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Variability in call structure and pairing success of male field crickets, *Gryllus bimaculatus*: the effects of age, size and parasite load

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Abstract. The effects of male body size, age and gregarine parasite load on the structure of calls and success at attracting mates were investigated in a natural population of the field cricket, *Gryllus bimaculatus*. The syllable rate within chirps was negatively related to male size, and the duration of syllables was positively related to size. Older males had more variable syllable rates within their chirps. Size did not influence pairing success. However, paired males were significantly older than solitary calling males. Parasitic infection influenced the pairing success of young males but not old males. These data are discussed in the context of direct and indirect selection for female mating preferences.

For many species, pair formation and mating involve a complex sequence of display and discrimination by members of each sex. While it is generally accepted that exaggerated mating displays are the product of sexual selection, their evolutionary origin remains unclear (Darwin 1871; Kirkpatrick & Ryan 1991; Maynard Smith 1991). Preferences may arise directly, through resource benefits obtained by the female and/or pleiotropic effects of preference genes (Kirkpatrick & Ryan 1991), or indirectly through increased offspring fitness (Zahavi 1975, 1977; Andersson 1986; Møller 1991).

The orthopteroid insects are well known for their acoustic displays (see Gwynne & Morris 1983 and references therein). Males produce calls that act as signals for mate attraction and the repulsion of rivals (Boake 1983; Simmons 1988a). Male field crickets call from aggregations to which females orient for mating (Cade 1981; Simmons 1988a). Such aggregations of calling males have been compared with 'lek' type mating systems where females come to choose between potential mates (Alexander 1975). However, few studies have addressed within-species variability in call structure and its possible significance for sexual selection and the evolution of mating preferences. We looked at variability in male calling song and its attractiveness to females in a wild population of the field cricket, *Gryllus bimaculatus*.

Female *G. bimaculatus* are known to exercise post-copulatory mate choice. After mating, males enter a period of post-copulatory guarding and will remate with the female once a new spermatophore has been generated (Loher & Rence 1978; Simmons 1990). The time a female spends with the male determines the frequency of matings, the amount of sperm received and ultimately the male's paternity expectation (Simmons 1986, 1987a, 1991). Females gain indirect benefits through mate choice by increasing the fitness of their offspring (Simmons 1987b). Thus, mate choice is an important component of the mating system of this species. It is not clear, however, whether females discriminate between males on the basis of their acoustic displays, prior to pair formation.

In a previous study male size was shown to be positively related to call intensity and syllable repetition rate (Simmons 1988a). Female *G. bimaculatus* are sensitive to variation in syllable rate (Doherty 1985; Schildberger 1985), preferring calls with higher syllable rates within the natural range for the species (Shuvalov & Popov 1973; Simmons 1988a). Whether large males attract more mates in natural populations is unknown.

Female *G. veletis* and *G. pennsylvanicus* preferentially oriented to older males within experimental populations, although the characteristics of the call that signal male age are unknown (Zuk 1987a). In natural populations, female *G. veletis* and *G. pennsylvanicus* were found to be paired with older males that also harboured significantly fewer

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gregarines, a protozoan gut parasite (Zuk 1988). Unlike male age, experimental manipulations failed to show a differential attractiveness related to parasite load (Zuk 1987a).

One of us (Zuk 1988) has argued that female choice for parasite-free males is most probably post-copulatory (as for *G. bimaculatus*, Simmons 1986), with females leaving parasitized males in search of other mating partners. Laboratory experiments with *G. bimaculatus* support this hypothesis. Uninfected males are more likely to remain in contact with the female during post-copulatory guarding (Simmons 1990). Female choice based on parasite load could provide indirect benefits to offspring if resistance to infection were heritable, because parasitic infection reduces development speed, longevity and the rate of spermatophore production in males (Zuk 1987b, c). The significance of gregarines for sexual selection in field crickets represents one of the few intraspecific tests of the controversial Hamilton & Zuk (1982) hypothesis (for a recent review see Møller 1990).

Here we estimate the degree of variation in body size, age and levels of gregarine infections within a natural population of *G. bimaculatus*. We determine the amount of information contained within the male's acoustic display that is related to these characteristics, and determine the relative importance of each in generating variability in male pairing success in the field.

