MATE CHOICE

Edited by

PATRICK BATESON

Reader in Animal Behaviour and
Director of the Sub-Department of Animal Behaviour
Department of Zoology, University of Cambridge

CAMBRIDGE UNIVERSITY PRESS
Cambridge
London New York New Rochelle
Melbourne Sydney
# CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>Introduction</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>T.R. Halliday             The study of mate choice</td>
<td>3</td>
</tr>
<tr>
<td>2</td>
<td>Wolfgang Wickler and Uta Seibt Monogamy: an ambiguous concept</td>
<td>33</td>
</tr>
<tr>
<td>II</td>
<td>Characteristics of sexual selection</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Peter O'Donald           Sexual selection by female choice</td>
<td>53</td>
</tr>
<tr>
<td>4</td>
<td>Stevan J. Arnold         Sexual selection: the interface of theory and empiricism</td>
<td>67</td>
</tr>
<tr>
<td>5</td>
<td>Jack W. Bradbury and Robert M. Gibson Leks and mate choice</td>
<td>109</td>
</tr>
<tr>
<td>III</td>
<td>Sex differences in choosiness</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>G.A. Parker               Mate quality and mating decisions</td>
<td>141</td>
</tr>
<tr>
<td>7</td>
<td>Marion Petrie             Mate choice in role-reversed species</td>
<td>167</td>
</tr>
<tr>
<td>8</td>
<td>Anthony AraK              Male–male competition and mate choice in anuran amphibians</td>
<td>181</td>
</tr>
<tr>
<td>9</td>
<td>Diana J. Bell             Mate choice in the European Rabbit</td>
<td>211</td>
</tr>
<tr>
<td>IV</td>
<td>Non-random mating</td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>Linda Partridge           Non-random mating and offspring fitness</td>
<td>227</td>
</tr>
<tr>
<td>11</td>
<td>Patrick Bateson           Optimal outbreeding</td>
<td>257</td>
</tr>
<tr>
<td>12</td>
<td>F. Cooke and J. C. Davies  Assortative mating, mate choice and reproductive fitness in Snow Geese</td>
<td>279</td>
</tr>
<tr>
<td>13</td>
<td>Diane M. Williams         Mate choice in the Mallard</td>
<td>297</td>
</tr>
<tr>
<td>14</td>
<td>Bruno D'Udine and Enrico Alleva Early experience and sexual preferences in rodents</td>
<td>311</td>
</tr>
<tr>
<td>V</td>
<td>Compatibility of mates</td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>Ian Rowley                Re-mating in birds</td>
<td>331</td>
</tr>
<tr>
<td>16</td>
<td>J.C. Coulson and C.S. Thomas Mate choice in the Kittiwake Gull</td>
<td>361</td>
</tr>
</tbody>
</table>
Contents

