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CHAPTER 6

General conclusion

Mate recognition and sexual selection in the calling song of Gryllus bimaculatus

The acoustic communication system of various orthopteran and anuran species is involved in sexual selection (e.g. Gray, 1997; Simmons, 1988; Simmons & Ritchie, 1996; Simmons & Zuk, 1992; Simmons *et al*., 2001). Simmons (1988) suggested that chirp duration, syllable rate and chirp rate convey information relating to male size in *G*. *bimaculatus*, and Bateman *et al*. (2001) and Simmons (1986a, b) showed that females prefer large males. In addition, it has been shown that older *G. bimaculatus* males have a significantly higher daily mating rate than younger males, and one of Simmons & Zuk's (1992) hypotheses was that females use syllable rate as an indicator of male age.

On the other hand, authors such as Boake *et al*. (1997), Ryan *et al*. (1996) and Schildberger *et al*. (1989) suggested that the communication system is also involved in species recognition. Bennet-Clark (1989) and Schildberger *et al*. (1989) showed through neurological studies that calling song frequency and syllable period are important mate recognition signaling traits in the calling song of *G*. *bimaculatus*.

Calling song traits under sexual selection and mate recognition

During the first 49 days after adult eclosion, males produced significantly longer chirp periods as they aged, suggesting that chirp traits can be used by females to judge male age. When the age and body size effects on the call traits were combined for the period of ten to 140 days post adult eclosion, it was shown that an older, large male called at a slower chirp and syllable rate than a younger, small male. Female preference studies that control for male size and male age respectively, need to be conducted to determine whether females use male song as an indicator for male size and/or male age. I therefore suggest that, while the chirp traits are potentially involved in sexual selection in *G*. *bimaculatus*, the

syllable traits and calling song frequency are potentially involved in mate recognition. Evidence below supports this interpretation.

Variation in the mate recognition and other call traits of G. bimaculatus

It has been predicted that mate recognition and sexual selection traits have different degrees of variation. Sexual selection has diversifying effects on mating signals (Lande, 1981; Panhuis *et al*., 2001), leading to large degrees of between-individual and between-population variation in these signals (Etges, 2002). Mate recognition, on the other hand, is suggested to exert stabilizing effects on mating signals across the geographic range of a species (Paterson, 1985), and one would expect these signals to have small degrees of between-individual and between-population variation. This study focused on several sources of variance that potentially contribute to the variation in the calling song of *G. bimaculatus*. Traits implicated in mate recognition were shown to have smaller degrees of variation than those traits implicated in sexual selection as follows:

a) Ferreira (2006a, Chapter 2) revealed that ageing effects contributed the least to the variation in the mate recognition traits (Table 2.1). The compensatory interaction between syllable duration and inter-syllable interval resulted in an extremely stable syllable period over the first 49 days of male ageing (Figures 2.4 & 2.5). The large degree of between-individual variation in the mate recognition traits compared with the chirp traits, are probably an artifact of the ANOVA since, when within-individual variation decreases (constant signal) then one would expect a larger between-individual variance component (Table 2.1).

b) Sources of variance that could contribute to within-population variation in the call traits were investigated in two South African populations, Makhado and Pretoria (Ferreira, 2006b, Chapter 3).

   i) Calling song frequency and syllable period had smaller degrees of between-chirp variation compared with the other call traits, suggesting a large degree of stability in the mate recognition traits of a particular male between chirps.

   ii) Principal components analysis (PCA) indicated that syllable traits contributed the least to the total within-population variation, while calling song frequency did not contribute to the total variation in either data set

(Table 3.4). On the other hand, the chirp traits contributed to a large degree to the total variation.

c) Supporting evidence was also found when investigating geographical variation in call traits (Ferreira, 2006c, Chapter 5).