METHODS

This study was conducted during late August and early September 1990 at the Doñana Biological Station, Southwestern Spain. Crickets were found in a narrow strip of meadow between the dried marshlands of the Guadalquivir river and the higher areas of Mediterranean shrubland to the west. This area remains moist during summer owing to the relatively higher water table (Rogers & Myers 1980). Meadows were dominated by tussocks of thrift, *Armeria alliacea*, in which males sheltered while calling to attract sexually receptive females.

Recording and Collection of Animals

We sampled males between 2230 and 0300 hours over 10 nights (*G. bimaculatus* are sexually active from dusk till dawn, Simmons 1988a). Each male was first located by ear and the microphone of a tape recorder was then positioned 0·25 m from its shelter. Once the male had resumed continuous calling for 2 min, a 1–2-min sample of the male's call was recorded. The ambient temperature was taken during the recording of each male's call. After the recording was made, the male was captured by teasing apart the tussock in which it was sheltering. Tussocks were checked thoroughly for any females that may have been attracted. During the recording of a number of males, females were captured as they approached the subject. We also searched tussocks from which courtship song was emanating and captured males and their partners. Throughout each night's sampling, the ground was scanned for crickets moving across the meadows. These individuals were also collected. All animals were taken to the laboratory and frozen.

Determination of Parasite Load

During the morning following collection, the animals were thawed and dissected under a microscope (30 × magnification) to determine gregarine parasite load. Gregarines (Sporozoa: Gregarinida) are gut parasites which develop from spores ingested by the host. Immature trophozoites can be found attached to the epithelial wall of the gastric caeca, while mature trophozoites and reproductive cysts can be found along the length of the mid- and hindguts (see Smyth 1976 for details of life cycle). The gut from each individual was removed and slit longitudinally to liberate its contents. Parasite load was estimated on a ranked scale of 1–4: (1) uninfected: no cysts or trophozoites present; (2) light: 1–10 cysts and/or trophozoites; (3) moderate: 11–30 cysts and/or trophozoites; (4) heavy: >30 cysts and/or trophozoites with the gut occluded by parasites. Prior to dissection, pronotum width was measured to 0·01 mm using vernier callipers.

Determination of Age

Age since adult moult was determined for males and females using the technique of Neville (1963). Cross sections of the hind tibia from each individual were viewed under phase contrast microscopy and the number of chitin rings counted; chitin rings form in response to daily exposure to light (see Zuk 1987d for detailed methodology and a demonstration of the technique's accuracy in determining age in gryllids).

Analysis of Calling Song

Temporal characteristics of calls were analysed by playing them through a Kay DSP digitizing

Sona-Graph (model 5500). Calling song consists of a series of repeated chirps composed of between three and five rapidly produced syllables. Characteristics of the call were measured as in Simmons (1988a). For each recording, two continuous sequences of 10 chirps were analysed. The duration of each chirp and the interval between chirps were measured from the screen tracing. Chirp rate was obtained by dividing the number of chirps by the total duration of the call sequence. The number of syllables within each chirp was also noted. The duration of 10 randomly selected syllables and the interval between 10 syllables were measured and the syllable rate for each chirp calculated as the number of syllables within the chirp divided by its duration. Thus, for each male we had 20 measures of chirp duration, inter-chirp interval, syllable duration, inter-syllable interval, and syllable rate within chirps. A mean value was calculated together with a coefficient of variation for use in analysis. The average of the two measures of chirp rate was taken as the estimate for analysis (for more details of the structure of calls see Simmons 1988a; Bennet-Clark 1989).

The fundamental frequency of each call was found from real time frequency analysis, by playing the recordings via a high pass filter into a Tektronics spectrum analyser (no. 5L4N). Measurements were made of log spectrum with its centre at 5 kHz and a band width of 200 Hz per division. The peak frequency was read directly from the screen while an estimate of its sharpness (Q) was calculated as the ratio of the peak frequency to the width of the frequency spectrum at −3 dB (Bennet-Clark 1989).

We used partial regression analysis to separate the effects of male age, size, parasite load and temperature on song characteristics and their variabilities. Partial correlation coefficients were first examined to determine which variables had a significant association with the call parameter in question. These variables were then entered into a multiple regression model.

