



MATING MALES

An Evolutionary Perspective on
Mammalian Reproduction

TIM GLOVER

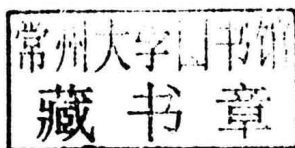
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TIMOTHY GLOVER

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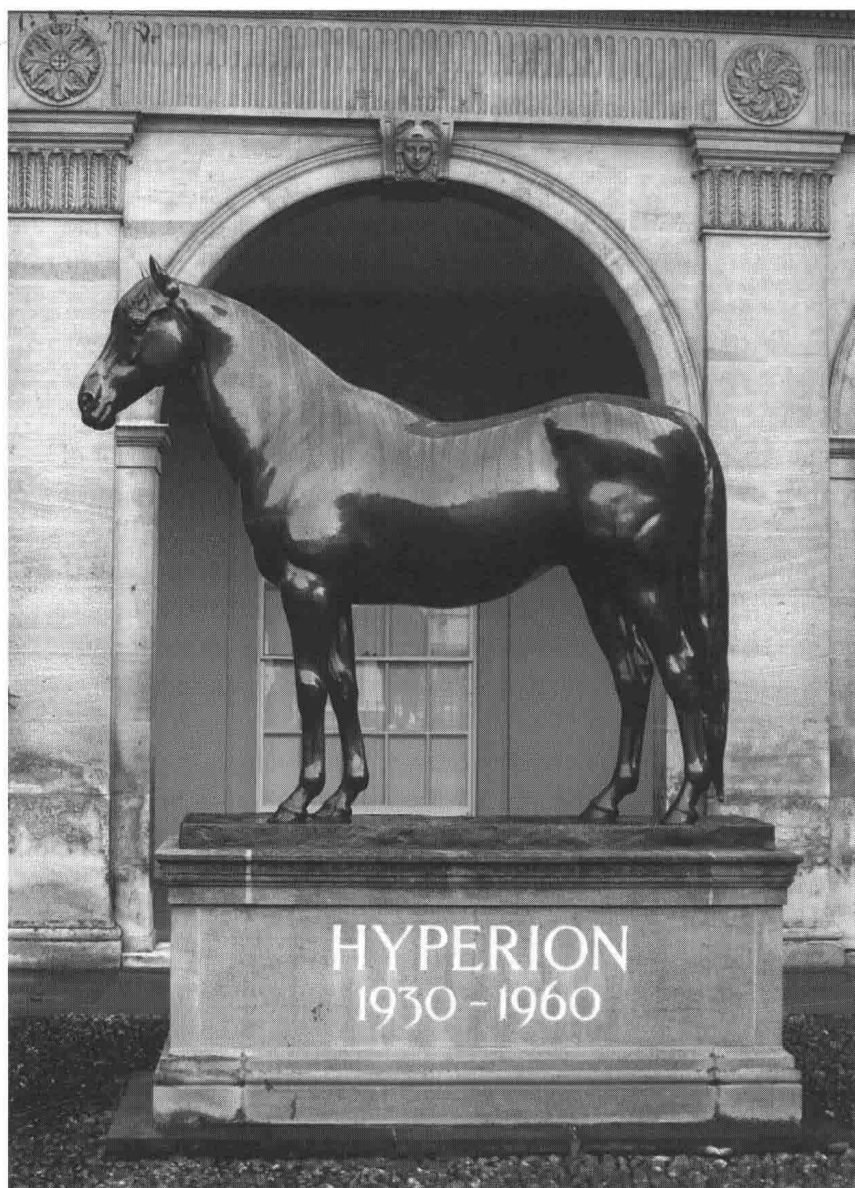
Mating Males

Examining mating from the male perspective, this book provides an overview of mammalian reproduction to illustrate the important role that males with a desire to mate play in the life of mammals.

Written in a conversational style that will appeal to those without specialist knowledge of the field, it begins with a broad overview of sexual reproduction in mammals, explaining the importance of mixing genes, sexual selection and the concept of mating seasons. Subsequent chapters examine some of the most important aspects in detail, including mating behaviour, the structure and function of the male organs of reproduction and their physiological control and modes of copulation. It also challenges some conventionally held notions about testicular descent and scrotal function and presents some new thoughts and ideas on these subjects.

A final chapter considers human reproduction, explaining how our physical and social evolution have contributed to the development of sexual behaviour that is markedly different from that of other mammals, due in particular to the absence of oestrus and seasonality in the human female.

TIM GLOVER is Emeritus Professor of Veterinary Anatomy at the University of Queensland. He has written over 100 papers on male reproduction and is the co-editor of *Male Fertility and Infertility* (Cambridge University Press, 1999).



