The Mandrill

A Case of Extreme Sexual Selection

Living in the remote forests of western central Africa, the mandrill (*Mandrillus sphinx*) is notoriously elusive and has evaded scientific scrutiny for decades. Yet, it is the largest and most sexually dimorphic of all the Old World monkeys, and perhaps the most colourful of all the mammals.

Synthesizing the results of more than 25 years of research, this is the first extensive treatment of the mandrill's reproductive and behavioural biology. Dixson explores in detail the role that sexual selection has played in shaping the mandrill's evolution, covering mechanisms of mate choice, intra-sexual competition, sperm competition and cryptic female choice. Bringing to life, through detailed descriptions and rich illustrations, the mandrill's communicatory biology and the functions of its brightly coloured adornments, this book sheds new light on the evolutionary biology of this fascinating primate.

Alan F. Dixson is a Professor in the School of Biological Sciences at Victoria University of Wellington, New Zealand. He is a world authority on the reproductive biology and evolution of sexuality in primates. During a distinguished career, he has held posts at the Zoological Society of London, Medical Research Council UK, International Medical Research Centre in Gabon, Sub-Department of Animal Behaviour, University of Cambridge and the Zoological Society of San Diego.

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To Amanda

And at home by the fire,

whenever you look up there I shall be –

and whenever I look up, there will be you.

Thomas Hardy *(Far from the Madding Crowd)*

Contents

The colour plate section appears between pages 112 and 113.

Preface

I am a kind of farthing dip, unfriendly to the nose and eyes.
A blue-behinded ape I skip, upon the trees of paradise.

Robert Louis Stevenson

Despite its great size, and colourful secondary sexual adornments, the behavioural biology of the mandrill (*Mandrillus sphinx*) remained shrouded in mystery until comparatively recently. It has given me much pleasure to study the behaviour and reproductive biology of mandrills in Gabon, and to supervise a number of research students who have helped to advance those studies. Indeed, I am indebted to a number of people who made the writing of this book possible. The late Dr Georges Roelants invited me to work at the International Medical Research Centre (CIRMF) in Gabon, and to direct research at its Primate Centre between the years 1989 and 1992. Dr Jean Wickings carried out all the genetic studies and hormone assay work on the mandrills during those years; these contributions were of vital importance. Two research students from the University of Zurich, Thomas Bossi (co-supervised with Professor Bob Martin) and Edi Frei (co-supervised with the late Professor Hans Kummer), helped to study the sexual behaviour and social organization of the mandrill. In later years, after I had returned to the UK to work at the Sub-Department of Animal Behaviour (University of Cambridge), Joanna Setchell joined our group as a PhD student, in order to research the socio-sexual development of male mandrills. After successfully completing her PhD, Jo Setchell continued to work on the mandrill groups at the CIRMF; her research publications, and those of her colleagues, have been of immense value to me.

The drill (*Mandrillus leucophaeus*) is even less well studied than the mandrill, but it is impossible to understand the evolutionary history of the genus *Mandrillus* without considering both these species. Thus, during six years spent in the USA, as Director of Conservation and Science for the Zoological Society of San Diego, I took the opportunity to initiate fieldwork on drills in Cameroon. In this regard, I owe a special debt of gratitude to Dr Bethan Morgan for her tireless efforts to gather data on free-ranging drills, and to Chris Wild who managed field operations in Cameroon from 2000 to 2005.

I should like to thank Martin Griffiths (formerly of Cambridge University Press), Katrina Halliday (Publisher: *Life Sciences*) and Megan Waddington (Editor: *Life Sciences*) for their encouragement and advice during the planning and production of this book. Dr Aimée Komugabe made many of the figures and maps, and she has done an outstanding job. Sincere thanks also go to Dr Jeanette Mitchell, who copy- edited the entire manuscript, and to Susan Leech for the great care she has taken in creating the index.

I am indebted to senior colleagues at Victoria University of Wellington, and especially to Professor Charles Daugherty and Professor David Bibby, who encouraged me to join the School of Biology in 2006. Since that time, I have enjoyed a positive intellectual environment in which to write research papers and books, as well as teaching undergraduates about the mysteries of human evolution and reproduction.

Writing a book is, by its very nature, a protracted and largely solitary process. However, I never feel alone, and this is entirely due to the strong support I receive from my family. My heartfelt thanks go especially to my wife Amanda, to our sons Alexander, Barny and Henry, and our daughter Charis.

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Professor Alan Dixson
Sandwalk
Paraparaumu Beach
New Zealand

Prologue

Among the mammals, sexual selection has sometimes resulted in the evolution of extreme sex differences in body size, weaponry and secondary sexual adornments. Nowhere is this observation more apposite than in the case of the mandrill (*Mandrillus sphinx*), as it offers numerous examples of the effects of sexual selection, especially in adult males. At over 30 kilogrammes in weight, the mature male mandrill is the largest of all the Old World monkeys, and it is more than three times the size of the adult female. The male's enormous jaws are equipped with long, dagger-like canine teeth, notably in the upper jaw. Most extraordinary, however, is the mandrill's colouration. Adult males of this species display large areas of bright blue and red skin (the so-called 'sexual skin') on the face, rump and genitalia. As young males transition to sexual maturity, boney paranasal swellings enlarge on each side of the snout, and cobalt blue sexual skin overlies these swellings in a series of ridges, flanking the scarlet mid-nasal strip and fleshy tip of the nose. Add to these extraordinary secondary sexual traits the possession of a yellow beard, a crest of hair on the scalp and nape of the neck, a mane, a large sternal cutaneous gland and marked enlargement of the colourful rump owing to deposition of fat, and the male mandrill ranks as the most visually striking of all primate species. Although adult female mandrills are certainly much less brightly coloured than the males, they are not lacking in secondary sexual adornments. Thus, there is a female sexual skin covering the perineal and genital areas, and this undergoes marked changes in swelling and colouration during the menstrual cycle.

