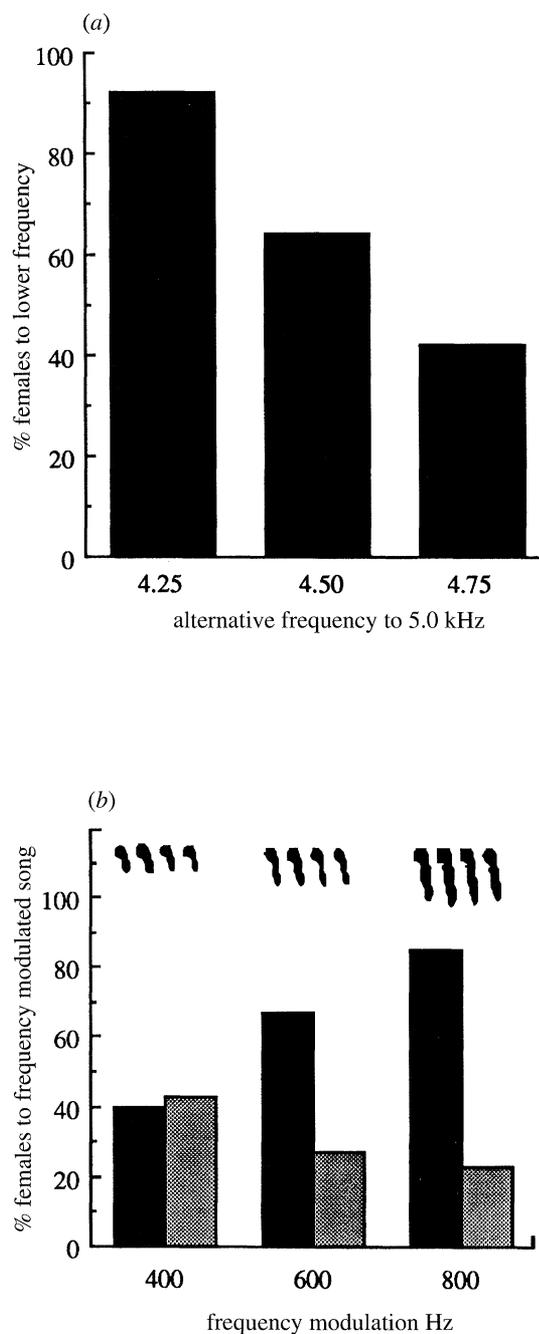


Figure 3. Phonotactic responses of female *Gryllus campestris* to simultaneously broadcast synthetic songs. (a) When offered songs of pure tone that decreased in frequency relative to a 5.0 kHz alternative. (b) When offered songs that had identical initial frequencies set at either 5.0 kHz (solid bars) or 4.25 kHz (shaded bars) but which increased in frequency modulation by 200 Hz steps relative to a pure tone alternative (sonograms of song models shown inset).

uncut meadows around the hamlet of Le Cauderc, in the Lot region of France.

#### (b) Results

When offered songs of pure tone, females oriented preferentially to songs of low frequency (figure 3a). A frequency of 5.0 kHz was tested against alternative models that decreased in frequency by 250 Hz steps. The data support a model of relative female choice, the

strength of female preference depending on the difference in dominant frequency between simultaneously broadcast songs (Forrest & Raspet 1994).

Female preferences based on the degree of frequency modulation were dependent on the initial frequency of the song models used (figure 3*b*). At high initial frequency, females showed a preference for frequency modulated song that increased with the degree of frequency modulation ( $\chi^2 = 6.029$ ,  $p < 0.05$ ,  $n = 40$ ) while at low initial frequency the degree of frequency modulation did not affect female phonotaxis ( $\chi^2 = 1.357$ , NS,  $n = 38$ ). Rather, females showed an absolute preference for pure frequency (26 of 38 females oriented to pure frequency songs, two-tailed binomial  $p = 0.034$ ). The change in female response to frequency modulation across the two trials was significant (McNamar's test,  $\chi^2 = 7.682$ ,  $p < 0.01$ ,  $n = 38$ ).

To examine further the interaction between initial frequency and frequency modulation we offered a choice between the two preferred song models, the 5.0 kHz song with 800 Hz frequency modulation and the pure tone at 4.25 kHz. Females preferred the low frequency song (24 of 35 females chose 4.25 kHz, two-tailed binomial  $p = 0.041$ ). However, when both 5.0 kHz and 4.25 kHz songs were frequency modulated by 800 Hz, females showed no preference for either song model (19 of 34 females chose the song of lower initial frequency, two-tailed binomial  $p = 0.608$ ).