I Mate choice in humans as an interpersonal process

17 STEVE DUCK AND DOROTHY MIELL Mate choice in humans as an interpersonal process 377

VI Hormonal mechanisms

18 J. B. HUTCHISON AND R. E. HUTCHISON Hormonal mechanisms of mate choice in birds 389

19 ERIC B. KEVERNE Endocrine determinants and constraints on sexual behaviour in monkeys 407

VII Decision rules

20 R. I. M. DUNBAR Life history tactics and alternative strategies of reproduction 423

21 JAMES F. WITTENBERGER Tactics of mate choice 435

Index 449
CONTRIBUTORS

Enrico Alleva, Consiglio Nazionale delle Ricerche, Laboratorio di Psicobiologia e Psicofarmacologia, Via Reno, 1, 00198 Roma, Italy
Anthony Arak, Department of Zoology, Downing Street, Cambridge CB2 3EJ, UK
Stevan J. Arnold, Department of Biology, University of Chicago, 1103 East 57th Street, Chicago, Illinois 60637, USA
Patrick Bateson, Sub-Department of Animal Behaviour, High Street, Madingley, Cambridge, CB3 8AA, UK
Diana J. Bell, School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK
Jack W. Bradbury, Department of Biology, C-016, University of California, La Jolla, California 92093, USA
F. Cooke, Department of Biology, Queen's University, Kingston, Canada K7L 3N6
J. C. Coulson, Department of Zoology, University of Durham, Science Laboratories, South Road, Durham DH1 3LE, UK
J. C. Davies, Department of Biology, Queen's University, Kingston, Canada K7L 3N6
Steve Duck, Department of Psychology, Fylde College, Bailrigg, Lancaster LA1 4YF, UK
Bruno D'Udine, Consiglio Nazionale delle Ricerche, Laboratorio di Psicobiologia e Psicofarmacologia, Via Reno, 1, 00198 Roma, Italy
R. I. M. Dunbar, Sub-Department of Animal Behaviour, High Street, Madingley, Cambridge CB3 8AA, UK
Robert M. Gibson, Department of Biology, C-016, University of California, La Jolla, California 92093, USA
T. R. Halliday, Department of Biology, The Open University, Walton Hall, Milton Keynes MK7 6AA, UK
J. B. Hutchison, M.R.C. Unit on The Development and Integration of Behaviour, Sub-Department of Animal Behaviour, High Street, Madingley, Cambridge CB3 8AA, UK
Contributors

R. E. Hutchison, Sub-Department of Animal Behaviour, High Street, Madingley, Cambridge CB3 8AA, UK

Eric B. Keverne, Department of Anatomy, Downing Street, Cambridge CB2 3DY, UK

Dorothy Miell, Department of Psychology, Fylde College, Bailrigg, Lancaster LA1 4YF, UK

Peter O'Donald, Department of Genetics, Downing Street, Cambridge CB2 3EH, UK

G. A. Parker, Department of Zoology, University of Liverpool, Brownlow Street, P.O. Box 147, Liverpool L69 3BX, UK

Linda Partridge, Department of Zoology, University of Edinburgh, West Mains Road, Edinburgh EH9 3JT, UK

Marion Petrie, School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK

Ian Rowley, CSIRO, Division of Wildlife, Clayton Road, Helena Valley, via Midland, Western Australia 6056

Uta Seibt, Max-Planck-Institut für Verhaltenphysiologie, D-8131, Seewiesen, W. Germany

C. S. Thomas, Department of Zoology, University of Durham, Science Laboratories, South Road, Durham DH1 3LE, UK

Wolfgang Wickler, Max-Planck-Institut für Verhaltenphysiologie, D-8131, Seewiesen, W. Germany

Diane M. Williams, 156 Queens Road, Yardley, Birmingham B26 2AJ, UK

James F. Wittenburger, Department of Zoology NJ-15, University of Washington, Seattle, Washington, 98195, USA
PREFACE

This book arose from a conference held by the Association for the Study of Animal Behaviour in Cambridge in July 1981. However, the book is emphatically not a set of conference proceedings. Some chapters were specially commissioned and contributors to both conference and book re-wrote their papers as surveys rather than as presentations of new data. The attempt has been to give a clear picture of the current state of the subject. Furthermore, wherever it was possible (and relevant), the chapters have been linked together so that, even when authors disagree, the reader will be aware of the areas of overlap.

The growing interest in mating preferences in animals has been generated in part by the renewed vitality of evolutionary biology. A characteristic that successfully attracts a member of the opposite sex might become increasingly common in the population simply because it is likely to be transmitted to offspring which in turn may be better than others at winning mates. This evolutionary process, which is a part of what is called sexual selection, could be an important source of genetic change. Even though sexual selection is uppermost in many minds, what animals actually do must not be confused with the hypothetical evolutionary process. When the term ‘mate selection’ is used for what animals do, it can quickly lead to unconscious punning and the assumption that a preference for a particular kind of mate necessarily has implications for sexual selection. As will become plain, the assumption is false. For these reasons, the immediate outcome of an animal’s mating preference is consistently referred to in this book as ‘mate choice’, ‘sexual selection’ is used for an evolutionary process and ‘mate selection’ is dropped.

