

## INTRODUCTION

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This book is a synthesis of recent advances in understanding of the ecological causes and consequences of variation in vertebrate mating systems. Each chapter was first presented as an invited lecture during a workshop of the International School of Ethology, held at the Ettore Majorana Centre for Scientific Culture in Erice, Sicily, in November 1998.

Research on vertebrate mating systems, including the ecological and evolutionary consequences of sexual selection, has made enormous progress over the past 15 years, partly because new ideas and techniques have been applied to observational and experimental field studies. There has been an increased emphasis on long-term monitoring of marked individuals, use of molecular techniques to identify biological parents, application of more realistic mathematical models and either manipulation of environmental variables or observation of the same species in different environments. In addition to a better understanding of the sources of variation in mating systems, ecologists have gained a better appreciation of the pervasive and sometimes unsuspected consequences of that variation for population dynamics, population genetics, morphology and, ultimately, management and conservation of vertebrates. Recent studies have led to substantial progress in both our knowledge of the mating systems of particular species and in the development of new theoretical frameworks that provide testable predictions. In some cases, new techniques, such as molecular identification of parentage, have revealed that commonly-held assumptions were erroneous, for example the belief that behavioural monogamy seen in many species of birds corresponds to genetic monogamy. Evidence of widespread extrapair and multiple paternity has forced a re-evaluation of theories of mate choice, sexual conflict, parental care and population genetics. Molecular techniques have also allowed researchers to quantify male reproductive success in species where it could not be estimated from behavioural observations alone, such as some phocids and ungulates. More recently, much interest in the study

of mating systems has been generated by the realisation of relevance to conservation: differences in mating systems can affect population genetics, age- and sex-specific mortality rates and density-dependence in population dynamics, all areas of great importance in the conservation of endangered species and management of vertebrate populations exploited by humans.

When we organized this workshop, it was therefore apparent to us that the study of vertebrate mating systems was entering a new phase. In addition to continuing to search for the proximate and ultimate causes of variation, many researchers were asking questions related to the consequences of variation in mating systems for other aspects of biology. We wished to convene a workshop to bring together active researchers who specialized on different taxa and employed very different approaches to the study of vertebrate mating systems. Rather than searching for an explanation of the diversity of mating systems, we requested authors to reflect on the consequences of that diversity. Each invited speaker provided a synthesis of how mating systems may affect a particular aspect of ecology, behaviour, conservation or population genetics. While many authors presented some of their own research, in all cases we asked them to underline the general relevance of their work and to speculate on future directions of scientific inquiry. The goal of this book is therefore to review the relationship of mating systems with other aspects of vertebrate biology, rather than to systematically analyse the mating systems adopted by various vertebrates. We chose to focus on how mating systems affect morphology, demography, genetics, parental care and conservation and included an examination of how changes in the environment affect mating systems. Many authors provide evidence of the importance of knowledge of mating systems for conservation of species and populations. This book presents stimulating new perspectives and ideas for the future of mating systems studies.

In the introductory first chapter, Haven Wiley explores three widely-applied models of sexual selection and provides a general framework for subsequent chapters. Wiley emphasizes the importance of a reliable signalling system and explores how the trade-offs faced by receivers of signals may affect the evolution of responses in a mate-assessment context.

The following section of the book deals with morphology and sexual selection, a subject where different researchers hold contrasting views and is tackled in chapters by Rauno Alatalo and Jacob Höglund. Alatalo explores the evolution of female choice for indirect benefits that are expressed only in the following generation. Two major theories have been proposed to explain indirect mate selection; the "Fisherian runaway process" and the "good genes hypothesis". Each theory has enjoyed considerable success during different periods. The rise and fall of these theories in the scientific literature is an example of classic Kuhnian paradigm shift: regardless of which theory was "dominant" at a given time, most empirical studies provided results that were interpreted as supporting the more popular theory of the day. The chapter examines some of the possible causes of this situation, focusing on the relationship between sample size and effect size in published studies. Alatalo concludes with a warning against widespread publication bias in favour of positive results and dominant theories in evolutionary research. Höglund then presents an example of the importance of interspecific analyses to study evolution of sexual dimorphism. Using lekking birds as a model, he shows that development of sexual dimorphism and sexual dichromatism is not necessarily associated with highly polygynous systems. He then examines five alternative explanations of this unexpected result, ranging from the limitations of the comparative method and the intensity of sexual selection on leks to divergent evolutionary histories of different species. The chapter concludes with an appeal for a balanced approach to the study of interspecific variation, which incorporates both the relevance of phylogeny and the importance of local adaptations.

The third part of the book links mating systems with demography. David Mc Donald illustrates the use of stage-classified matrix population models to analyse demographic consequences of variation in mating systems. After a brief introduction where the basic elements and assumptions of the technique are clearly explained, he uses three contrasting case studies (Florida scrub-jays, sage grouse and long-tailed manakins) to show how this method can identify which vital rates have the greatest effect on population growth rate. His analyses suggest that critical vital rates are directly related to differences in mating systems. This chapter clearly illustrates the importance of information on mating systems to formulate sustainable policies for consumptive use of wildlife and protection of endangered species.

