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978-0-521-15957-9 — Mating Males: An Evolutionary Perspective on Mammalian Reproduction
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Excerpt
More Information

1 The system

Since this book is about mammals, it is reasonable to ask the question: 'What is a mammal?'. A mammal is a vertebrate, which means it has a vertebral column or backbone – a facetious answer to the question could be that a mammal is a mammal when it is not a fish, an amphibian, a reptile or a bird. All of these are also vertebrates, you see. Most mammals have hair, wool or fur, but not all; some have spines and others scales, whilst man has little or no such covering. So there is great variety among mammals, which makes it all the more confusing when it comes to definition. However, the correct answer to the question is that mammals are those creatures that suckle their young. This distinguishes them from other animals, including the other vertebrates mentioned.

Reproductively speaking, there are three kinds of mammal. There are those that lay eggs, such as the duck-billed platypus and echidna (what used to be called the spiny anteater), those that give birth to embryos – the marsupials, including kangaroos among others (you can accommodate up to a dozen newly born opossums on a teaspoon) – and those such as ourselves, who give birth to relatively well-developed foetuses after nurturing them for longer periods in the womb (the uterus). Each of these groups is classified sequentially as being *prototherian*, *metatherian* or *eutherian* mammals. Thus, the completion of body form occurs in the uterus of eutherian mammals in contrast to that of a 'joey' (baby kangaroo or any other marsupial), for example, whose longest period of development is at the teat, having been born as a young embryo.

Nevertheless, there is quite a lot of variation in the degree of development of newly born eutherian mammals. Guinea pigs, or cavies as they are sometimes known, are virtually independent as soon

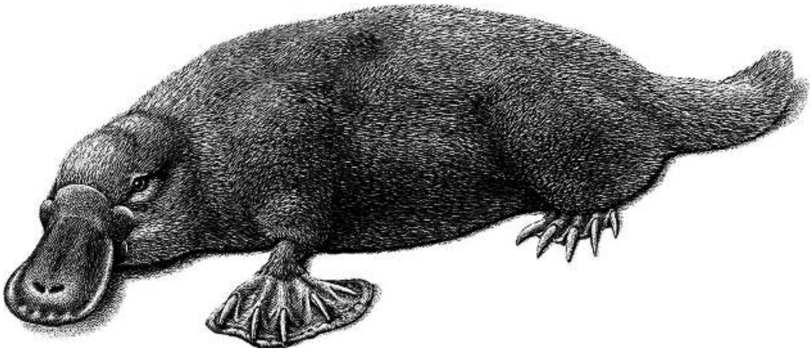

FIGURE 1.1 A rather curious mammal! The strange and mysterious platypus lays eggs, but although she has no teats, she suckles her young. Her milk is ejected over the surface of her abdomen for the young ones to drink. © Photolibrary.com

as they are born, whereas the newly born of other species – such as humans, elephants or pandas – need a much longer period of maternal care before they are capable of fending for themselves. Animals that give birth to live young whose earliest development takes place in the uterus are known as being *viviparous* and typify eutherian mammals, while mammals that lay eggs (i.e. the monotremes, such as the duck-billed platypus – Figure 1.1) are, like birds, referred to as being *oviparous*. Some fishes and reptiles (e.g. the adder) are viviparous; while some fishes are said to be *ovoviviparous* (or oviviviparous), because they provide advanced development in the egg and yet give birth to live young.

The above information is all by way of background explanation, but let's get back to mating. It is often equated with the act of copulation, which means 'to couple' or 'be fastened together'. But mating may have wider meaning than this; sniffing around or fore-play is also part of the process and, in some species, mutual care of young between male and female may come into it. So perhaps mating is best regarded as a drawing together of male and female for purposes of successful sexual reproduction.

By mating with different females, a male is able to scatter his genes widely, and since most mammals mate with several females rather than one, the dispersal of his genes may be quite extensive. His aim is to outdo his peers in the distribution of his own genes. From a purely biological standpoint, a male mammal may be thought of as simply being testicles on legs, because its body functions mainly to transport the testicles from place to place. This function is all-important in sexual reproduction, since it is the testicles that produce the gene-bearing sperms.

The more females a male impregnates, the greater, we say, is his reproductive fitness, because thereby, the wider his genetic stamp will be. Moreover, such a successful male will provide a greater mix of genes (whilst sustaining his personal hallmark in the offspring), than his less successful rival, who may mate with fewer females or none at all.