Anybody who is at all unfamiliar with the subject would do well to start reading the book at the beginning. In Chapter 1 Halliday provides an essential curtain-raiser for what follows. He reviews the major issues which
Preface

recur throughout the book and points to both the possibilities and the difficulties of testing some of the current theories about mate choice. As in many rapidly expanding subjects, the concepts have been inadequately defined and are liable to generate considerable confusion. The trouble has arisen in part because interests in mate choice and mating systems have converged from a number of quite different directions. The point is brought out well by Wickler & Seibt who, in Chapter 2, show how ‘monogamy’ had quite different origins in the social sciences, evolutionary biology and population genetics. Much muddle, disagreement and inconsistency could be avoided if the different meanings were clearly recognised.

The second part of the book is devoted to the evolutionary process of sexual selection and how it might work. In Chapter 3 O’Donald summarises succinctly the results of his computer simulations and recent thinking. He criticises the widely held view derived from R. A. Fisher that sexual selection has a runaway character to it. In other words, he does not believe that once a choosy female mates preferentially with a male bearing a particular character, that character must necessarily grow in size or conspicuousness in subsequent generations at a geometric rate. The view of another modern theorist, Lande, is summarised and made understandable to a non-mathematical audience by Arnold in Chapter 4. Lande’s modelling approach is very different from O’Donald’s and leads him to re-affirm that Fisher’s runaway evolutionary process could have occurred sometimes. However, Lande’s work also suggests that under certain conditions, equilibria are to be expected. If and when they occur, the frequency of females with a preference for a particular kind of male and the frequency of that type of male have both stabilised.

All the evolutionary theorists are concerned about the interplay between sexual and natural selection pressures. In the second part of his chapter Arnold provides a method for distinguishing between current pressures due to sexual selection and those due to natural selection. This method does not provide any solution to the problem of what has happened in the past in a particular case, but could provide an indication as to what will happen in the future. The need to provide good ways of distinguishing between rival hypotheses is the major message of Bradbury & Gibson’s contribution in Chapter 5. They consider the phenomena of leks which are assemblies of adult males visited by females solely for the purpose of copulation. Leks have been treated as classic examples of male competition and female choice. Bradbury & Gibson see the promise of using leks for testing controversial ideas about males being chosen on the basis of cues that
Preface

indicate the adaptedness of the male. However, they point to the many factors that can complicate the interpretation of such tests.

The third part of the book on sex differences in choosiness is closely linked to the second and many of the contributors start from the position which is commonly held in the sexual selection literature, that males compete with each other for opportunities to mate with females, and females choose their mates. In Chapter 6 Parker presents several theoretical grounds for doubting the generality of this conclusion, and shows that a variety of possibilities is evolutionarily stable. He also argues strongly against the notion that choice by either sex is made on the basis of qualities that are likely to be transmitted genetically to offspring. Petrie takes a different view in Chapter 7, suggesting a number of circumstances in which female choice of mates on the basis of genetically transmitted quality could be maintained in the population. She goes on to consider the conditions in which the male might become the choosy sex, but agrees with one of Parker's points when she notes that male choosiness is not exclusively found in polyandrous species.

The next two chapters are more empirical in character and review what is known to happen during the mating of respectively anuran amphibians and rabbits. The frogs and toads have proved a particularly rich source of material for studies of mate choice. Arak's survey in Chapter 8 provides ample evidence for major differences between the sexes in terms of competition and choosiness. However, he also underscores the point that many pressures have probably contributed to the evolution of the observed behaviour and, like Bradbury & Gibson, he argues against squeezing everything into the framework of a theory about sexual selection. A very similar point emerges from Bell's survey of mate choice in the rabbit in Chapter 9. She notes that while female 'choice' in this species is primarily determined by intrasexual competition for warren littering sites, females do nonetheless prefer the odour of socially dominant males in laboratory tests.

