

The inheritance of female preference functions in a mate recognition system

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Mate recognition systems (MRSs) play a major role in sexual selection and speciation, yet few studies have analysed both male and female components in detail. Here, female preference functions have been characterized for the tettigoniid bushcricket *Ephippiger ephippiger*, and the inheritance of male song and female preference functions followed in crosses between subspecies. Songs are disproportionately determined by sex-linked genes. However, there is no evidence for a role of maternally derived sex-linked genes in female preference or of maternal effects. At the genetic level, there is a mismatch between peak preferences and male song, consistent with an evolutionary history of persistent directional preferences. Such a pattern of inheritance could contribute to the process of speciation via the evolution of new MRSs.

Keywords: behaviour; speciation; genetics; courtship song; female preference

1. INTRODUCTION

The mate recognition system (MRS) of a species comprises the signals and preferences involved in communication, stimulation and choice of sexual partners. Sexual selection arises due to non-random variation in the mating success of individuals, which often results from variation in the components of an MRS. The evolution of new MRSs can cause sexual isolation and, hence, speciation. There are several examples where organisms are apparently primarily isolated by sexual behaviours and comparative studies of male traits suggest this form of speciation may be particularly fast in some animal groups (Butlin & Ritchie 1994; Hollocher *et al.* 1997; Turner 1999). However, if female preference functions among species are similar, differences in male components may not represent isolation (Ryan & Rand 1995). For example, ‘open-ended’ preference functions favouring males with long tails may be common among species of birds and fish (Price 1998; Basolo 1999). The characterization and inheritance of MRSs is therefore important in understanding sexual selection and speciation, yet little empirical progress has been made, particularly in the combined analysis of both male and female components (Butlin 1993; Ryan & Rand 1993; Jennions & Petrie 1997; Wagner 1998).

A particularly interesting question concerns the inheritance of MRSs and the role of sex-linked genes. Ewing (1969) suggested that sex-linked genes may play a large role in MRS evolution as hemizygosity would allow fast evolution of male traits. General reviews (Charlesworth *et al.* 1987; Ritchie & Phillips 1998) have failed to find convincing evidence in support of this, but a recent quantitative analysis found evidence that traits subject to sexual selection were more prone to apparent sex-linkage effects than non-sexually selected traits. Reinhold (1998) quantified the extent to which traits differed between reciprocal F_1 hybrids between strains or species and found greater differences for traits considered likely to be under sexual selection than for control traits, though this analysis could not distinguish sex linkage from maternal

effects. As many sexually selected traits are likely to influence MRSs, this study suggests that the sex-linkage hypothesis is worthy of renewed attention (see also Hastings 1994; Sperling 1994; Davies *et al.* 1997; Noor 1997; Prowell 1998).

Phonotaxis experiments with acoustic insects allow detailed analysis of preference functions in MRSs (Wagner *et al.* 1995; Ritchie 1996). For example, *Teleogryllus* species show large differences in the structure of the male song between reciprocal hybrids and, curiously, reciprocal female hybrids prefer the song of the appropriate hybrid genotype (Hoy *et al.* 1977). This result was interpreted as evidence of the sex linkage of preference genes with preferential inactivation of the paternally derived sex chromosome for dosage compensation, therefore providing an example where both components of the MRS are largely influenced by sex-linked genes.

The tettigoniid bushcricket (katydid) *Ephippiger ephippiger* has different ‘song races’ which vary in the syllable number of the calling song (Busnel 1963; Duijm 1990). Previous studies involving phonotaxis experiments have shown that differences in female preference match this song variation, with females having strong preferences for a song typical of their own song race (Ritchie 1991, 1992a). Furthermore, these differences in song and preference have a genetic basis, because F_1 hybrids are intermediate (Ritchie 1992b, 1996). Here, I examine the distribution of song and preference functions in a full set of crosses between the song races, quantify the relative effect of sex-linked genes and examine the correlation between female preferences and the male trait in these crosses.