It is important to recognize that reproduction involving two individuals is by no means confined to vertebrates, let alone to mammals. The transfer of nuclear material from one individual to another is even to be seen in single-celled organisms such as the paramecium and single strands of the simple plant, spyrogyra (conjugation). Furthermore, RNA and DNA are not confined to nuclei, so we can have bacteria and viruses, which are without a nucleus, spontaneously reproducing and sending modification messages between them. But actual sexual reproduction (the union of eggs and sperms) occurs commonly among invertebrate multicellular organisms, including worms, insects and other arthropods, so beetles, moths and butterflies, as well as a host of marine animals including octopuses and their relatives, and crabs, lobsters and their relatives, are included. In some animal species, sexual reproduction appears to have been tried and then discarded during their evolutionary history. In others, such as the malarial parasite, it is periodically introduced into what is essentially an asexual reproductive cycle. But sexual reproduction seems to have been fairly efficient, because it is so widespread throughout the animal kingdom, even, for example, in hermaphrodite worms, such as the tapeworm.

With the exception of hermaphrodites, the popularity, as it were, of sexual means of propagation is most likely to be due to the flexibility and versatility that results from a mostly random mixing of genes. It has been argued that this notion needs a rethink, but until we get one, the principle makes reasonable sense. This genetic amphimixis, however, demands that sperms and eggs (in mammals, each carrying half the number of chromosomes carried by other cells in the body) unite in order to yield viable offspring. The success of the system depends on their being some biological assurance that this will happen.

PROTECTION OF SPERMS AND EGGS

Male and female sex cells (gametes) cannot unite if they are unable to survive long enough to do so. This is obvious, but it does mean that they need to avoid environments that are fiercely adverse to their wellbeing. In addition, it is clearly desirable that they should not be deposited too far from each other. If these needs can be met, then their chances of meeting each other in good condition are increased and they can get away with a relatively short lifespan. Thus, we see that sperms and eggs are not only protected in terms of space and territory, but also by timing and individual longevity.

Spatial protection is achieved by males and females moving closer together as the time for sperm and egg deposition approaches. As far as temporal protection is concerned, we find that reproductive activity tends to be intermittent rather than constant, and in a large number of animals it is confined to certain seasons of the year. This seasonal activity has a side-effect, in that it also saves on the number of sperms and eggs necessary for the process to work. This can be important, because producing eggs, in particular, requires considerable energy.

Most males produce a prodigious number of sperms, which is a powerful instrument in ensuring that, in spite of inevitable wastage, there remains enough of them to reach the site of fertilization. Nevertheless, there are safety mechanisms built into the system, because the life and survival of a sperm can be precarious. For example, the sperms of some species can resist differing environmental conditions. But even so, when sperms and eggs are deposited in a watery environment – as they are in most fishes, where fertilization is external to the body – dilution by the surrounding medium, predation and purely adventitious wastage are all hazards that sperms and eggs must face. Extremes of temperature, serious changes in pH (acidity and alkalinity) or osmolarity are not likely to be easily tolerated, so the environment needs to be stable enough to be congenial to these reproductive cells. The sperms of many marine animals are isosmotic with sea water (that is, they do not draw in or push out more fluid than is good for them), but fishes that live in either fresh water or sea water might find one more conducive to the protection of their gametes than the other. Salmon, for example, move from sea water to fresh water for spawning. Thus, there is a level of vulnerability beyond which gametes will not be able to survive, so the adult animals that produce them must behave accordingly.

Sexual rituals, by both some vertebrate and invertebrate males, lure females to come as close to potentially fertilizing sperms as possible. In amphibians such as salamanders and axolotls, the male literally guides his female to sperms that he has deposited on the ground. Eventually she will snatch them up into her genital opening or cloaca. In the case of the salamander, she gets her directions to the sperms through a male dance of courtship. Newts also induce their females to pick up sperm packages in claspers that are situated in their hind parts. Among the invertebrates, male dragonflies do an alluring dance and scorpions have a similar, if slightly more complicated ritual; among vertebrates, female salmon emit a chemical that blends with another one from the male and attracts him to come closer to her. Spatial protection of sperms and eggs, therefore, can sometimes be a combined effort by both sexes.

In most of these animals, and we see it in other vertebrate and invertebrate species, as well as in some cartilaginous fishes, there is an added protection for sperms in that they are encased, as if wrapped up in a parcel, before being called upon to go forth and fertilize. These wrapping cases are called 'spermatophores'.

The invertebrate octopus, several species of shark (all species of which have a backbone consisting entirely of cartilage rather than bone) and other fish, including many bony fishes, produce spermatophores. There are some marine invertebrates, however, which agglutinate their sperms during internal transportation, so that groups of them stick together in small packages without being wrapped up. They are only released to be individually free when they hit the sea water.

At first sight, it might seem that when fertilization takes place within the female body (so-called internal fertilization), with sperms being deposited directly into the female tract, the sperms are especially well protected and that this is the safest procedure of all for them. However, it turns out that this is more apparent than real, because the female tract is not always as hospitable to invading sperms as might be imagined. On the contrary, provided the sperms are shed fairly close to eggs, external fertilization in water is probably safer. It may come as something of a surprise to know that there is at least one species of fish that releases 1000 times fewer sperms than are to be found in the ejaculate of a reindeer, for example. Surely, this discrepancy in numbers suggests that there are more hidden dangers for sperms in the female tract of a mammal than there may be for those released into the sea. With internal fertilization, though, there must be less risk of sperms wandering off in the wrong direction and getting lost.