Part III of the book is concerned with non-random mating and the evolutionary and developmental processes that lead to preferences for particular kinds of mates. These chapters provide direct evidence for mating preferences in both sexes. They also provide examples of mating preferences, such as those for non-siblings, that are very unlikely to facilitate sexual selection and may sometimes oppose it. In Chapter 10 Partridge leads off with a general discussion of the ways in which offspring fitness can be enhanced by non-random mating. Many of her examples are
xii  Preface

taken from studies of the fruitfly, but her points can be usefully
generalised to other species. She stresses the advantage of avoiding
inbreeding and also points to the value of assortative mating where it
maintains local adaptations. I take up this point on the balance between
inbreeding and outbreeding in Chapter 11 and suggest a sharply-tuned
preference might be required. I go on to ask how an animal might be able
to recognise an optimally related mate and conclude that early experience
with close kin is frequently essential for developing mating preferences for
individuals that are related by an optimal amount. Cooke & Davies
provide support for part of this conclusion from their long-term study of
the polymorphic Snow Goose in Chapter 12. The geese generally mate with
the morphs which have the same colour as themselves but can be fooled
when reared by foster-parents of a different colour. However, Cooke &
Davies fail to find any reduction of fitness in the offspring when different
morphs mate with each other. Even so, they do not altogether rule out the
possibility that fine tuning of its preference could enable a bird to choose
the partner that would maximise its reproductive success.

Williams reviews the evidence from another wildfowl species, the
Mallard, in Chapter 13. Here again, early experience plays an important
role in influencing the mating preference – but only in the male. The
females' preferences for males are much less obviously influenced by
learning in ontogeny and are strongly influenced during courtship by the
condition of the male plumage, a point which ties her chapter in with
Parker's and Petrie's discussions of mate quality. The important influence
of early experience emerges once more in the review of rodents' sexual
preferences by D'Udine & Alleva in Chapter 14. The evidence also
indicates the subtle and complex interactions which can occur between
learning and other ontogenetic processes that influence sexual preferences.
As with evolutionary processes, a question about developmental influences
on mate choice does not reduce conveniently to a single answer.

Learning about close kin and choosing mates that are a bit different
provides a way of obtaining the best genetic mix for the offspring.
However, compatibility between mates also operates at a behavioural level,
particularly in monogamous species in which both sexes care for the young.
In such cases, successful behavioural meshing of mates can crucially
influence whether or not the young are adequately looked after. Part V
raises some of these issues of compatibility. Long-term monogamous
pair-bonds are particularly common in birds. Rowley provides, in Chapter
15, a thorough review of this phenomenon and of what precedes and
follows the break-up of a pair-bond. A pair often becomes separated
outside the breeding season, but Rowley argues that there is usually considerable value in re-mating with the same individual. However, a new partner may be sought if the old one was incompatible. Some of the evidence for this view comes from the long-term studies of Coulson and his co-workers on the Kittiwake, summarised in Chapter 16. They find that ‘divorce’ is correlated with failure to breed successfully in the previous year which, in turn, is likely to be associated with incompatibility of the pairs particularly during incubation of their eggs. Coulson & Thomas also find that breeding success increases in birds that retain their mate for the previous year. This suggests that, in some long-lived species at least, the achievement of compatibility is not just a matter of initial choice but is also a consequence of experience with a partner.

Chapter 17 by Duck & Miell is the only one written explicitly about humans, and is the only one written by non-biologists. They are concerned to show that friendships, sexual as well as non-sexual, are not simply determined by initial attraction. The level at which judgements are made about whether or not a person is or is not a friend, deepens as he or she becomes more familiar. This occurs as a result of the transactions taking place with that person. Although it is easy to be glib about such comparisons, there does seem to be considerable value in linking Duck & Miell’s conclusions to those of Rowley and Coulson & Thomas.