2. METHODS

(a) General methods

The animals used were derived from collections of *E. ephippiger* made in southern France. Currently, *E. ephippiger* is recognized as a variable ‘superspecies’ *Ephippiger ephippiger diurnus* Kruseman (Hartley & Warne 1984; Oudman *et al.* 1990). Poly-syllabic individuals from the eastern Pyrenees were of the ‘cunii’

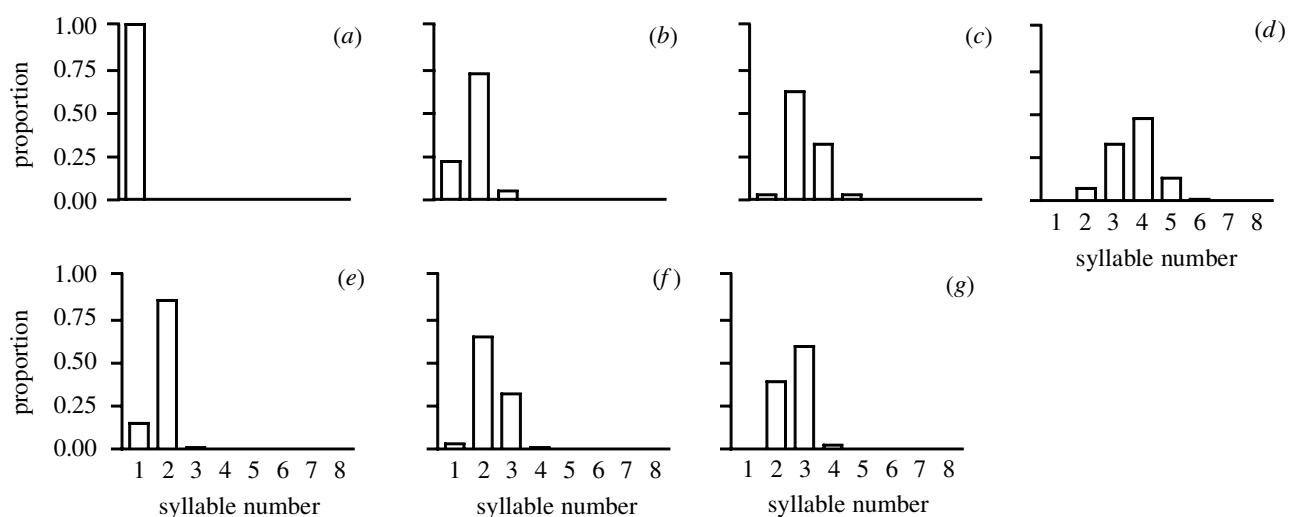


Figure 1. The distribution of male syllable number in crosses between the song races of *E. ephippiger*. The histograms show the overall distribution for each genotype (sample sizes per male vary, but this is allowed for in statistical analyses). (a) Monosyllabic, (b) monosyllabic \times polysyllabic, (c) polysyllabic \times monosyllabic, (d) polysyllabic, (e) BX (monosyllabic), (f) F₂ and (g) BX (polysyllabic). (Maternal genotypes are indicated first for the F₁ hybrids.)

form and monosyllabic individuals from the Mediterranean coast were intermediate between the ‘cruciger’ and ‘vitium’ forms (Kidd & Ritchie 2000). There was no obvious reduction in the viability of hybrid offspring, but the animal is not easy to rear in the laboratory.

(b) Male song

The mean syllable number of males is independent of temperature (over the range used in the laboratory) and age and is highly repeatable (Ritchie 1992a, 1996). Where the same populations have been studied in both the laboratory and field, males sing similarly (M. G. Ritchie, personal observation). The syllable numbers of parental polysyllabic and hybrid males were recorded once each. The monosyllabic stock is strictly monomorphic.

(c) Female preference functions

Female preference functions are characterized by mapping the frequency with which females choose native song made to vary in syllable number over non-native song (Ritchie 1996). Virgins were given a choice between synthetic songs replayed through two loudspeakers. The songs were synthesized using the SIGNAL software system at a D/A rate of 250 kHz replayed via a two-track TEAC reel-to-reel tape recorder (X-2000M, 38 cm⁻¹) and Ultrasound Advice amplifiers (S55) and speakers (S56) and monitored using a Brüel and Kjær (2231M) sound-level meter with a 0.25 in (1 in = 0.0254 m) microphone (4135). Subtle details of the song models are faithfully reproduced with this equipment (Ritchie *et al.* 1995). The sound pressure level was equalized at the release point of a T-junction which females walk along to approach the speakers.

Each trial consisted of playing a pair of songs to a female four times and switching songs between speakers for consecutive presentations. Four choices of one song requires three consecutive changes of direction, so strong preferences are unambiguous (no preference results in a score of 0.5). Between trials, the native song was changed in syllable number. Song of the other song race was used for the non-native song for parental females. Monosyllabic song was used for F₁ hybrids and the opposite of the parental genotype used in the cross was used for back-cross

females. For F₂ females, I used mono- or polysyllabic song to alternate females and combined the results (there were no obvious differences). Traits other than syllable number also influence preference so females can choose between, for example, one syllable of polysyllabic versus monosyllabic song. A complete set of trials was given in random sequence, then another set completed with a different sequence of syllable number (this does not provide sufficient replication within females to allow calculation of the repeatability of female preferences). Random sequence presentation controlled for sequence effects and swapping songs between speakers between each choice controlled for side biases. Any female who failed to complete all trials readily was omitted from the final data set.

