Alternative Reproductive Tactics

An Integrative Approach

Consistent variation in the reproductive behavior of males and females within a species is an evolutionary puzzle. How two forms of male can develop in one species, for example, and how such variation can be maintained in one population at the same time, offers a special opportunity to study the evolution and functional causes of phenotypic variation, which is a general problem in the field of evolutionary biology. By integrating both proximate (physiological) and ultimate (evolutionary) perspectives and by covering a great diversity of species, *Alternative Reproductive Tactics* addresses this exciting topic of longstanding interest, bringing together a multitude of information in an accessible form that is ideal for graduate students and researchers in evolutionary biology, behavior, and reproductive physiology.

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Contents

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Preface

The study of alternative reproductive tactics (ARTs) is a hot topic in evolutionary and behavioral ecology. ART refers to consistent variation in the reproductive behavior (involving, e.g., mating, nesting, fighting) of males or females within one population. This variation offers a special opportunity to study the evolution and functional causes of phenotypic variation, a general problem in evolutionary biology. A large body of published data exists on ARTs, but there has been no conceptual unification of the available information, nor any strong effort to integrate it into a general framework. Apart from a recent book by S. M. Shuster and M. J. Wade (2003) (*Mating Systems and Strategies*, Princeton, NJ: Princeton University Press) that addresses the topic of ARTs within the larger scope of mating systems, there has been no major publication covering this topic. Moreover, the few reviews available in the literature are taxon specific and do not fully integrate the proximate and ultimate levels of analysis in understanding ARTs. Clearly, integration of data, concepts, and analysis levels is overdue. In trying to meet this challenge, Rui Oliveira joined forces with Michael Taborsky and Jane Brockmann, who were among the contributors to a symposium on ARTs at the 27th International Ethological Conference in Tübingen. The three of us have complementary connections to active researchers in the field and all three have been studying ARTs from very different perspectives. Following the Tübingen conference we started a fruitful discussion in order to establish the plan of a book, identifying the areas to be covered and who would be the most appropriate to write about each of quite a few essential topics. We decided to use an integrative approach to the field inviting people both from the area of ultimate causes (evolutionary and behavioral ecology) and from the field of proximate mechanisms (behavioral physiology). We asked authors to write a chapter on a specific issue selected by us and not to write short reviews about their own work, so that this book can be more than the sum of its parts. It is with great pleasure that we thank all the authors for investing a lot of time and effort in writing their chapters to meet these requirements, and for their generous patience with successive delays in finalizing the book.

Since ARTs can be viewed as a model system for studying the evolution of variation, which is one of the central questions in evolutionary biology, the potential audience for this book is very broad, including readers interested in animal behavior, life histories, phenotypic plasticity, biological game theory, evolutionary theory, and ecology in general. Thus, although this is not a textbook we hope it may become a reference for postgraduate courses in the above-mentioned areas.

We have organized the book in four parts, together with an opening general introduction and a final concluding chapter.

In the opening chapter we try to clarify concepts and address the levels at which questions about the evolution of ARTs should be asked. This is important because alternative hypotheses often turn out to be simply a matter of asking questions at different levels. Therefore, in this chapter we also attempt to provide a framework, language, and theoretical basis for studying ARTs. It is important to note, though, that we did not impose our framework on the other authors of this volume. In accordance with the topic, which deals with the intriguing wealth of biological variation between individuals of a population, we intended to allow different concepts and frameworks within the pages of this book. As with ARTs existing in a population, only time will show which concepts will finally persist.

Part I of the book summarizes the study of ultimate causes and origins of ARTs. It opens with a chapter on the evolution, life histories, and adaptiveness of ARTs viewed within the scope of alternative allocation phenotypes (Brockmann and Taborsky). It is followed by a chapter in which the use of comparative methods is proposed as a tool with a large potential to reveal phylogenetic patterns of ARTs in the study of their evolution (Almada and Robalo). This part ends with a chapter where dynamic game modeling is applied to the study of ARTs (Lucas and Howard).

Part II summarizes our current knowledge of the proximate mechanisms of ARTs. It starts with a chapter on the interaction between genetic and environmental factors on

the development of ARTs (Emlen), which is followed by two chapters on neural (Bass and Forlano) and endocrine mechanisms underlying ARTs (Oliveira, Canário, Ros).

Part III is a compilation of taxonomic reviews with the goal to provide an overview of the occurrence of ARTs in the animal kingdom. This part covers most animal taxa for which ARTs have been described, namely insects (Brockmann), crustaceans (Shuster), fish (Taborsky), amphibians (Zamudio and Chan), reptiles (Calsbeek and Sinervo), birds (Krüger), nonprimate mammals (Wolff), and primates (Setchell). The few examples of ARTs in invertebrates not covered by these taxonomic reviews were addressed where appropriate in text boxes of other chapters.

Part IV is a compilation of chapters on emerging perspectives on ARTs, such as the role of animal communication in the evolution of ARTs (Gonçalves, Oliveira, and McGregor), the relationship between ARTs and mate choice for good genes or good care (Neff), a co-evolutionary approach to sexual conflict and ARTs within a sex (Alonzo), and the viewing of cooperative breeding as an ART (Koenig and Dickinson).

In the final chapter the editors reflect on what emerges from all the contributions to this book as the current status of the study of ARTs, and the prospects for future research in this field. It is a summarizing chapter attempting to pull all the topics together, pointing to major questions and suggesting the importance of studying the evolution of ARTs integratively.

All chapters were reviewed by the three editors and by external reviewers. We are very pleased that the authors made an extraordinary effort in considering the editors' and reviewers' comments in revising and amending their contributions. A large body of external reviewers made a significant contribution to the contents of this book and we would like to express our gratitude to their extensive criticisms and suggestions about each manuscript.

Apart from the dedicated work of authors and reviewers, this book would not have been possible in its current format without the contribution and support from various people and institutions. We are grateful to Desmond Morris who kindly permitted us to use one of his paintings for the cover of this book. Desmond Morris was one of the earliest ethologists to describe ARTs (in sticklebacks: Morris, D. 1954. The causation of pseudofemale and pseudomale behaviour: a further comment. *Behaviour* 7, 46–56) so we felt his artwork was particularly appropriate for this book. The Mayor Gallery (London) kindly provided technical support for the reproduction of this painting. The editors at Cambridge University Press, Martin Griffiths, Clare Georgy, and Shana Coates, were both patient and supportive and we thank them for their efforts.

Grace Kiltie worked directly with HJB on the formatting and copy-editing of all chapters. She also compiled the remissive index for the book and the figure and table lists. Her commitment and enthusiasm were decisive for the success of this enterprise. Joana Jordão also provided valuable help during the final phase of proofreading. RFO is supported by the Portuguese Foundation for Science and Technology (FCT; Pluriannual programme: R and D unit 331/2001) and the editing of this book was supported partially by a FCT research grant. ISPA and RFO generously hosted MT and HJB in Portugal during September 2004. MT was supported by SNF grant 3100A0-105626. HJB was supported by the National Science Foundation, Florida Foundation and Department of Zoology, University of Florida. Finally, Catarina and João Oliveira, Xana Lopes, Barbara Taborsky, and Tom Rider merit special thanks. They unconditionally supported us along the long and winded ways of compiling this book.