RESULTS

Variation in Size, Age and Parasite Load

There was no sexual dimorphism in body size within the population sampled. However, calling males were significantly older than acoustically orienting females (Table I). These results might be expected, because males develop faster than females (Simmons 1987c).

Table I. Sexual dimorphism ($\bar{X}\pm$SE) in the size and age of sexually active *G. bimaculatus* in the field

	Pronotum width (mm)	Age (days)
Males (97)	7·35±0·07	12·6±0·4*
Females (39)	7·49±0·09	10·8±0·5

*$t=3{\cdot}258$, $P=0{\cdot}003$.

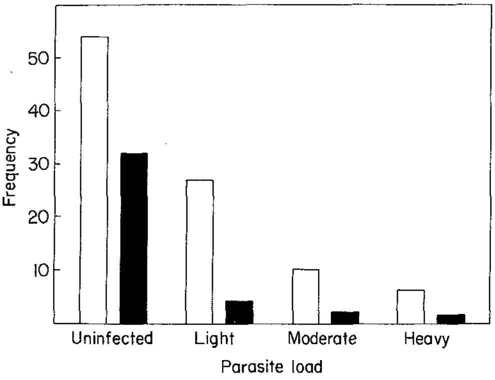

Figure 1. The distribution of gregarine infections in male (☐) and female, (■) *G. bimaculatus.*

There was a significant sexual difference in the prevalence (proportion of individuals infected) of gregarine infection; males were more likely to be infected than were females (44·3% versus 17·9%, $\chi^2=7{\cdot}23$, $P<0{\cdot}01$; see Fig. 1). Amongst infected individuals, the intensity of infection did not differ between the sexes ($\chi^2=0{\cdot}102$, NS). Typical of parasitic infections, gregarine parasite loads were positively skewed, as found in laboratory populations of this species (Simmons 1990), and natural populations of other species of field cricket (Zuk 1987e). There was no significant correlation, for either sex, between parasite load and pronotum width (males: $r_S=-0{\cdot}074$, $N=97$, NS; females $r_S=0{\cdot}210$, $N=39$, NS) or parasite load and age (males: $r_S=0{\cdot}014$, $N=97$, NS; females: $r_S=-0{\cdot}049$, $N=39$, NS).

Variation in Male Calls

Of the 15 call characteristics that we measured, only syllable rate and syllable duration showed any variation that could be explained by characteristics

Table II. The effects of temperature, body size, age and parasite load on call structure

	Independent variable				
	Temperature	Pronotum width	Age	Parasite load	*P*
FRQ	0·150	−0·293*	0·024	−0·095	0·037
Q_3	−0·153	0·151	0·128	−0·240	—
CHDUR	−0·262	0·228	0·004	0·074	—
CV	0·088	0·299*	0·085	−0·125	0·033
CHINT	−0·143	0·133	0·004	0·084	—
CV	0·197	0·218	0·075	−0·110	—
CHRATE	−0·017	−0·212	0·043	−0·087	—
SYLCH	−0·084	0·003	−0·089	0·017	—
CV	−0·029	0·283*	0·119	−0·028	0·044
SYLDUR	−0·421**	0·363**	0·156	0·137	0·001
CV	0·347**	−0·218	−0·070	0·107	0·013
SYLINT	0·067	0·125	0·169	−0·102	—
CV	0·267	0·027	−0·047	−0·206	—
SYLRATE	0·492***	−0·512***	−0·206	−0·150	0·000
CV	0·056	0·125	0·364**	−0·124	0·009

The significance of the regression models is shown where independent variables showing an association with call parameters were used in the analysis. The calls of 51 males were analysed. FRQ: fundamental frequency; Q3: tuning at −3dB (see Methods); CHDUR: chirp duration; CHINT: chirp interval; CHRATE: chirp rate; SYLCH: syllables per chirp; SYLDUR: syllable duration; SYLINT: syllable interval; SYLRATE: syllable rate; CV: coefficient of variation in associated variable.