i) Although there was a large degree of between-population variation in call traits, PCA indicated that calling song frequency and syllable period did not contribute to the total variation in the data set consisting of ten wild-caught populations (Table 5.3). In a captive-reared F_1 data set (consisting of six populations) calling song frequency did not contribute to the total variation in the data set and the syllable traits contributed less to the total variation than the other call traits (Table 5.3).

ii) The large degrees of inter-continental stability in the mate recognition traits (Table 5.2), supports the findings of Henderson & Lambert (1982) who found considerable stability in the mate recognition system of worldwide populations of *Drosophila melanogaster*. This suggests that inter-continental variation forms only a subset of the total variation that exists in the signaling traits of *G. bimaculatus*.

d) For mate recognition traits, captive-reared F_1 offspring had a smaller degree of between-population variance than their wild-caught parents. This suggests that environmentally-induced variance is more important for the mate recognition traits and also implies that genetic variation may be less for these traits.

The above results are consistent with the idea that mate recognition traits and sexual selection traits are separate aspects of communication. One could therefore predict that the mate recognition traits show stabilizing selection across a significant part of the geographical range of *G. bimaculatus*, and are therefore consistent with the prediction of Paterson (1985). In addition, the mate recognition traits also have smaller degrees of variation compared with other call traits, which is consistent with the predictions of Etges (2002), Lande (1981) and Panhuis *et al*. (2001). On the other hand, the geographical study (Ferreira, 2006c, Chapter 5) showed that the mate recognition traits of two South African populations (Hotazel and Queenstown) differed significantly from the other South African and European populations (Table 5.2). This could be consistent with Fisher's runaway process that predicts no predictable between-population differences in courtship signals

(Fisher, 1958). However, one should expect to see larger degrees of between-population differences within South Africa, if the Fisher process is operational in South Africa. In order to conclude whether geographical variation in the communication system of *G. bimaculatus* is consistent with Paterson's or Fisher's predictions, inter-population female preference studies where females are subjected to male calling songs from different populations need to be conducted. The outcome of the female preference studies will be important for understanding the evolution of communication for this species. For instance, if Queenstown females only prefer local males (i.e. Queenstown males), then this might be suggestive of covariance between the male signal and the female preference. On the other hand, if the Queenstown females do not have a preference for native males above foreign males, then stabilizing selection is probably acting on this signaling system and the species is probably not susceptible to speciation.

Effect of the environment on mate recognition traits of G. bimaculatus

Based on the comparative results of wild-caught populations from South Africa and Europe with their captive-reared F_1 offspring (Ferreira, 2006c, Chapter 5), this study suggests that a significant part of the geographical variation in mate recognition traits is probably caused by environmental effects (Table 5.2; Figure 5.4). These environmental effects could act as noise affecting the acoustic communication system of *G. bimaculatus*. Ferreira (2006b, Chapter 3) revealed large seasonal differences with large between-season variance components in the mate recognition traits. However, these results were not consistent between the two populations (Makhado and Pretoria), suggesting that the environmental component contributing to variation in signaling traits is not predictable and that several factors such as food availability, temperature, rainfall and population density probably contribute collectively to this variation. If environmental effects largely comprise temperature effects, it could be negated through 'temperature coupling'. Doherty (1985) showed that there is parallel coupling of female preferences to the effect that temperature has on the male signaling system in *G. bimaculatus*. A full-scale quantitative study needs to be undertaken to estimate the environmental component of variance in call traits.

Gene flow and mate recognition in G. bimaculatus

Surprisingly, the phylogeographical study (Ferreira, 2006d, Chapter 4) revealed a large degree of gene flow among seven South African populations, as well as between populations in Spain and Italy. The inter-continental estimates of gene flow were lower than for within-continent gene flow estimates. The fact that one haplotype was shared among all the populations suggest that there is ongoing inter-continental gene flow within this species. This could explain the observed stability in the mate recognition traits, and suggests that female *G. bimaculatus* from Europe should be able to recognise males from South Africa as conspecific, and *vice versa*.

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