The two chapters in Part VI are markedly different in character from all the others in the book in as much as they deal with the internal control of mate choice. While this book is primarily concerned with behaviour and not with underlying mechanisms, it seemed important that something should be included about the role of sex hormones. These play a fundamental role both in inducing the development of sexual behaviour and also as integrating agents that hold the sexual repertoire together. In their chapter, the Hutchisons show that androgen in adult male birds is directly involved with the expression of a learnt preference for a particular type of female. They go on to argue that changing levels of androgen and its metabolites during courtship facilitate the processes of assessment and synchronisation during courtship. In Chapter 19 Keverne deals with the involvement of sex and stress hormones in the mating behaviour of monkeys. He considers the ways in which hormonal levels and social status interact. Both play their part in influencing the sexual attractiveness of males and females. For the would-be reductionist, Keverne’s analysis is salutary because what might seem an obvious index of mating quality (testosterone in the case of males and oestrogen in the case of females) cannot be used on its own.
xiv  Preface

A final change of direction occurs in the last part of the book. This part deals with the kinds of decisions an animal must take in relation both to the long-term mating strategy that it should adopt in the environmental and social conditions in which it finds itself, and to short-term tactics. Should it plump for the member of the opposite sex in front of it or wait for another which might prove even more satisfactory? Dunbar considers alternative mating strategies in Chapter 20. He develops points alluded to by both Bradbury & Gibson and Arak earlier in the book. It is particularly obvious in leks that it is not only the vigorously displaying males that copulate successfully. Other males adopt a very different mode of behaviour, quietly sneaking copulations without any explicit competitions with other males. Since reproductive success is determined by many components, an individual can trade losses on one component such as rate of mating against gains on another such as length of reproductive life which may be greater in uncompetitive males. Dunbar makes the point that alternative reproductive strategies that yield comparable net gains are possible.

Wittenberger in Chapter 21, concludes the book by considering the tactics of mate choice. Ideally, a mate should be maximally attractive, optimally related, highly fertile or fecund, a holder of valuable resources, and so forth. In practice, he or she is unlikely to combine all these qualities. Even in the simplest situation where all the likely potential mates are available, the chooser must be equipped with rules for deciding on the relative weight that should be given to each independent set of characteristics, such as a set based on kinship and a set based on physical well-being. The problem becomes more complex when the potential mates are not available simultaneously and mating with one reduces the likelihood of mating with another. It is a familiar enough human dilemma. A better possibility (pub, picnic site or petrol pump) might be found round the next corner. Fortunately it is not a problem which defies solution and Wittenberger points the way to how animals might solve it in the case of choosing a mate.

While many people are interested in mate choice because of its relevance to sexual selection, it will be obvious from the contents of the book that interest in the subject has also arisen for quite other reasons. For instance, the problems of how particular preferences develop in an individual's lifetime are logically distinct from the evolutionary issues. Nonetheless, it becomes apparent that when a coherent topic like mate choice is examined in different ways, the various approaches to it can help each other. The value of evolutionary theory as a cohesive force, even in areas of biology that are not directly concerned with problems of evolution, is well known.
Preface

But the evolutionary biologist can also benefit from contact with people working on problems of development and control. A familiar criticism directed at theories of evolution is that they are not amenable to testing because history cannot be replayed. Some of this criticism is scientifically illiterate since the theories and the comparative approach they encourage have certainly brought order to the existing material in all its astonishing diversity.

Furthermore, even in a non-experimental subject, theory can offer guidance on where to gather fresh evidence and, quite properly, can be embarrassed by the collecting of such evidence. It is in this respect that contact with other biologists can be helpful to the evolutionary theorists. The relevant and sometimes embarrassing evidence may have already been collected. More importantly, different perspectives contributed by each specialist inevitably provide a more complete picture of the requirements of the whole animal than is obtained by any one view.

My sense is that the various approaches to mate choice are combining in important and valuable ways. As a result, the face of the subject is changing rapidly and, as with a developing embryo, its various features are more easily distinguished. If this book contributes to these processes of growth and differentiation, it will have served its purpose.

Patrick Bateson

Cambridge, May 1982