Hyperion – by Gainsborough, out of Selene. One of the most famous thoroughbred sires of all time (if not arguably the most famous). He was a chestnut and stood only 15 hands high (1 hand is just over 11 cm).

To Claire

Preface

In some quarters it is fashionable to try and argue that mating males (especially human ones) are surplus to requirements when it comes to the progress and continuation of their species. That animals can be cloned and that technology enables some men without sperms in their ejaculate to father children appear to confirm this. But this book aims to dispel any such contention and to explain how, through mating, a male mammal fulfils an indispensable role in the maintenance of its own species.

Reproduction by means of cloning can only have a stultifying effect in the long run, and is ultimately likely to be lethal. Like those of a clockwork toy, the mechanisms of survival need to be wound up from time to time, if for no other reason than to survive the vagaries of the environment. In mammals, including man, this is achieved by the periodic injection of new and randomly different genes through sexual reproduction. The evolutionary development of sex has thereby introduced an extra dimension to the natural selection (survival of the fittest through accidental mutation) of asexually reproducing species.

In mammals, the unison of eggs and sperms, each having half of the normal complement of chromosomes, has facilitated a reduction in the incidence of too many morbid mutations, whilst enhancing the possibility of good ones being introduced. The importance of this arrangement is that favourable characteristics can be achieved in one generation, or a few, without significantly affecting the phenotype (overall body characteristics) of the species. Survival in mammals has depended upon this method of ensuring adequate genetic variation. It is facilitated by having males in the population in addition to females. The wider the mix of genes by different types within a

species, or even from a closely related species, the tougher the offspring are likely to be. Cross breeding (*hybridization*) between different species of baboons has demonstrated that new and doubtless beneficial characteristics can soon make their appearance in a group.

Farmers have known about the importance of this sexual genetic variation for years and have continuously cross bred sheep, for example, because they have been aware of the principle of so-called *hybrid vigour*. This means that cross breeds are often sturdier than inbred animals. Crossing Swaledale ewes with a ram such as a Dorset Horn, for instance, yields what are called 'mules', sheep which withstand the harshness of the Yorkshire winters best, whilst producing meat and wool of the highest quality. There are other examples, exemplified, for instance, by improving the hunting capacity or augmenting scent skills in dogs. Also, it is particularly noteworthy that mongrels are much more likely to enjoy better health than closely inbred animals.

By contrast, it is well known that inbreeding, and even worse, cloning, is not desirable, if the aim in the long term is to produce really good healthy stock. Reducing or eliminating genetic variation, therefore, has not proved to be biologically advantageous, and in the wild there are usually plenty of unrelated males wandering around to ensure that it doesn't happen. Rarely, for example, does one see male cheetah siblings mating with the same female. If they did so too often, it would be contrary to the principle of genetic variation. Why distribute most of your genes with a particular female if your brother has already done it for you? For the sake of genetic variation, it is much better to go off and mate with an entirely different female in order to increase genetic mix. A single cloning in cows, sheep or any other animal can be very useful, but probably not far beyond one generation. The production of 'Dolly' was a fantastic achievement. However, I think it unwise to over-interpret the potential of cloning and of producing transgenic animals, even though our ability to do so has been an amazing advance in biological knowledge.

Victorians recognized that it could be inadvisable for close relatives to marry. It was commonly held that if cousins married, they would be likely to yield offspring who were mentally deficient or lunatic. This is not necessarily so, of course, but was among the mores of the time, presumably intended to discourage too much inbreeding. It was already understood all that time ago, that to reproduce your kind with an initial stranger is more likely to improve the stock – hence our distaste for incest. An apparently unrecognized flaw in the philosophy of ‘planned eugenics’, which was quite fashionable among some intellectuals before the Second World War, was that reduction in the randomness of the gene mix can only end in tears. People in Sardinia appear, at first sight, to be an exception, in that they are long lived and yet go in for quite a bit of inbreeding. But human longevity is a complex business and not a good example of natural survival.

The most striking example of the adverse effects of inbreeding is to be seen among pedigree dogs. By breeding dogs from parental and first-generation animals or from siblings, abnormalities of conformation and even genetic disease are perpetuated or created. Fashions at Crufts (not entirely their fault) have turned many excellent basic breeds into cripples. Governments are unlikely to legislate against this, lest the self-righteous indignation of those blinkered breeders and their societies leads to electoral disadvantage.

But what is the point or the sense of legislating against docking spaniels’ and boxers’ tails, whilst allowing Pekingese to be bred so they cannot breathe properly? To breed dogs that are so specialized that they cannot mate spontaneously must be the ultimate in absurdity. If something is not done, it must be obvious that many good breeds of dog will die out altogether, with an awful lot of suffering en route. Readers might gather that I feel strongly about this! Micro-pigs also pander to human whim, yet society is up in arms at the very mention of designer babies. What’s good for the goose is surely good for the gander!

