

Preface

During the Brazilian Ethology Meeting in 2010 in Alfenas, a small city in the state of Minas Gerais, Brazil, we sat over coffee and discussed the various talks presented during the meeting. We were simultaneously discouraged and hopeful: discouraged because we could not fathom why some of the terrific talks and exciting information on sexual selection and mating systems presented during the meeting remained virtually unknown to the scientific world outside Latin America, and then hopeful because we could imagine producing a book based on the studies of sexual selection being conducted by researchers throughout the Neotropics. Thus was hatched the idea of a book about sexual selection of neotropical animals. It has since become apparent that putting together such a book is a somewhat harder endeavor than we had originally envisioned. It has been a lengthy process, and we have had to nag colleagues about deadlines, and also question ourselves about preconceived concepts that we thought were well-established. But now that we are on the verge of publication, we definitely think this has been a thoroughly worthwhile mission.

Initially, we scrutinized the literature to see what was available relative to tropical biology, sexual selection, and mating systems. Although there are many recent academic books that cover diverse aspects of tropical biology, and many more that concentrate on sexual selection and mating systems, there are none that integrate these two areas. One that approaches this merging of theoretical framework with geographical scope is *Behavioral Ecology of Tropical Birds* (Stutchbury and Morton, 2001), but the book is restricted to birds and broad-based, covering behavioral ecology as a whole. We wondered why no book had ever been published examining sexual selection of neotropical organisms, given the explosive growth in publications about sexual selection in general, and the enormous diversity of tropical organisms and biological interactions available for study in tropical America. Furthermore, we pondered why even those books that concentrate on sexual selection rarely cite studies of tropical animals. Below, we attempt to answer these questions by addressing two issues. First, we rationalize why this book will contribute to the burgeoning theoretical and empirical foundations of sexual selection. Second, we focus on why the study of the abundant animals and systems in the Neotropics has been appallingly neglected. We follow up by introducing the concepts and themes explored in each chapter.

Which explanations validate examination of the interface between sexual selection and the Neotropics? Is there a reason to assume major differences in the pressures that shape sexual adaptations in temperate and tropical organisms? The neotropical region, broadly defined for the purposes of this book,

encompasses vast tropical areas as well as large altitudinal variations. Climatic and geographic factors promote elevated faunal and vegetational diversity, which in turn results in complex selective pressures upon organisms, generating assorted and unique reproductive behaviors and morphological traits. The vast diversity harbored by the Neotropics is both a difficulty and a wonderful phenomenon, resulting in many organisms lacking even basic descriptions and taxonomic classification. The enormous diversity of animal life yields another type of diversity, that of biological interactions, which peaks in neotropical regions but is much less varied in temperate regions. The study of this type of diversity is markedly absent from the literature.

Despite the diversity of species, interactions, and behaviors harbored by the Neotropics, most biological research has focused upon temperate region species and systems. Dobzhansky mentioned this problem over 60 years ago: "Temperate faunas and floras, and species domesticated by or associated with man, have supplied, up to now, practically all the material for studies on population genetics and genetical ecology" (Dobzhansky, 1950). In the field of sexual selection, in particular, most theoretical concepts are indeed based on studies of the less diverse North American and European faunas. Even these studies in temperate regions of the northern hemisphere focus on a relatively small number of model species that, because of logistical factors or abundance, became the object of numerous studies.

The main goal of this book, then, is to present relatively new sexual selection study models based upon neotropical species that have been intensively studied during the past 20 years. These studies have shown both convergences as well as unexpected divergences relative to the traditional models that have been studied in North America and Europe. We hope that by providing comparisons with well-known species and models, this book will help to integrate various concepts in sexual selection. Another objective of the book is to combine different perspectives and levels of analysis using a broad taxonomic basis. These approaches distinguish this book from current publications in sexual selection mainly because of the geographic and taxonomic focus, so that readers will be introduced to systems and information largely unknown outside the tropics, some of which diverge from well-established patterns for temperate regions.

Given the potential for important contributions to biological research, why then has this wealth of knowledge been overlooked? Although this book is not about history and politics, it is a fact that such issues can shape (or misshape) the value placed on as well as the progress of science. Thus, acknowledging the role of politics and history in science is an important step toward understanding, and perhaps changing, the scientific scenario. Historically, most of Latin America has been both politically and economically turbulent, usually with unfortunate consequences for the establishment of educational systems and modern research. Using Brazil, the country we are most familiar with, we can illustrate how politics and economic turbulence have dominated cultural and educational initiatives, and generated obstacles to education, research, and scientific progress.

