Identification of the factors that lead to dispersal and inbreeding

by

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Submitted in partial fulfilment of the requirements for the degree PhD Genetics
In the Faculty of Natural and Agricultural Science
University of Pretoria
Pretoria
August 2009
Summary

Individual-based simulation modelling is an excellent method for testing hypotheses, while including realistic and stochastic population parameters. This thesis considers the evolution of dispersal or inbreeding through individual-based simulation modelling.

The occurrence of exclusive inbreeding and exclusive outbreeding is found in a number of organisms and are referred to as mixed mating. Mixed mating is suggested to be in response to low levels of inbreeding depression as well as simultaneous inbreeding- and outbreeding depression while intermediately related mating partners are not available. The results of this thesis show that stable mixed mating strategies evolve in the presence of both inbreeding and outbreeding depression, as well as, under conditions where low levels of inbreeding depression are present. Also, inclusive fitness allows higher levels of inbreeding in genetic systems where the mating partners are more related to each other.

Dispersal evidently evolves in response to inbreeding depression. A number of other factors, such as local mate competition and the cost of dispersal also influence the rate of dispersal. In addition to these factors, it is shown in this thesis that male dispersal evolves when there is variation in patch sex ratios. Simulation data also supports parent offspring conflict models, as males have reduced dispersal rates when they, rather than their parents, determine the dispersal rate.

Population structure is affected by dispersal rates. Using individual-based simulation modelling and various sampling strategies, reveals that few molecular markers, for a few individuals, are sufficient to accurately detect population subdivision, especially when the sub-populations are large. It is, however, indicated that planning prior to sampling are important for proper assessment of population structure.

Lastly, molecular data from the pollinating fig wasp *Platyscapa awekei* reveals that this species suffers from low levels of inbreeding depression. However, when this data are simulated, stable mixed mating did not evolve although it is observed in *P. awekei*. Sex ratio variation, high local mate competitions and male only broods are therefore suggested to drive male dispersal. It is consequently advantageous to use various techniques to unravel the evolution of a trait and gain insight into the system.
To: My Grandfather

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I thank my supervisor, Jaco Greeff, for his support during my research, allowing me the freedom to choose my topics of research, and subsequently to wander into the realm of individual-based simulation modelling. Many hours were spent discussing various aspects of evolution, biology and statistics and I learned a great deal from him and it has been a privilege to work together.

I thank my family for all the love and encouragement. To my parents, many thanks for the support, both financial and otherwise, provided over the years. To my sibling, Cindy, thanks for all the visits in the lab and often participating in various discussions on evolution and related matters.

I am very grateful to everyone who read, commented and pointed to errors in the manuscripts: Chapter 2 – Jaco Greeff, Carina Schlebusch, Marié Warren and two anonymous reviewers; Chapter 3 – Jaco Greeff, Carina Schlebusch and Marié Warren; Chapter 4 – Jaco Greeff, Carina Schlebusch, Marié Warren and Pam de Waal and Chapter 5 – Jaco Greeff, Carina Schlebusch and Marié Warren. A special thanks to Marié Warren, who patiently corrected my English throughout the thesis.

To the Department of Genetics at the University of Pretoria and my fellow lab members, past and present Annie, Aret, Christoff, David, Duncan, Heike, Joscha, Marié, Mel, Motoaki, Okkie, Pam, Soné, Vinet, and Zee, many thanks for making the work environment a fun place to be and your companionship during this study.

I am grateful to the National Botanical Gardens of South Africa that allowed me to collect figs and fig wasps on their premises. I also extend my appreciation to the University of Pretoria and the National Research Foundation for their financial support during this study.

Lastly, I owe a massive debt of gratitude to my wife, Carina. I am thankful for her constant support of my research while doing her own PhD. Her love, encouragement and understanding made life a pleasure during this study.
Preface

Each chapter in this thesis, except for the introduction and conclusion, is written as a journal article and is either submitted or in preparation for submission and as such includes its own introduction, and discussion section. In chapters 2 and 3 the results and discussion sections are combined respectively as a discussion naturally follows a description of the generated data.

Jaco Greeff, my supervisor, is included as co-author for the submitted manuscripts for chapters 2, 3 and 4. The reasons for this are twofold. First, the models were developed with suggestions from him, although the underlying ideas as well as the simulation models themselves are my own. Secondly, all of the financing and facilities required to complete these studies were provided through funding secured by him.

In this thesis I extend a number of existing ideas with the use of individual-based simulation modelling within the Delphi environment, compiled for the Windows operating system. As such, these programs and source code are available in the electronic appendix submitted with this thesis. Although these programs are merely the tools used to test ideas, the following can be mentioned regarding the code itself: the program discussed in chapter 4 was created first, followed by the program for chapter 2 and lastly the program for chapter 3. Starting with no formal education in programming and no experience with the Delphi environment the program code may be somewhat informal. Therefore, the code for the last program is more efficient than the first. Additionally, in the general introduction, I deal with individual-based simulation modelling as a tool to study evolutionary processes to avoid repetition in the chapters where it was employed.

Lastly, to keep all the theory and models grounded in reality, much of the research in this thesis refer to pollinating fig wasp biology. While the simulation models are not exclusive for the pollinating fig wasp system they are applicable to them. Furthermore, chapter 5 deals with empirical data from this system and for these reasons I introduce the pollinating fig wasp system in the in general introduction.
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