In addition to providing for more immediate survival of a species in new and alien environments, the mixing of genes with

attendant mutations can be augmented and added to naturally, if more randomly, over very long periods and thus, in typical Darwinian fashion, create a new species. But new species cannot naturally be created overnight and may indeed take thousands of years. Natural speciation is generally a very slow process.

The means whereby genetic amphimixis in mammals is assured (through spontaneous mating) is discussed in the pages that follow.

This book is about mammals – reference to other animals is only made out of passing interest or for comparison. This is simply because my main interest over the past 50 years or more has been in the biology of mammals and I feel ill-qualified to write about other animals in any detail. This is not to imply that they are any less fascinating. I have also confined my attentions to the male, because most of my earlier work was focused on sperm production and the interpretation of semen quality. In this I was privileged at Cambridge to have three great masters of reproductive physiology as my mentors. These were Sir John Hammond, Dr Arthur Walton (pioneers of artificial insemination in British cattle) and Professor Thaddeus Mann. Professor Mann was an unswervingly supportive personal friend for many years after Sir John and Dr Walton died. I am deeply indebted to all of them and hope they would have enjoyed this presentation (though doubtless, they would have had their criticisms!).

In this text I examine the structure and arrangement of the organs of reproduction, not just for the sake of it, but rather as a demonstration of how their shape and form in different species of mammals reflect reproductive strategies and sexual tactics that have evolved over the ages according to biological circumstance. The final aim of every sexually active male is to reproduce, but details of the means of doing so differ in different species, even though mating is always involved. Only the intellectually deprived, those people who are unable to recognize overwhelming scientific evidence when they see it, can fail to accept and embrace the principles of evolution

through natural selection, as set out by Darwin in his work on the origin of species. So, in examining differences in structure and form we need to seek evidence for how it might have happened.

I hope that by approaching the subject of mating in different mammalian species, I might be able to offer a new slant on the way we look at the process in ourselves. A word of caution is needed, however. Whilst this book is not for those who giggle at the very mention of mating, nor for those who consider the subject vulgar and not to be mentioned at all, it is certainly not for the prurient. Neither, though, is it for the squeamish or faint-hearted. This is not a drawing-room story, but is intended to be a glance at what is a really interesting evolutionary development in the spectrum of biological functions.

The book is a light canter through the field and, in the final chapter, I expressed some personal opinions. For several years I worked as an andrologist in an infertility clinic and I have to make clear that some of these opinions are based on clinical experience and anecdotal evidence rather than experimental data. I have also served as a professional witness in a variety of court cases and some of my remarks in the last chapter are drawn from that experience. So, although this chapter may in parts appear to be unduly empirical, its intention is to provide ideas and some new ways of looking at the subject of human reproduction. Apart from this, some of the issues raised and conclusions reached, whilst based on scientific evidence and observation, may be regarded by some authorities as being debatable. But ideas and discussion of them must surely be one route to getting things right, and differences in interpretation can be useful in this context. The text is written deliberately by way of a discourse, in the hope that it might be more readable than a more conventional work and, if nothing else, might periodically entertain, rather than induce somnolence. The book, you see, is not really intended for bedtime reading.

I have not interrupted the narrative by inserting hundreds of references into the text, more scholarly though that might appear to

have been. This is not only because I have not wanted to spoil the flow of the story, but also because much of the material is based on papers written in the last century. By and large, it seems to me, contemporary biologists rarely read papers written more than about ten years back, so listing older papers might be regarded as a waste of time. But I have given just a brief list of key works at the end of each chapter for anyone, especially students, who might wish to take things further. In so doing, I am putting in a plea for older works to be consulted frequently, because a broad background can only provide better perspective.

It has not been too easy to choose the most appropriate and useful references, because the book consists of a distillation of information acquired over many years of observation and reading, and much of it is well known. Many, if not most, of the references cited are to books or reviews, and if a student dips into these, many more references to individual papers will be found. A few of these, including some of my own, are provided when I have considered them to be of particular relevance in understanding the subject under discussion. The list does not, therefore, necessarily refer to specific points made in the text, but is rather provided for wider general reading. I hope the text might prove to be of sufficient intrinsic interest to those outside the field, without the need for further reading, so addressing the references is simply a matter of choice or need.

Domesticated and laboratory animals receive most attention in this book. This is because, in the context of the subjects discussed, more is known about them than other mammals. It could also reflect a certain bias, due to my having been reared as a boy on a farm, and having bred rabbits and rats in my schooldays. This is not to mention my frequently being asked, on our farm, to hold mares while the stallion covered (served) them. Much of the information presented here on wild mammals stems from my own observations at zoos, especially Chester Zoo in the United Kingdom, and in the African countryside. This was Africa when you could spend a whole day in

the bush (or 'bundu') and never see a human being, but could alone share the rather savage beauty of the Rift Valley with the indigenous animals. In those days, there were no Volkswagens painted like zebras or chattering tourists with their frantically clicking cameras to mar the curious majesty of Kenya, a quite magical place.