A curve was fitted to the distribution of choices using cubic splines, smoothed using penalized maximum likelihood. This analysis is particularly appropriate when the shape of the function is the feature under study, as it involves no *a priori* assumptions concerning shape (Schluter 1988; Ritchie 1996). Potentially, any shape up to straight lines between consecutive points can be fitted, with the best smoothing parameter found by iteration (I used -7.4, the average of that found for nonlinear functions). The syllable number reflects an underlying continuous trait and female preferences are likely to be continuous (Ritchie 1992a).

(d) Model fitting

Restricted maximum likelihood (REML) was used for both song and preferences to estimate the effect of the different components of the genetic models using the REML function of Genstat 5 (Genstat 5 Committee 1993). The significance of the terms was assessed with Wald tests, distributed as χ^2 with one degree of freedom (see Hastings & Veerkamp (1993) and Ritchie & Kyriacou (1996) for examples of such analyses). Fixed terms represented the effects of autosomes, the X chromosome and cytoplasm (representing maternal effects; recombinant X chromosomes were entered as 0.5, allowing cytoplasmic and X effects to be distinguished). For females it is not possible to fit separate terms for autosomes and sex chromosomes. However, a term was entered representing the

Table 1. Basic statistics for each cross

(The means reported are pooled estimates derived from one data point (the mean) per male. The standard deviations (s.d.) are also pooled estimates from one-way ANOVA across males.)

	mono-syllabic	polysyllabic	monosyllabic × polysyllabic	polysyllabic × monosyllabic	F ₂	back-cross (BX) to monosyllabic	back-cross (BX) to polysyllabic	total
number of males	—	25	9	18	12	4	6	74
number of chirps	—	1832	691	1614	1133	308	651	6225
mean syllable number	1	3.57	1.85	2.31	2.33	1.85	2.76	—
s.e.	—	0.56	0.34	0.34	0.40	0.35	0.41	—
number of females	10	7	10	10	7	7	10	61
number of choices	480	448	480	480	444	336	560	3228
peak of preference	1.40	4.59	2.60	3.15	4.11	2.42	3.62	—
s.d.	0.97	0.75	0.87	0.51	2.27	0.66	1.48	—

maternal sex chromosome, following the suggestion of paternal sex-chromosome inactivation in *Teleogryllus* (Hoy *et al.* 1977). Thus, for females, the model contained fixed terms for autosomes, maternal X chromosomes and cytoplasm (representing maternal effects). For both analyses, individuals were included as a random term.

3. RESULTS

(a) Male song

The inheritance of syllable number generally followed that expected for an additive quantitative character (figure 1 and table 1). However, reciprocal F₁ hybrids differed and were more like their maternal genotype, consistent with sex linkage or maternal effects. Balanced nested ANOVA of 18 hybrid males showed that these differences are significant ($F_{1,16}=11.45$ and $p=0.004$; denominator mean square = males within genotypes). From these data, Reinhold's (1998) Ix (the proportion of the parental difference attributable to sex-linked genes or maternal effects) was 0.26.

A reduced data set containing 2237 chirps from 50 males (including values representing 50 chirps each from five monosyllabic males) was analysed using REML with the genetic model. This showed that the difference between reciprocal hybrids clearly represents sex-linked genes rather than maternal effects (table 2). Once again, the X chromosome was responsible for *ca.* 25% of the difference between parental genotypes, with the remainder corresponding to simple additive autosomal effects. *Ephippiger* has 15 chromosome pairs of approximately equal size, so this is a very disproportionate effect.

(b) Female preference functions

The parental strains clearly differed substantially in the shape of their preference functions (figure 2), with their preferences broadly matching the male song type. F₁ hybrids showed intermediate preferences. Those with polysyllabic mothers showed a clearly defined peak at three syllables per chirp, whereas those with monosyllabic mothers showed a broader preference from two to four syllables per chirp, so there was not a large difference in the peak preferences between reciprocal hybrids. F₂ females showed intermediate and rather weak preferences. As expected for an additive quantitative trait,

back-cross females' preferences were displaced towards the parental type used, but the parental preferences were not fully recovered. Back-crosses to monosyllabic individuals were sharply peaked, but around song containing two syllables per chirp and back-crosses in the other direction showed a strong preference for polysyllabic song (though peaked around three or four syllables, compared with a peak for five syllables in the parental strain).

