Evolutionary implications of variation in the calling song of the cricket *Gryllus bimaculatus* De Geer (Orthoptera: Gryllidae)

By Marna Ferreira

Submitted in partial fulfilment of the requirements for the degree Magister Scientiae

in the Faculty of Natural and Agricultural Sciences Department of Zoology and Entomology University of Pretoria Pretoria South Africa

July 2006

Evolutionary implications of variation in the calling song of the cricket *Gryllus bimaculatus* De Geer (Orthoptera: Gryllidae)

by Marna Ferreira

for the degree Magister Scientiae

Supervisor:	Prof. J. Willem H. Ferguson
Department:	Centre for Environmental Studies, University of Pretoria,
	Pretoria, 0002, South Africa

Abstract

The acoustic communication system of the field cricket, *Gryllus bimaculatus*, comprises male signals that elicit phonotaxis by females. Although calling song traits have been implicated in mate recognition as well as sexual selection, the degree to which these two categories of call traits differ as well as the sources of variation that affect them have not been investigated. Variation in signaling traits implicated in mate recognition or sexual selection can bring about speciation. *Gryllus bimaculatus* occurs in Africa, Asia and Europe, and its communication system is easily measured, making it an ideal study organism to investigate the evolutionary implications of variation in signaling traits.

Calling song data was used to investigate how call traits change with male ageing in order to determine if call traits can be used by females to judge male age. In general, older males produced shorter syllables and slower chirp rates. It has been predicted that females can use call traits to judge male size. However, this study found only weak correlations of male size with call traits and therefore suggests that females probably cannot use the calling song as an indicator of male size. Environmental effects could act as noise on the cricket's signaling system and, in turn, influence the reliability with which a male signal reflects his quality. Within-male variation in call traits was mostly caused by large degrees of between-chirp variance. There were significant between-season differences in call and morphometric measurements, with large degrees of seasonal stability across years. Geographical variation in call traits and morphometrics of eight South African and two European populations as well as six captive-reared F_1 populations was also investigated. I found larger degrees of between-population differences within regions than between continents. An isolation-by-distance effect could not explain inter-continental and regional variation in call and morphological traits. To determine to what degree environmental effects contribute to geographical variation in these traits, variances of wild populations were compared with variances of their captive reared F_1 offspring. This study found that a significant part of the geographical variation is due to an environmental component.

Intraspecific patterns of genetic variation were investigated in seven South African and two European populations, by sequencing part of the mitochondrial cytochrome *b* gene. There was a small degree of within-population genetic variation in Europe and a large degree of within-population genetic variation in South Africa. Thirty one haplotypes were identified from 161 individuals, one of which occurred in all nine populations. While some gene flow did occur among South African and European populations, large amounts of gene flow occurred within South Africa. Nested clade analysis predicted that isolation by distance in combination with restricted gene flow explained gene flow patterns within South Africa. The genetic diversity of *G. bimaculatus* is probably maintained by a large gene pool, and inter-continental and regional gene flow is possibly maintained by means of land, sea or air transport.

Keywords: *Gryllus bimaculatus*, Orthoptera, Gryllidae, South Africa, Europe, Wild-caught populations, Captive-reared F₁ populations, Calling song variation, Morphometrics, Mitochondrial DNA, Cytochrome *b*, Phylogeography

ii

Acknowledgements

I would like to thank my supervisor, Prof. Willem Ferguson, for his guidance, patience, advice and support.

I would like to thank my parents, Mac & Ellen, and grandmother, Mara, for their love, support, encouragement and prayers. To my husband, André, thank you for your love, support and most of all your patience. With you behind me, I will be able to achieve anything. To my dear friend, Lizandé Kellerman, thank you for your support, encouragement, prayers and assistance in the field.

I would like to thank Wayne Delport for his assistance with the Cesium Chloride DNA extractions as well as for assisting me with most of the genetic analyses. To Luke Verburgt, thank you for your assistance with the cricket recordings. I would like to thank everyone who has assisted me in the field and laboratory. I appreciate it immensely.

The farmers from Dullstroom, Dundee, Makhado, Paarl and Wolmaransstad are thanked for allowing me to catch crickets on their properties as well as for their kindness and hospitality. Doors le Roux is thanked for providing me with rainfall data for Makhado.

The National Research Foundation (NRF) and University of Pretoria is thanked for financial support.

Table of Contents

Page

Abstracti - ii
Acknowledgementsiii
Table of Contents iv
Chapter 1: General introduction 1 - 12
Chapter 2: Interactive effects of age and body size on calling song traits
of male field crickets, Gryllus bimaculatus De Geer
(Orthoptera: Gryllidae) 13 - 44
Chapter 3: High levels of environmentally-induced variation in the calling
song of the field cricket, Gryllus bimaculatus De Geer
(Orthoptera: Gryllidae) 45 - 78
Chapter 4: Inter-continental phylogeography and regional gene flow in
the field cricket, Gryllus bimaculatus De Geer (Orthoptera:
Gryllidae)79 - 107
Chapter 5: Environmentally-induced geographical variation in the
calling song of the field cricket, Gryllus bimaculatus De Geer
(Orthoptera: Gryllidae) 140
Chapter 6: General conclusion 141 - 147
Appendix 1