Biologists have long speculated as to why the mandrill should exhibit such an extreme expression of so many sexually dimorphic traits. When Charles Darwin (1871, 1876) was formulating his ideas concerning evolution by sexual selection, he observed that 'no other member in the whole class of mammals is coloured in so extraordinary a manner as the adult male mandrill'. Darwin regarded the male mandrill as the mammalian equivalent of the peacock, suggesting that its bright colouration had also evolved to 'serve as a sexual ornament and attraction' to females. In Darwin's opinion, the mandrill's colours were thus the products of inter-sexual selection, via female choice, the most attractive males being likely to gain a reproductive advantage by achieving more matings and siring more offspring than less colourful individuals. However, he also noted that 'with mammals the male appears to win the female much more through the law of battle than through the display of his charms'. Thus, the male mandrill's great size and impressive canine teeth might represent the outcome of intra-sexual selection owing to aggressive competition between males for access to mates.

These tentative explanations left unresolved the question of why inter-sexual and intra-sexual selection should have operated in such an extreme fashion in males of this particular primate species. Why should female mandrills also display attractive cues in the form of their sexual skin swellings? A resolution of these problems, and many other questions concerning the mandrill's evolution, requires a detailed knowledge of its ecology and behaviour, social organization, mating system and reproductive biology. How is the sexual behaviour of this species organized, and what governs sexual attractiveness and mate choice? What is the nature of dominance relationships between males and between females? What environmental factors determine the mandrill's social behaviour and the changing composition of its unusual supergroups and subgroups? Exploration of the mechanisms governing sexual selection and reproductive success in the mandrill is of intrinsic interest, as it helps us to understand the biology of this spectacular animal. Moreover, studies of the mandrill will certainly contribute to our wider understanding of how sexual selection operates in other mammals.

Unfortunately, in Darwin's time, almost nothing was known about these matters. Indeed, the natural life of mandrills, within the remote forests of western central Africa, has not been studied until comparatively recently. Super-groups of these magnificent monkeys, numbering as many as 800 individuals, traverse vast areas within the rain-forested interior of Gabon. They travel rapidly on the ground, but frequently take to the trees during daily foraging and in order to seek refuge at night. Hordes also split into smaller subgroups, and for a long time it was assumed that these might represent polygynous one-male units, such as those that occur in geladas and hamadryas baboons. As we shall see in later chapters of this book, such assumptions arose in the absence of detailed information about the mandrill's behaviour and reproductive biology. So difficult are these monkeys to locate and observe in the wild that it is not surprising that the true nature of their behaviour and ecology has evaded scientific scrutiny for so long.

During the 1960s and 1970s, primate field studies were undergoing something of a renaissance. Detailed field investigations of the African and Asian apes, as well as of various monkey species, Malagasy lemurs and other prosimians, were initiated during those two decades. It was an exciting time, and books and journals began to appear devoted to the field of 'Primatology'. Yet, the mandrill (*Mandrillus sphinx*) and its close relative the drill (*M. leucophaeus*) remained unstudied and relatively unknown. Both species were thought of as 'forest baboons', and as such they were assumed to be similar in many ways to the well-studied savannah baboons (*Papio* spp.). John and Prue Napier (1967) had published their *Handbook of Living Primates*, which provided scholars with a valuable guide to current knowledge of the prosimians, monkeys and apes. However, readers of the *Handbook* were informed that 'information on drills and mandrills in the wild is wholly anecdotal'.

This declaration of ignorance of mandrill field biology did not discourage me as a young undergraduate. I was full of naïve enthusiasm but, alas, totally lacking in any practical experience of primatology. I had read George Schaller's (1963) splendid monograph *The Mountain Gorilla: Ecology and Behavior*, and Irven DeVore's (1964) edited volume on *Primate Behavior: Field Studies of Monkeys and Apes* (including work

on baboons and macaques, as well as Jane Goodall's ground-breaking observations of chimpanzees at Gombe). If these pioneers could achieve so much, surely it should also be possible to study mandrills in the wild?

At that time, Dr John Hurrel Crook was the leader of a research group in the Department of Psychology at Bristol University and he supervised a number of PhD students who were carrying out fieldwork in Africa. I visited him in 1969, in an attempt to persuade him to take me on, in order to conduct fieldwork on the mandrill. He was very kind and patient with me, as I recall, gently pointing out the near impossibility of finding mandrills in the wild, let alone tracking them in the depths of the rainforest. For an inexperienced student to attempt such a project, working unsupported in remote areas, would be dangerous and also professionally very risky. For how could anyone guarantee that enough data might be generated to justify a PhD?

John Hurrel Crook was, of course, absolutely right and I was obliged to abandon the idea, but not the ambition, to study mandrills in Africa.

Twenty years were to elapse before I had the opportunity to conduct work on mandrill behaviour and reproductive biology at the International Medical Research Centre (CIRMF) in Gabon. Subsequently, the first studies of mandrill supergroups were carried out by fieldworkers based at the CIRMF Field Station in the Lopé National Park. Enough is now known about the mandrill to justify a synthesis of knowledge concerning its behaviour, reproductive biology and evolution. We are presently in a position to examine its natural history and reproductive biology, and to evaluate more critically the role that sexual selection may have played during its remarkable evolutionary history.