In order to fit an REML model to the preferences, the peak of the preference function of each individual female was entered into a data set (for two females, the mean of two equal peaks was used). Neither the maternal X or cytoplasmic effects explained a significant proportion of the data and the autosomal additive term had a fitted effect representing some 75% of the difference between parental strains (table 2).

4. DISCUSSION

This study allowed analysis of both of the major components (male song and female preferences) of the MRS of *Ephippiger*. In general, the preference functions broadly matched the distribution of the male trait. However, closer examination revealed a mismatch between the two behaviours. Consider the preference function of the females from the polysyllabic population. The peak preference was at five syllables per chirp, which is rare in the population (figures 1 and 2). Thus, the preference function would have the net effect of exerting directional selection on the males (though it is not an 'open-ended' preference). Net directional preferences are also seen at the genetic level in each of the crosses. The mean peak preference of females from each cross was higher than the mean syllable number of males from the same cross (table 1 and figure 3) and this effect was more pronounced for more polysyllabic genotypes. The most likely explanation for this is that female preferences have persistently favoured longer chirps, with stronger preferences among polysyllabic females, perhaps associated with greater variance in the male trait (Gerhardt 1991).

Persistent directional preferences might be favoured if longer chirps are more easily localized, although directional preferences would also be favoured if male chirp length was correlated with male quality (Welch *et al.*

Table 2. Fitted effects and their standard errors (s.e.) for genetic terms in REML models

term	autosomes	X/maternal X	cytoplasm
males			
effect (s.e.)	1.812 (0.259)	0.632 (0.251)	0.090 (0.197)
Wald test	194.000*	14.300*	0.200
females			
effect (s.e.)	2.351 (0.752)	0.915 (0.680)	-0.128 (0.605)
Wald test	34.600*	2.800	0.000

* $p < 0.001$ (other terms not significant).

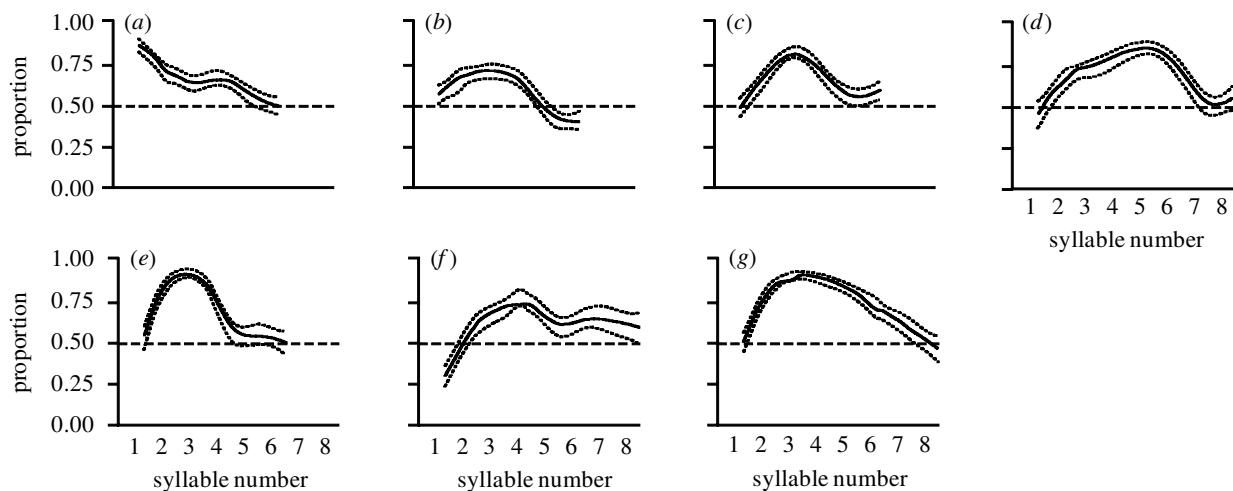


Figure 2. Female preference functions in crosses between the song races of *E. ephippiger*. A preference score of 1 indicates that each female chooses the song of that syllable number on all occasions. The horizontal dotted line indicates random phonotaxis, i.e. no preference. Preference functions are fitted cubic splines and error intervals are ± 1 s.d. calculated from 1000 bootstrap replicates. (a) Monosyllabic, (b) monosyllabic \times polysyllabic, (c) polysyllabic \times monosyllabic, (d) polysyllabic, (e) BX (monosyllabic), (f) F₂ and (g) BX (polysyllabic). (Maternal genotypes are indicated first for the F₁ hybrids.)

