

CHAPTER 1

General introduction

The effects of sexual selection and mate recognition on signaling traits

The process of intersexual selection includes female preference whereby she prefers to mate with some males above others. Various sexual selection models have been proposed to explain female preference. Some indirect selection models include the 'good genes' hypothesis where female preference involves traits that enhance the lifetime fitness of offspring (Endler & Houde, 1995; see review in Møller & Alatalo, 1999), the 'Hamilton-Zuk' hypothesis where female preference involves traits whose expressions are health-dependent and reflect resistance to genetic diseases (Hamilton & Zuk, 1982), e.g. pathogen resistance in house crickets, *Acheta domesticus* (Ryder & Siva-Jothy, 2000), or the 'chase-away' model described by Holland & Rice (1998). In this model antagonistic coevolution occurs between the sexes whereby females had a preexisting sensory bias for a specific trait, but they now prefer not to mate with males that display this trait since they might induce females to mate in a suboptimal manner, leaving males to evolve even more elaborate display traits (Holland & Rice, 1998). On the other hand, females might prefer traits that are correlated with some aspect of male quality from which they can benefit directly, e.g. female decorated crickets, *Gryllodes sigillatus*, would obtain greater nutritional awards when mating with larger males (Sakaluk *et al.*, 1992). It has been predicted that traits involved in sexual selection should show directional selection and have large degrees of between-male variation (Etges, 2002; Klappert & Reinhold, 2003). Sexual selection also has between-population diversifying effects on mating signals (Panhuis *et al.*, 2001).

Sexual selection implies that a female prefers to mate with a particular male, either by having prior preferences or by preferring to mate with a male that is more active and persistent in competing for her attention (O' Donald, 1983). Mate recognition, on the other hand, is regarded by Paterson (1985) as '...a specific response by one partner to a specific signal from the other', ensuring that an animal mates with an appropriate partner. The function of mate recognition is

therefore, to ensure mating between conspecific individuals. Paterson's Specific-Mate Recognition System (SMRS) includes signals and responses that lead to fertilization and Paterson (1985) predicted that mate recognition traits that form part of the fertilization system is subject to stabilizing selection throughout a species range while this species occupies its normal habitat. Butlin (1995) suggested that, if there are between-population differences in mate recognition traits, then it is probably due to environmental effects. Furthermore, one would expect mate recognition signals to have small degrees of between-individual variation (Etges, 2002). Indeed, Ryan *et al.* (1996) and Ferreira & Ferguson (2002) showed that call traits important for mate recognition in the túngara frog, *Physalaemus pustulosus*, and the field cricket, *Gryllus bimaculatus*, respectively had lower degrees of variation compared with other call traits. Henderson & Lambert (1982) found considerable stability in the mate recognition system among worldwide populations of the fruit fly, *Drosophila melanogaster*.

Some authors suggested that sexual selection and mate recognition are independent processes (e.g. Paterson, 1993) while others believe the contrary is true (Pfennig, 1998). Several studies have shown that different traits are involved in mate recognition and sexual selection (European green toad, *Bufo viridis*: Castellano & Giacoma, 1998; Hawaiian picture-winged fly, *D. heteroneura*: Boake *et al.*, 1997; Túngara frog, *P. pustulosus*: Ryan *et al.*, 1996). Ryan & Rand (1993) suggested that mate recognition and mate choice through sexual selection are separate processes, but with recognition having effects on mate choice and *vice versa*. On the other hand, Backwell & Jennions (1993) argued that mate choice involves selection on all aspects of communication systems, including mate recognition, and that mate recognition systems can therefore not be distinct from mate choice systems.

The role of signaling traits in speciation

Paterson (1985) suggested that if a small population becomes isolated in a new and distinct environment, then mate recognition traits of the fertilization system could be subjected to directional selection. However, once the SMRS has improved its effectiveness in the new habitat, the mate recognition traits will again be under stabilizing selection. If this new fertilization system is different from the parental one, then speciation has occurred.