**P*<0·05; ***P*<0·01; ****P*<0·001; significance of individual partial correlation coefficients. Note that with the number of partial regression analyses contained within this table a high level of type I errors is expected, see text.

of the male (Table II). Male size was positively related to syllable duration and negatively related to syllable rate. The only aspect of the call influenced by male age was the variability in syllable rate; older males had higher coefficients of variation. Syllable rate, syllable duration and the variability in syllable duration were also influenced by temperature (Table II). Parasitic infection did not influence call structure.

There are a number of relationships in Table II significant at the 0·05 level. However, given that we performed 15 simultaneous partial regression analyses we expect to obtain some significant results by chance alone. Adopting the sequential Bonferroni test (Rice 1989) for the 15 separate partial regression analyses leaves only the syllable duration and syllable rate regressions significant at a table-wide significance level of 0·05.

Variability in Pairing Success

We compared the characteristics of males that had been successful in attracting a female with those that were not (i.e. solitary calling males versus non-calling paired males). There was no significant heterogeneity in the representation of infected and uninfected males within the calling male and paired male samples; parasite prevalence did not influence pairing success (χ^2=0·496, NS; see Table III). Neither was there an influence of the intensity of infection on pairing success of infected males (mean rank intensity ± SE for paired males was 2·58 ± 0·14 versus 2·30 ± 0·15 for calling males, U=189·5, NS). The ages of paired and calling males differed significantly although this difference appeared to be dependent on infection status; infected paired males were significantly older than infected calling males (Table III). There was no significant correlation between male and female age within pairs (r=0·230, df=23, NS).

To investigate the apparent interaction between infection and age in male pairing success, we divided males into either 'old' (equal to or older than the mean male age of 12 days, see Table I) or 'young' (younger than the mean) groupings and

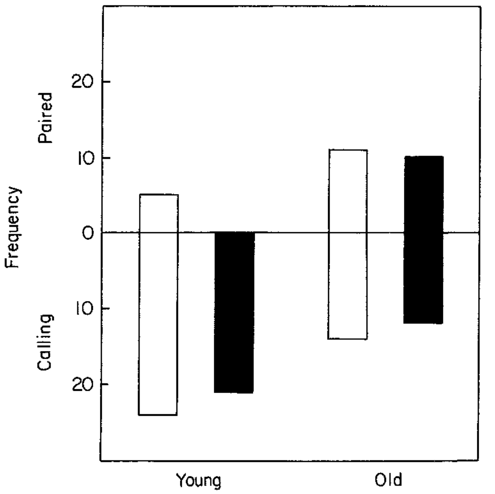

Figure 2. The frequencies of infected (■) and uninfected males (□) that were successful in attracting females relative to age (see text for statistics).

looked at the probability of being paired using a log-likelihood ratio test (Zar 1984). There was a significant interaction at the infection category × age class × paired status level (G=4·91, df=1, P=0·027; Fig. 2). Simple effects testing revealed the source of interaction. While, overall, young males were less likely to be paired than old males (10% versus 44·7%, G=15·64, df=1, P<0·001), amongst young males the probability of being paired was dependent on infection status; young infected males were never found paired while 10% of uninfected young males had mates (G=5·85, df=1, P=0·016; see Fig. 2). There was no influence of infection on pairing probability for old males (G=0·10, df=1, NS). Finally, irrespective of infection status, there was no significant difference in size between paired and calling males (Table III).

Table III. Characteristics ($\bar{X}$ ± SE) of males successful in attracting females (paired) and those found calling

	Calling	Paired
Uninfected		
Frequency	38	16
Pronotum width (mm)	7·29 ± 0·11	7·58 ± 0·15
Age (days)	12·2 ± 0·6	13·3 ± 0·7
Infected		
Frequency	33	10
Pronotum width (mm)	7·31 ± 0·12	7·36 ± 0·18
Age (days)	12·1 ± 0·7	15·1 ± 0·7*

*Mann–Whitney U, P=0·01.

DISCUSSION

The strongest relationship to emerge from these data is that between male pairing success and age. This relationship was previously shown in two other species of field cricket, *G. pennsylvanicus* and *G. veletis* (Zuk 1988). There are at least two possible explanations for our results. First, females may orientate preferentially to older males using cues present in the call. Alternatively, females may exercise post-copulatory choice by leaving young males in search of additional mates (Simmons 1986, 1990, 1991).