The Portuguese arrived in Brazil in 1500, only 8 years after Christopher Columbus set foot in the Caribbean islands. Portugal did not allow higher education institutions to be established in its colonies, in contrast with England, which was mostly responsible for colonizing North America. The three oldest universities in the United States, for instance, are Harvard, established in 1636, the University of Pennsylvania, established in 1740, and the College of William and Mary, which opened its doors in 1779. In comparison, the oldest higher education establishment in Brazil was inaugurated over 300 years later, in 1934 – only 80 years ago! In this simple historical fact, it is easy to perceive how politics and knowledge are intrinsically linked.

Political instability has posed overwhelming challenges to the establishment of educational institutions and economic prosperity all across Latin America. In comparison to the United States, where citizens over the past 200 years have grown used to the idea of democracy and casting votes to choose their leaders, Brazilian citizens have had only intermittent access to voting rights for approximately 77 years, the past 30 of which have had an enormous and positive impact upon the country. In general, throughout Latin America, dictatorships have been a pervasive feature of the political landscape since the colonial period. With the exception of Costa Rica, Mexico, and French Guiana, all other former colonies of France, Portugal, and Spain experienced periods of military dictatorship during the second half of the 20th century (Calleros, 2009). Dictatorships have lasted from a few years to decades, with the record going to Cuba (54 years), followed by Paraguay (35 years) and the Dominican Republic (31 years). But even short dictatorships are disruptive, when one considers the 9000–30,000 disappeared and dead individuals in Argentina between 1976 and 1983, or the approximately 60,000 people (2% of the population) detained during the military regime in Uruguay from 1973 to 1983. Considering political instability, one has only to realize that about 200,000 people died during the Guatemalan civil war, which lasted 36 years (1960–1996), to appreciate that research and science can very much become low priorities for a society.

During the 1980s and 1990s, elected democratic governments coming into power after periods of dictatorship in Latin America were faced with high economic inequality, high inflation, and macroeconomic instability (Bittencourt, 2012). We contend that economic instability has also been a hindrance to the establishment of educational systems and modern research. In the second half of the 1980s, monthly inflation in Brazil ranged from 6% to 83%. Thus, a researcher who submitted a research proposal to a funding agency in that period would have to have been granted approximately four times the amount requested to compensate for the loss due to inflation during the 3-month proposal evaluation period of the funding agency. Obviously, such an adjustment was never incorporated into the funding mechanism, resulting in serious negative consequences to successful implementation of most projects. Inflation not only engulfed a large part of research funds, but also influenced governmental investment policies. In Brazil, this meant fewer resources devoted to education, particularly for research funding.

Thankfully, this disheartening scenario is rapidly changing throughout Latin America in the 21st century. The Democracy Index (a measure of the state of democracy worldwide; compiled by the Economist Intelligence Unit [EIU, 2013]) suggests that most of Latin America and the Caribbean currently boast what is termed a "flawed democracy", which is second only to the "full democracies" of North America and Western Europe. This state of democratic transition ranks above "hybrid regimes" (Asia, Australasia, Central and Eastern Europe, sub-Saharan Africa) and "authoritarian regimes" (Middle, East, and North Africa). And while a "flawed democracy" may still be far from ideal, its favorable impact can already be felt in the surging educational institutions, universities, and research outputs.

In Brazil, the past decade has seen a phenomenal increase in the number of universities and a significant impact upon research. Moreover, the economic stability attained nearly 15 years ago promoted fast and profound changes in academia, with great benefits to research funding. For the first time in Brazilian history, students and researchers are being encouraged to publish their studies in high-impact journals in their fields of expertise. As an initial result of this investment-and-reward policy, the number of peer-reviewed publications by Brazilian researchers jumped from 6000 per year in 1995 to 32,000 in 2009 (Regalado, 2010). Increasingly, research is being conducted by native researchers who have now accumulated many years of data on neotropical model organisms. As more long-term data emerge, so do surprising and interesting details that either enrich known ecological models or pose challenges to existing paradigms.

Despite the enormous advances observed, it is naïve to assume that a centuries-old gap in scientific knowledge can be eradicated in a few years. Scientific activity in many countries in Latin America continues to require strenuous effort to overcome commercial barriers or high taxes that complicate the acquisition of scientific equipment and supplies crucial to research. Additionally, in some historically neglected areas of research, such as behavioral ecology, the scientific community is small and sparsely distributed within and among countries, making it difficult for researchers to exchange information and to organize themselves into societies with political leverage, both of which are essential for the advancement of knowledge. Environmental laws that are extremely restrictive to researchers, particularly foreigners, also have slowed research in areas such as ecology and systematics by making data collection and international collaboration more difficult. Finally, some cultural barriers remain in various Latin American countries – for example, where members of the scientific community resist publishing their studies in languages other than their own.