## 5. DISCUSSION

The results of both our analyses and experimental manipulations strongly suggest that size and directional asymmetry of the sound resonators or harps influences the spectral properties of cricket song. Our results support the mechanism of sound production in crickets, proposed by Elliot & Koch (1985) and Koch *et al.* (1988); an increase in the mass of the harps is predicted to result in a decrease in resonant frequency and tooth impact rate so that the song generated has a lower frequency. Frequency modulation in cricket song has not previously been described although it is noticeable in other published sonograms (Leroy 1966; Simmons 1988). The relation between harp asymmetry and frequency modulation is also consistent with the notion that harp mass is an important determinate of song frequency. Nocke (1971) found asymmetries in the resonant frequency of left and right harps of the same order as our measures of harp area; left harps had a higher resonant frequency. Changes in resonant frequency during the course of the sound pulse would lead to frequency modulation. Stephens & Hartley (1995) have recently shown that *G. bimaeculatus* calling song has two frequency components, and relate one to the tooth impact rate and the other to the resonant frequency of the wing. They argue that the clockwork mechanism of Elliot & Koch (1985) and Koch *et al.* (1988) is without foundation, proposing a very different mechanism that involves the resonance of the subalar air space which both tunes and amplifies the cricket song (see also Morris & Mason 1994). The negative relation between male size and song frequency could arguably arise because of increased volume, and thus decreased

resonant frequency of, the subalar space in males with larger tegmen. Nevertheless, our observation of frequency modulation is inconsistent with Stephens & Hartley's (1995) model. As the tegmen close during the course of the sound pulse, the subalar space will reduce in size leading to an increase in its resonant frequency. This should result in an increase in song frequency across the sound pulse rather than the decrease in frequency that we demonstrate here. Nocke (1971) did not find the subalar volume to have any resonant properties. Stephens & Hartley (1995) argue that the singing animal can adjust the size of the subalar space to maximize its tuning properties. It seems likely that this will be matched to the resonant frequencies of the tegmenal structures, so that the two models of sound production may compliment rather than contradict each other.

Recent examinations of asymmetry in secondary sexual traits have suggested fluctuating asymmetry can reliably reflect individual quality (Møller & Høglund 1991; Møller 1992*b*; Møller & Pomiankowski 1993), and that females find both large and symmetrical males more attractive (Møller 1992*a*; Swaddle & Cuthill 1994). Traits that show signs of directional asymmetry are generally rejected as possible indicators of individual quality (Palmer & Strobeck 1986; Swaddle *et al.* 1994). However, theoretical simulations show that directional asymmetry, like fluctuating asymmetry, can arise because of stress if there is a bias towards one side of the body (Graham *et al.* 1993). The right-over-left method of stridulation predisposes crickets to directional asymmetry (Masaki *et al.* 1987). Decreased body size in crickets is an indicator of developmental stress (Simmons 1987) and was associated with increased levels of fluctuating asymmetry in a morphological trait, tibia length, both within and between populations. The positive correlation between fluctuating asymmetry and directional asymmetry found in this study is evidence that directional asymmetry can also reveal developmental stability.

Here, we have shown that small males produce high frequency songs that are less attractive to sexually receptive females. Nevertheless, small males have the potential to improve their attractiveness by developing asymmetrical harps. Among song models with a high initial frequency, those with greater frequency modulation were more attractive to females. This in part may result from the observed preference for low frequency song. Increasing the degree of frequency modulation, by increasing the size of the right harp would have the effect of adding some low frequency elements to the song so that the mean frequency across the pulse was reduced. Among large males however, females showed an absolute preference for the pure tone characteristic of symmetrical harps. The observation that the preference for low frequency song was lost when songs were frequency modulated, despite the fact that the mean frequency across the sound pulse would have been reduced by increasing frequency modulation, suggests that female preference for low frequency is not open ended. Neurophysiological studies provide a proximate explanation for the

observed female preferences. On average, the female's ear is tuned to a carrier frequency around 4 kHz (Nocke 1972), thus the preference for lower frequency calls in our phonotaxis trials. At low frequencies, frequency modulation would have the effect of moving a male's song away from the female's optimal response frequency making the song less attractive. At high frequencies, frequency modulation would have the effect of moving a male's song closer to the female's optimal response frequency making the song more attractive.

Increased costs of asymmetry for males that develop large harps may maintain honesty in the signalling system of *G. campestris*; only males capable of developing large harps while maintaining symmetry will benefit from the increased attractiveness of low frequency songs. Size dependent costs and benefits of directional asymmetry such as those reported here are expected to generate a negative relation between trait asymmetry and size (Møller & Høglund 1991; Møller 1992*b*; Evans *et al.* 1994). Although the relation between mean harp area and harp asymmetry was negative it was not significant.

The results of our laboratory experiments account for the observation in the field, that male *G. campestris* who are successful in attracting females are larger and more symmetrical than their unsuccessful neighbours (Simmons 1995). Patterns of directional asymmetry in sexually selected traits may thus prove equally revealing of individual quality as those of fluctuating asymmetry (Møller 1994), although clearly the patterns observed must be interpreted within a framework of the functional significance of asymmetry.

We thank Dale Roberts, Win Bailey, and Innes Cuthill for their comments which greatly improved the manuscript. L.W.S. is supported by an ARC Senior Research Fellowship and M.G.R. by NERC Fellowship GT5/92/TLS/16.

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Received 14 May 1996; accepted 18 June 1996