Several sexual selection models aim to explain geographic divergence in sexually selected traits and female preferences (see review in Andersson, 1994). Fisher's runaway process predicts diversity in courtship signals through genetic correlation between female preferences and male traits (Fisher, 1958). Lande (1981) predicted through modeling on polygenic traits that the male-female signaling system may be unstable, depending on the genetic covariance between the male signal and the female preference. This will lead to rapid between-population differentiation in the signaling system, as was shown in female preferences of guppies, *Poecilia reticulata* (Brooks & Endler, 2001). Iwasa & Pomiankowski (1995) and Pomiankowski & Iwasa (1998) predicted through mathematical modelling that Fisher's runaway process is unstable and naturally leads to continual change in sexual traits.

When the same trait or genetically correlated traits are used for both species recognition and sexual selection (i.e. mate quality recognition), conflict could arise between species recognition and sexual selection, resulting in inappropriate mate choices (i.e. preferences for heterospecifics or lower-quality males; Pfennig, 1998). It has been shown in laboratory studies that females could respond to calls of heterospecific males (Ryan & Rand, 1993; Backwell & Jennions, 1993) or that they could prefer heterospecifics above conspecifics in the absence of a mate recognition cue (Hankison & Morris, 2002). Female túngara frogs, *P. pustulosus*, had a preference for heterospecific male song when part of a heterospecific male's song was added to the conspecific call (Ryan & Rand, 1993). Although female Neotropical frogs, *Hyla ebraccata*, preferred conspecific male calls, they did respond to heterospecific male calls when no alternative was available (Backwell & Jennions, 1993). Female pygmy swordtails, *Xiphophorus pygmaeus*, use multiple cues for mate recognition and sexual selection and Hankison & Morris (2002) found that females do prefer heterospecific males when subjected to certain choices in laboratory tests. An understanding of how mate recognition and sexual selection processes affect signaling systems should therefore enable scientists to predict what the evolutionary implications of variation in signaling systems could be, and if a species might be susceptible to speciation.

Rationale for this thesis

Understanding the sources and magnitude of variation in the communication systems of animals, enables one to have a better understanding of the

mechanisms of mate recognition and sexual selection within a species, as well as their potential interaction. I will investigate several sources of variance that potentially contribute to variation in the signaling traits of the field cricket, *G. bimaculatus*. This includes variation within an individual, between individuals, between populations, between continents and between seasons. I will also investigate whether different call traits are involved in sexual selection and mate recognition.

The male signals of *G. bimaculatus* are stereotyped and easily quantified, which makes it an ideal species for studying variation in signaling traits. In addition, these crickets occur almost worldwide (Harrison & Bogdanowicz, 1995; Ragge, 1972), giving one the opportunity to study large-scale geographical variation in signaling traits. It is also relatively easy to sample these crickets in the field, since calling males can be tracked easily. It is also easy to breed and rear them in captive conditions, which makes it easy to study variation in the signaling traits of captive-reared F₁ offspring.

The acoustic communication system and call production in G. bimaculatus

The acoustic communication system of *G. bimaculatus* comprises calling songs, courtship songs and aggressive songs (Alexander, 1962). Males produce calling songs to attract females. The calling song consists of chirps and each chirp comprises three to six syllables (Desutter-Grandcolas & Robillard, 2003). Syllables are produced by wing closing movements, when the plectrum of the one wing traverses the file of the other wing. Wing opening movements result in quiet inter-syllable intervals (Bennet-Clark, 1989). Several calling song characteristics have been implicated in mate recognition (Bennet-Clark, 1989) and sexual selection (Simmons, 1988; Simmons & Zuk, 1992).

Mate recognition and sexual selection in the calling song of G. bimaculatus

Two calling song characteristics, namely calling song frequency and syllable period, are important for mate recognition in *G. bimaculatus* (Bennet-Clark, 1989; Schildberger *et al.*, 1989) while chirp duration, chirp rate and syllable rate have been identified as sexually selected call traits (Simmons, 1988). Within this framework of mate recognition, I addressed the following question: Do between-individual, between-population and between-seasonal factors have a smaller

effect on variation in mate recognition traits than on other call and morphological traits in *G. bimaculatus*?