Either or both of the above hypotheses could account for the fact that males found paired were significantly older than calling males in this and Zuk's (1988) study. Under experimental conditions (Zuk 1987a), more females fell into pitfall traps over which old calling males had been suspended, supporting the former hypothesis for the apparent old male advantage. However, no characteristic in the call was found that females could use to discriminate between potential males. Cade & Wyatt (1984) found no effect of male age on the duration of nightly calling activity for laboratory reared *G. veletis* or *G. pennsylvanicus*. Our data suggest that, for *G. bimaculatus*, there may be variation in the finer structure of male calls that conveys information related to age. For *G. bimaculatus*, the variability in syllable rate within chirps increased with male age. While on a table-wide basis this relationship was short of significance, it was individually significant at less than the 1% level. Given that this was the only parameter of the call related to male age and that age and success at attracting mates are highly correlated, we believe that it is a genuine relationship and not one generated by chance alone. Why syllable rate should be influenced by male age is not clear to us. It may be the consequence of increasing muscle fatigue in old males or perhaps some physical wearing of the sound-producing apparatus that corrupts sensory feedback (Elliot & Koch 1983 detail the mechanics of stable stridulation). Stiedl et al. (1991) have recently shown an effect of male age on stridulatory file wear in the tettigoniid, *Ephippiger ephippiger*, that reduces the number of impulses per syllable in the call.

Interestingly, female *E. ephippiger* prefer the calls of younger males.

The apparent preference for older males is paradoxical since, for *G. bimaculatus*, the rate of spermatophore production and fertility per mating decrease with male age (Simmons 1988b). However, if females obtained indirect benefits by mating with older males, these could outweigh the apparent costs; selection could then still favour females that discriminated on the basis of male age. A variety of benefits related to selection by females on the basis of age have been proposed. These include the proven ability to survive (Trivers 1972; Halliday 1978) or the possession of fewer deleterious mutations (Manning 1985).

Alternatively, the apparent preference for older males need not be adaptive at all but may be the consequence of physiological constraints of the female's nervous system. West-Eberhard (1983, 1984) suggested that habituation to continued or repeated stimuli (of which the calls of some cricket species are a classic example, Elliott & Koch 1985) may favour signals that alternate, such that novelty becomes an advantage. The increased variability in syllable rate with male age may simply be a geriatric effect in males to which the female's nervous system is prone to respond. However, given that there may be a selective disadvantage to mating with older males (Simmons 1988b) we would expect that females able to overcome such passive attraction (sensu Parker 1983) would be favoured by selection if there were no indirect benefits to the mating pattern.

A previous study (Zuk 1988) also showed that males with lower levels of gregarine infections are more likely to be paired. For *G. bimaculatus* an effect of gregarine infection was apparent only among young males and there was no relationship between infection and call characteristics. Another study (Simmons 1990) showed a relationship between gregarine parasite load and male post-copulatory mate guarding ability: the duration of guarding decreases with parasite load. Thus, on the assumption that females prefer older males as mates, the data obtained in the present study could be explained if females encountering young males attempt to leave during post-copulatory mating decisions and only uninfected males were able to prevent them from doing so. It has been shown elsewhere that female *G. bimaculatus* paired with their preferred mating partners do not attempt to leave (Simmons 1989) and therefore do not 'test' them in this manner. Clearly the complex relationship between various male characteristics and female mating decisions warrants further investigation.

Finally, the syllable rate within male calls was negatively related to male size. This is in direct contrast to a previous study (Simmons 1988a) which reported a positive relationship. In laboratory trials (Shuvalov & Popov 1973; Simmons 1988a), females prefer calls with faster syllable rates and we should therefore have expected smaller males to attract more mates in our field population. However, the present analysis also revealed a significant positive relationship between male size and syllable duration, not apparent in Simmons' (1988a) data. It may be that syllable rate and syllable duration are compensatory in their effects on net signal output such that pairing success would not be influenced by male size (see Doherty 1985). Certainly male size did not influence pairing success in the population studied here although laboratory studies suggest that it may be important in post-copulatory discrimination (Simmons 1986).

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