We believe that the strong and weak points in this book, along with the taxonomic gaps and oversights in relation to some topics, reflect the current state of knowledge about sexual selection in the Neotropics. We attempted to include the largest possible taxonomic diversity and number of topics in the book, but in many cases we met with lack of information or specialists to contribute to our proposal. Our final list of authors includes researchers that live

in the Neotropics as well as researchers from other regions. All of these, however, have been engaged in research on the neotropical fauna for a considerable number of years, and publish in excellent international journals. Authors were asked to highlight how their studies of neotropical fauna can contribute toward the theoretical and empirical advancement of sexual selection theory. In what follows, we briefly summarize the content of the chapters. We decided to open the book with two general chapters, which encompass broad theoretical issues, and then to structure the remaining contents following a taxonomic order, given the great array of topics presented by authors.

In Chapter 1, Macías-Ordóñez and collaborators provide a theoretical framework to approach the study of sexual selection on a broad geographic scale. They call this approach *macroecology of sexual selection*, formally defined as large-scale influence of climatic conditions on sexually selected traits. Using the Neotropics as a reference, the authors postulate broad predictions concerning the effect of biotic and abiotic factors on the life history, reproductive behavior, and sexually selected traits of arthropods, and ectothermic and endothermic vertebrates. The main goal of this chapter is to show that variation in climatic conditions, in terms of either precipitation or temperature, should be a powerful predictor of sexually selective forces.

Chapter 2 addresses an important conceptual issue in science: our ability to recognize differences between established biological patterns and exceptions. Peretti begins by examining what are rules and exceptions in biology and, particularly, in reproduction. Then he explores the two most important changes that may occur in criteria and concepts within subject areas: when a rule comes to be viewed as an exception, and when something that was considered an exception becomes a rule. Studies of scorpions are used to exemplify these two major changes, and to highlight how new data from neotropical species may provide information to confirm, limit, or refute general rules in sexual selection.

Chapter 3 outlines the contribution of neotropical insects to the study of ecoimmunology – a relatively new field that investigates immunity from an ecological and evolutionary perspective. Contreras-Garduño and Canales Lazcano focus on the importance of pathogen/parasite pressure on the evolution of secondary sexual characteristics, reviewing the available data and discussing how future studies should take into account natural parasite or pathogen infections. The authors also stimulate interpopulation comparisons using neotropical insect species to investigate the existence of possible latitudinal gradients in the intensity of both immune responses and secondary sexual characteristics.

The theoretical ideas proposed in Chapter 1 are revisited in two other chapters, which provide empirical tests for some macroecological predictions related to mating systems. In Chapter 4, Peixoto and Mendoza-Cuenca use butterflies to analyze how the frequency of territorial mating systems and the intensity of male–male competition for access to females may vary according to climate. In Chapter 5, Buzatto and collaborators show that the occurrence of maternal care and the length of the mating season in harvestmen may be

influenced by an interaction between environmental temperature and precipitation, and discuss how these influences may extend to the types of mating systems found in species of the order Opiliones.

Chapters 6, 7, and 8 focus on arthropod species in which males exhibit high reproductive investment, in the form of either exclusive post-ovipositional paternal care or expensive nuptial gifts. In Chapter 6, Aisenberg presents the reproductive ecology of the sand-dwelling wolf spider *Allocosa brasiliensis*, which shows reversal in both the sex roles and the sexual size dimorphism found in most spiders. She discusses hypotheses about the evolution of reversed sexual patterns, and shows how this species provides a unique opportunity to explore the pressures driving sex roles in spiders. In Chapter 7, Albo and collaborators compare the function and evolution of nuptial gifts in two spider species, the neotropical *Paratrechalea ornata* and the palearctic *Pisaura mirabilis*. Although these two species belong to different families and show several differences in their ecology, their reproductive behavior is remarkably similar, suggesting convergent evolution of several sexually selected traits. In Chapter 8, Requena and collaborators review the theoretical background for the evolution of parental investment and sex roles, contrasting classical views with the most recent criticisms and advances proposed by mathematical models. They then introduce the cases in which male arthropods care exclusively for offspring, stressing the contribution of neotropical species to our understanding of the role of paternal care in male attractiveness and in sex role reversal.