It is not clear to what extent the calling song of *G. bimaculatus* is used in sexual selection. It has been suggested that females use the calling song to determine male age and male size. Simmons & Zuk (1992) predicted that females either decide post-copulatory whether they intend to mate with a certain male or they use a cue in the calling song to determine a male's age. Older males had a significantly higher daily mating rate than younger males, even though gregarine infection did not influence the mating success of older *G. bimaculatus* males (Simmons & Zuk, 1992). It is known that *G. bimaculatus* females prefer large males and they accept more sperm from large males compared with small males (Bateman *et al.*, 2001; Simmons, 1986a, b). It has been shown in several cricket species that females could use call traits to assess male size (Brown *et al.*, 1996; Gray, 1997; Simmons, 1988) and Simmons (1988) suggested that call traits provide information relating to male size. However, there are energetic costs involved in calling song production and Prestwich (1994) showed that the energetic cost of calling increases linearly with calling rate in several cricket species. Within the framework of sexual selection, the following questions were addressed: (a) Do the calling song characteristics change with male ageing? (b) Do larger males spend more hours per day calling than smaller males? (c) Do males with shorter life spans spend more hours per day calling than males with longer life spans? (d) Do larger males have longer life spans than smaller males? (e) Is there a correlation between male size and calling song characteristics? (f) What is the contribution of the within-individual variance to the total population-level variation in call traits? (g) Does rearing temperature affects male and female body sizes at adult eclosion?

Phylogeography of G. bimaculatus

One of the aims in population genetics is to determine the amount of genetic variation that exists in natural populations and to ideally explain this variation in terms of its origin, maintenance and evolutionary importance (Hartl, 1987). The mitochondrial (mt) DNA genome is maternally inherited, haploid and non-recombining (Hartl, 1987) which make it useful for studying intraspecific patterns of genetic differentiation among populations with the use of gene trees (i.e. phylogeography). Phylogeographical analyses could provide information about the

present and historical processes that gave rise to the present geographical distribution of *G. bimaculatus* (Templeton *et al.*, 1995; Templeton, 1998). Although the phylogeny of *Gryllus* is well understood, little is known about the intraspecific patterns of gene flow and population structure of *G. bimaculatus*. By sequencing part of the cytochrome *b* mtDNA gene, I addressed the following questions: (a) What is the degree of gene flow that occur among South African and European populations (i.e. inter-continental) as well as within South Africa and Europe (i.e. regional)? (b) Which biogeographical processes provide the best explanation for the current genetic structure of seven South African populations of *G. bimaculatus*?

Geographical variation in the calling song and morphometrics of wild-caught and captive-reared F₁ populations of G. bimaculatus

“Patterns of geographic variation within species give some indication of both the potential for future evolution and the past history of selection and constraints” (Ryan *et al.*, 1996). It is important to have an estimate of between-population variability in the calling song of *G. bimaculatus*, since the calling song is regarded as one of the most important premating barriers in crickets (Otte, 1989). Isolation-by-distance effects explained geographical variation in the mating call of the green treefrog, *Hyla cinerea* (Asquith *et al.*, 1988) and the advertisement call of the túngara frog, *P. pustulosus* (Ryan *et al.*, 1996). However, it is not clear what caused geographical variation in the advertisement call of the frog, *Leptodactylus fuscus* (Heyer & Reid, 2003) or the calling song of the bushcricket, *Ephippiger ephippiger* (Ritchie, 1992). Genetic and environmental variation, as well as an interaction between them, contributes to the total phenotypic variation of a trait (Falconer & Mackay, 1996). Mousseau & Howard (1998) compared wild-caught with laboratory-reared populations of two species of ground crickets, *Allonemobius fasciatus* and *A. socius*, as well as a hybrid population and they found a significant effect of the environment on call traits. My aims incorporated the following questions: (a) Does an isolation-by-distance effect explain the geographical variation in the call and morphological traits of *G. bimaculatus* males from South Africa and Europe? (b) Does geographical variation in the call and morphological traits resemble gene flow patterns? (c) When comparing geographical variation in call and morphological traits in wild-caught populations

from South Africa and Europe with captive-reared F_1 populations, can part of this variation be due to environmental effects?

Knowledge of the degree of variation that exists in sexually selected traits compared with mate recognition traits, as well as having an estimate of environmental effects on the communication system, could therefore help us to understand whether these classes of signals are distinct in crickets and how sexual selection and mate recognition act on the signaling system of *G. bimaculatus*. This study aspires to make a contribution towards such a better understanding.

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