The fourth section reverts to a more classical approach to the study of mating systems because it is mostly concerned with how differences in the environment affect the type of mating system seen in different populations of the same or related species. Two authors contributed to this section: Juan Carranza examines research on endotherms and Mandy Dyson research on ectotherms. This taxonomic subdivision was justified by the very different influences that environmental variables can have on vertebrates differing in type or metabolism. Carranza suggests that much of the interspecific and intraspecific variation in mating systems of mammals and birds can be related to environmental factors, using examples from his study on red deer mating behaviour to illustrate his ideas. It is well known that the distribution of resources in the environment affects female distribution, which in turn affects the reproductive strategy of males and therefore the mating system of a population (Clutton-Brock 1989). Carranza takes the argument one step further and explores how human alterations of the environment, including some modifications specifically intended for wildlife management (such as fencing and artificial feeding), can affect the degree of polygyny in ungulates. Sometimes the ecological and genetic consequences are opposite to those desired by wildlife managers. Carranza's chapter, therefore, provides another key example of how knowledge of the behaviour of individuals can assist the management of exploited wildlife populations. Clearly, one important message of this chapter, that was heard repeatedly throughout the workshop, is that wildlife managers should not limit themselves to counting animals: individual differences in behaviour can have important effects on population growth rate and genetic variability. The chapter concludes with a consideration of the effect of environmental variation on sexual selection. Dyson starts from the classical framework proposed by Emlen and Oring (1977) to discuss how environmental variations can influence ectotherm mating systems. In ectotherms, the major environmental factors affecting operational sex ratio and potential reproductive rate are temperature, food availability and nesting sites. These factors can determine duration of paternal care because there is a fitness trade-off between caring for offspring and competing for mates. Changes in environmental variables, together with density of potential mates and risk of predation, can also affect the fitness trade-offs of mate choice and in some cases, environmental variables may limit the ability of both sexes to choose among potential mates.

The relationship between mating systems and parental care is explored in the fifth section of the book. First, Tamas Szekely, James Webb and Innes Cuthill together argue for an integrated approach to the study of mating patterns, mating opportunities and parental care. They suggest that because there are feedback relationships linking mating strategies, mating opportunities and parental care strategies, these three aspects of reproductive behaviour cannot be considered in isolation. They present a framework linking mating behaviour and parental care and analyse each element of this framework using a dynamic game approach. The chapter concludes with an examination of the need to include realistic life-history trade-offs in models. Relevant trade-offs vary among species and cannot be simply inferred or imagined: field data must be the foundation of any modelling approach that aims to advance scientific knowledge rather than simply generate more theoretical models.

Although the relationship between mating systems and conservation are considered in several of the chapters, it is the specific focus of the two chapters in the sixth part of the book. Philip Stevens and Bill Sutherland focus on the many and sometimes unsuspected roles of Allee effects, those situations where the presence of conspecifics can provide a fitness benefit to individuals, rather than the more usual competitive situation. Stevens and Sutherland first examine reciprocity between Allee effects and mating systems, then explore how Allee effects on mating systems can affect the ecology of different species in ways that bear directly on conservation. The authors suggest that there are three areas of conservation biology in which an understanding of mating systems is crucial: management of exploited species, avoidance of genetic pollution and hybridization and planning of reintroductions and captive breeding programs. In the next chapter, Jack Hogg approaches mating systems and conservation from the perspective of long-term field research on native populations of exploited ungulates. The chapter begins with a general synthesis of how mating system studies can contribute to population genetics, population ecology and population viability analysis, all subjects of great importance to the conservation of biodiversity. Hogg then goes on to consider the use of behavioural observation and molecular techniques to estimate effective population size. Finally, he shows how a male's choice of where to breed varies according to social status and distribution of competitors within a metapopulation of bighorn sheep. Because trophy hunting before the rut

removes many of the largest rams, average competitive ability of rams alive at the beginning of the rut is lower in hunted than in protected areas. As a result, there is net genetic emigration from protected areas, possibly leading to a loss of genetic diversity over the long term. This chapter raises important questions about the genetic consequences of a patchwork of different wildlife management regimes over a landscape.

The last section of the book deals with mating systems and genetics, another subject that is also considered in previous chapters. The contributions by David Westneat on the role of genetics in mating systems and by Peter Boag and Laurene Ratcliffe on the genetics of avian mating systems consider in detail this important subject. It is unquestionable that recent developments in molecular genetic techniques have substantially accelerated the progress of our understanding of vertebrate mating systems. Westneat begins with a personal view of the history of how our understanding of mating patterns has been revolutionized by the use of molecular markers: the distribution of genetic parentage can be very different from the impression one may have from watching behavioural interactions. The ability to identify parentage through molecular markers has allowed a much greater understanding of evolution of reproductive strategies, relationships between behavioural and genetic paternity and paternal care, strength of sexual selection and ecology of mating patterns, including a better appreciation of sexual conflict. The chapter concludes with several pertinent suggestions on how future studies of mating systems could take advantage of the wide range of molecular tools available to measure individual reproductive success. The final chapter, by Boag and Ratcliffe, details the use and limits of genetic tools for parentage analysis, paying particular attention to recent developments in the identification of multiple and extra-pair paternity. The authors review the advantages and disadvantages of the two more common methods used to identify paternity: microsatellites and multilocus DNA fingerprinting, and go on to consider two examples of practical difficulties that can be encountered in studies of reproductive success in birds with very complex (and until recently unsuspected) mating systems. In tree swallows, extra-pair copulations are so widespread that it is extremely difficult to assign parentage without extensive sampling of many individuals over a wide area. The second example on two species of cooperatively breeding Australian Miners, illustrates the limits of our current ability to assess parentage when potential parents are relatives. Boag and Ratcliffe then

examine some of the assumptions of the most common genetic explanations for mate choice (good genes, heterozygosity, genetic diversity and genetic compatibility) and review recent studies testing these assumptions. Like many other contributors to this book, they conclude with a reminder of the need for rigorous field studies, to provide detailed knowledge of the natural history of the species that is being examined in the light of mating systems. Although the application of recent developments in technical and modelling tools has allowed great progress in our understanding of vertebrate mating systems, we suggest that much of the future progress will continue to depend primarily on intensive, long-term field studies of marked individuals.

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