Chapters 9 and 10 focus on fish, but their approaches are entirely different. In Chapter 9, Morris and Ríos-Cardenas stress the importance of incorporating selection due to female mate preference and sexual conflict when considering the evolution of alternative reproductive tactics. They use neotropical live-bearing fishes belonging to the genus *Xiphophorus* to investigate some fundamental yet poorly explored questions, such as to what extent one of the alternative tactics relies on the presence of the other to gain reproductive success. In Chapter 10, Macías García explores how the interaction of complex geological history and mode of reproduction may have promoted the diversification of a Mexican fish clade, the Goodeinae. He suggests that viviparity is linked to a consensual method of sperm transfer that allows the evolution of costly male ornaments via female mate choice. Moreover, he argues that both male mating selectivity and female ornamentation provide a mechanism of morphological diversification promoting speciation.

In Chapter 11, Summers and Tumulty discuss the ecology and evolution of parental care in neotropical poison frogs, highlighting how sexual selection may affect and be affected by parental care. Although this chapter focuses on frogs, the theoretical background is analogous to that presented in Chapter 8 for arthropods. In fact, both chapters share a very similar structure, wherein the authors first review relevant theory and then present empirical research on the forms of parental care, stressing their consequences for mating systems and sexual selection. Contrary to the situation for arthropods, however, knowledge

concerning poison frogs has benefited from a large number of field studies, a great amount of naturalistic information available in the literature, and well-resolved phylogenies. The group, therefore, offers unique opportunities to test hypotheses on the evolution of parental care, and the chapter fully explores this subject.

The next four chapters (Chapters 12–15) focus on birds, but emphasize entirely different theoretical and empirical topics. In Chapter 12, Wingfield and collaborators examine hormonal patterns of birds in the Neotropics. Questions surrounding differences in hormonal cycles in birds of the southern versus northern hemispheres have scarcely been explored. Given the differences in the endocrine regulatory systems of birds adapted to northern and southern photoperiods, it is expected that many reproductive and social patterns should be profoundly different. This issue is explored by examining the limited evidence currently available, especially with regard to testosterone production, and in a few better-studied species, such as the rufous-collared sparrow (*Zonotrichia capensis*).

Chapter 13 explores the evolution of vocal signaling in neotropical birds. Podos evaluates whether, and in what ways, the neotropical environment may have shaped patterns of vocal evolution that differ from those known for temperate birds. He examines this question by contrasting vocal behavior and acoustic structure of song of neotropical birds with their temperate counterparts. He ends the chapter by arguing that sexual selection has not operated differently in neotropical versus temperate zone birds. Rather, he suggests that in the Neotropics sexual selection achieves a greater range of outcomes, given the more extensive scale of diversity and interactions among organisms.

Chapters 14 and 15 differ from the two previous ones in that they focus on long-term studies of single species that exhibit remarkable sexual ornamentation and behavior: the long-wattled umbrellabird (*Cephalopterus penduliger*) and the blue-black grassquit (*Volatinia jacarina*). In Chapter 14, Karubian and Durães examine sexual traits from a fresh angle and ask how these may impact interspecific ecological interactions that include predation, parasitism, and mutualistic interactions. They use the long-wattled umbrellabird, a most unusual looking lek-breeding bird, to examine how its mating behavior may be important in seed dispersal in a neotropical forest. They first present a theoretical overview of lekking birds and point out an important difference between lekking species of tropical versus temperate regions: nearly all tropical species are frugivorous, whereas temperate species are primarily granivorous and insectivorous. The rest of the chapter focuses on the demographic and genetic consequences of animal-mediated seed dispersal, and how sexual selection and mating systems, particularly lek-breeding, can influence seed dispersal outcomes. They end the chapter by illustrating these concepts using empirical results from their longstanding study of the long-wattled umbrellabird.

In the last of the four bird chapters, Chapter 15, Manica and collaborators review the evolution of ornaments through sexual selection and examine the

mechanisms that may drive polygamy in the socially monogamous blue-black grassquit. The authors begin by appraising concepts relative to sexual selection in general, and then zoom in on sexual selection and mating systems in birds before finally focusing the discussion on extra-pair paternity in tropical birds. Long-term studies of the blue-black grassquit mating system provide the basis for the various considerations that follow, covering the evolution of sexual ornamentation, ranging from iridescent, UV-based structural plumage to acoustic signals and display behavior.

Finally, in Chapter 16, Voigt reviews case studies of neotropical bats to identify morphological traits and behaviors that have been shaped by sexual selection, and also discusses the possible underlying mechanisms of sexual selection in these specific cases. Each one of the six bat species treated in the chapter sheds light on a specific aspect of sexual selection, such as female mate choice, including the precise sensory modalities used by a species for mate-choice decisions, or mechanisms of male-male competition.

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