1998) or if females had been selected to increase their resistance to current levels of male stimulation (Rice & Holland 1997; Holland & Rice 1998). Most tests of arbitrary Fisherian processes emphasize an expected close match between trait and preference and strong genetic covariance between the two (Bakker 1993; Butlin 1993; Pomiankowski & Sheridan 1994; Bakker & Pomiankowski 1995), but persistent viability selection against longer chirps (e.g. through the energetic cost of singing or the incidental attraction of acoustically orientating predators or parasites) could result in female preferences always being directional but not open ended (Lande 1981).

The genetic control of the MRS described here largely conforms to a simple polygenic additive model. Other studies of acoustic signals have implied that polygenic determination is common, even where the trait difference is superficially very simple, such as a change in call timing (Shaw 1996). Polygenic determination seems likely for female preferences, though there is some suggestive evidence that single genes of large effect could play their part (Bakker & Pomiankowski 1995). Single-gene systems are more commonly found among pheromonal communication systems (Ritchie & Phillips 1998) and it seems more likely that molecular characterization of the genes involved in sexual isolation will make progress with such systems, though other systems are

also yielding candidate 'speciation genes' (Wheeler *et al.* 1991; Ting *et al.* 1998).

The current study supports recent suggestions that sex-linked genes could be disproportionately involved in sexual communication systems (Reinhold 1998). The analysis of female preferences does not allow any direct estimate of the relative role of sex-linked genes in female preferences, although it fails to support any particular role for maternally derived sex-linked genes. It is not clear why sex-linked genes should have a large effect in sexual behaviour. Ewing (1969) suggested male hemizygosity will facilitate selection on advantageous recessive genes, but this should apply to all traits (Charlesworth *et al.* 1987). Associations between meiotic drive and sexual selection could favour linkage (Wilkinson *et al.* 1998), though perhaps a more simple explanation is that most traits involved in sexual communication are sex limited in expression, favouring sex linkage in the hemizygous sex (Rice 1984; Reinhold 1999).

The pattern of inheritance of an MRS is also of potential importance in determining the contribution of MRSs to speciation. Comparative studies show that sexual isolation can evolve rapidly, sometimes before post-mating isolation is detectable and that this is more likely to occur when species ranges overlap (Coyne & Orr 1989, 1997). Reinforcing selection (Noor 1999) is unlikely to be

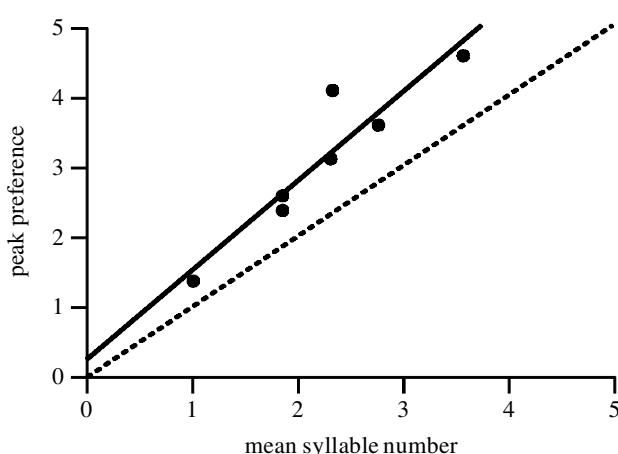


Figure 3. Peak preference versus mean syllable number across genotypes. Each point is the mean peak of individual females' preference functions plotted against the mean syllable number per male. The solid line is a least-squares regression ($\text{preference} = 1.26 \text{ trait} + 0.30; F_{1,5} = 34.2$ and $p = 0.002$) and the dotted line is that expected if preferences and traits matched perfectly. The peak female preferences are always for greater values of the trait than males actually produce.

involved in the absence of post-mating isolation. An alternative source of selection is that hybrid MRSs may be aberrant, for example if hybrid males produce a signal which is not preferred by any type of female (Coyne & Orr 1989; Hatfield & Schlüter 1996). In *Ephippiger*, hybrid swarms would be most likely to develop (in the absence of viability selection) because assortative mating between hybrids will lead to the production of an F_2 generation and subsequent recombinant genotypes. However, between species with more distinct and tightly tuned preference functions, sex linkage would mean hybrid hemizygous males have traits not favoured by heterozygous hybrid females and such a mismatch could form a subtle source of selection against hybrids.

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