Writing objectively about mating is not always easy without appearing indelicate. I think this is largely because a lot of people interpret animal behaviour anthropopathically – they ascribe the feelings and passions of man to other animals. I have a clear memory of a photographic exhibition in Liverpool in the United Kingdom, where I once worked, showing two butterflies in sexual union. The caption read 'Butterflies fornicating'. Maybe Liverpool butterflies do fornicate, but it seemed rather anthropopathic to me!

Occasionally, I have toyed with a little anthropopathy in this book, but only humorously or as an explanatory metaphor. If we want a broad and meaningful perspective on the behaviour of non-primate mammals, it is better not to try and connect it with human behaviour at all. Worse still, we tend to think it is funny to be anthropomorphic and put animal heads on humans or dress animals up to make them appear like humans. Most of us have indulged a little in this sort of thing, and Walt Disney did it rather charmingly and respectfully. We also see it in circuses. It is a sort of habit, and it existed even before Aesop's fables. For example, sexual activity for tasteful human beings is a private affair, and in writing this book I have occasionally felt guilty, lest I might have intruded too far into the private lives of other mammals. But we can be assured that no such sense of privacy is likely to prevail among those mammals when a female is in heat.

Research into DNA relationships between mammalian species is very useful in all sorts of ways, but that we share some patterns of DNA with pigs and guinea pigs does not mean to say that we are all that close to them or that we behave like them. We even share aspects of our DNA with some invertebrates. I honestly believe, and this is not a condescending comment at all, that scientists must be

cautious not to mislead the public in efforts to communicate their science. Without details, it is easy for people to get hold of the wrong end of the stick. It should no longer be necessary to produce further evidence of Darwinism (no longer a mere theory). Of course, we are likely to have some aspects of our DNA which relate to that of other animals, but that is to be expected during evolution. We are descended from a sub-human primate, but this does not mean that we need to behave like other sub-human primates. It is puzzling why this is so difficult for some people to grasp.

Yet magazines and television programmes, in particular, are repeatedly tempted into trying to relate the sexual behaviour of wild animals to that of man, and vice versa. This is wrong and very misleading. Indeed, the final chapter of this book explains how human mating behaviour is likely to be unique among mammals as a result of the special nature of human evolution. A major theme in this book, for instance, is that animals that have no periods of sexual desire (periods of heat or oestrus) behave quite differently from those that have.

In writing this material, I have tried my best not to offend, but if there are parts of the text where I have failed, I hope any reader will understand the difficulty and be forgiving. In trying to arrive at a suitable balance, a certain moral detachment might show through. But the book is about biology, and it is intended to be informative, yet thought provoking.

Timothy Glover
Brisbane, Queensland, 2011

Acknowledgements

First, I want to thank all those good scientists who have contributed to knowledge in the field of reproductive biology. I have usually found their work, whether presented verbally or in print, to be arresting and absorbing. I apologize at the outset to the authors of many splendid works that have not been cited in the listed references of this book. The constraints of space and logistics have been pressing and, therefore, I decided that I would simply try to provide an entrée to each subject covered in the text. Thereby, the gate can be opened into the field and a deeper look at the literature should then provide a pathway across it. Information on this subject is extensive and experts will recognize that such a compact volume as this can only be a broad pastiche. Of course, I want to thank those whose books and reviews have been cited here. I believe they will prove a very valuable guide to those who wish to look into the subject more deeply.

However, there are some people whose special help leads me to name them. This I do gladly. I am greatly indebted to Ron Hunter of Edinburgh for his relentless encouragement and support. Without this, and, therefore, without him, I doubt whether the book would ever have been completed. I am appreciative of the help received from Keith Harrison and Frank Carrick of Brisbane. I am also particularly grateful to 'Twink' Allen, former Professor of Equine Reproduction at Cambridge for permitting me to use the drawing shown in Figure 5.2, and members of his staff for their help and interest and for permitting me to use the photographs shown in Figures 2.5 and 5.7, and to Roger Short and Jim Cummins for their interest and help. I am indebted also to Sandra Wilsher for the

photograph of the statue of Hyperion, which appears as a frontispiece and for her great help with other figures.

It is a friend indeed, who can be bothered to read one's material and so I want to express my sincere appreciation to Michael Bryden, Emeritus Professor of Veterinary Anatomy at the University of Sydney, and John Tesh of the University of Surrey, UK, for agreeing to help me in this way for helpful suggestions.

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