In mammals, there are particular regions of the female tract that are less of a menace to sperms than others. Indeed, some areas of the tract may be regarded as safe havens. In some invertebrates such as crabs, there are receptacles in the female tract that provide such havens, and in mammals the neck of the womb or the cervix and the junction between the uterus and the Fallopian tubes (uterotubal junction) are less dangerous regions for sperms than other parts of the tract such as the vagina or the body or horns of the uterus itself. As might be expected, mammalian sperms move out of the trickiest environments within the female tract as soon as they can and head for these safer places. There are exceptions, as in biology there nearly always are! Some bats store sperms in the wall of the uterus, a normally hostile place, for up to six months, but this is an unusual specialization for mammals.

When fertilization is internal, sperms can be deposited into the female in a variety of ways. They may be injected under the skin as if from a syringe, or limbs may be used for insertion, as in the hectocotyledonous arm of the octopus. Insemination in most birds and some fishes is achieved by apposition of the male and female cloacae, although some birds have a phallus or penis – the ostrich and the duck are the most notable, but there are a few others. These penes have a ventral sulcus or groove, rather like the embryonic phallus of a mammal, so they do not actually ejaculate through it, though semen may in part be directed by it. The penis of the waterfowl is a very elaborate affair, designed, it seems, to try and overcome structural barriers within the female. This underscores the fact that birds, as we shall see in the next chapter, can be quite selective in the males they permit to impregnate them. So, in sexual reproduction, the existence of a penis is not consistent in all species and it seems first to have evolved in some of the flatworms (platyhelminths).

SYNCHRONIZING MALES AND FEMALES IN MAMMALIAN SPECIES

Internal fertilization and its attendant need for copulation characterizes mammals, so when the time is ripe, males and females need to draw closer together, with a view to being very close. This is because their form of mating involves bodily contact between the sexes. To achieve this, the male must draw attention to himself and encourage the female to accept such a physical liaison. In the majority of mammals this acceptance is only periodic and is restricted to her periods of desire – when she is 'in heat' or 'oestrus'. These periods might only occur in a mating season and are non-existent out of season. Some mammals have discarded the idea of mating in specific seasons of the year, but to argue that all mammals are fundamentally seasonal breeders, or have tended to be so in the past, is compelling.

In sexual reproduction it is obviously essential that the release of sperms and eggs is properly synchronized, and this means that copulation should occur at a particular and appropriate time. In mammals, this synchrony is achieved by the ovary releasing eggs during or shortly after the periods of a female's acceptance of a male. The release constitutes the process of **ovulation**. It ensures that a female receives sperms at a time which corresponds closely to the release of her eggs. But the length and frequency of the female's period of desire and, therefore, the opportunity for copulation, vary widely between mammalian species.

Horses, dogs and cats (and their relatives in the wild) have a fairly long period of oestrus, whilst in cows and ewes, it is only short. Cows may be in heat for only five or six hours in the winter, and it might not even be noticed, but in the summer it usually lasts for about a day. Oestrus in ewes in the northern hemisphere is confined to a breeding season between October or November and about March (except for the Dorset Horn in Britain, which breeds twice per year) and it lasts between one and two days only. Sows have a slightly longer period of two to three days.

However, within the mating period, be it seasonal, intermittent or constant throughout the year, the frequency with which females come into heat or oestrus also differs between different species. The period between one heat and another is known as an 'oestrous cycle'. In horses and cats, this is about three weeks long, but ewes come into heat every 16 days. There are quite a lot of heat periods in these animals and they are thus referred to as being 'polyoestrous'. In the last century, the Hunters' Improvement Society (HIS) registered stallions used to travel around the country by road, covering mares at different stables and farms. They would call back in three weeks and repeat the procedure if the mares had again come into oestrus. This was rather unreliable, since mares can ovulate (and thus come into heat) in early pregnancy or even with foal at foot, but the method seemed to work quite successfully.

Dogs – and their wild relatives such as wolves and foxes – only come into heat every year or every six months, making them

FIGURE 1.2 'Mighty Power' by Radium out of The Waif (a descendant of the great St Simon, through his dam). Champion HIS thoroughbred premium stallion in the 1930s (see text). He was also a chestnut, but stood 16.5 hands high.

'monoestrous' animals, although their carnivorous relatives, the hyenas, are polyoestrous. Among the smaller laboratory animals, rats have a distinct oestrous cycle, but rabbits do not. If rabbits are not receptive to a buck, they are always either pregnant or displaying false pregnancy (which is quite a common condition in rabbits). In most other mammals, though, there is a regular oestrous cycle and this results from an equally regular cycle of activity of the ovary (Table 1.1).

The majority of mammals ovulate spontaneously during their periods of oestrus (cows being an exception in that they ovulate shortly after their heat period has ended), but a number of mammals are unable to do so. Ovulation in these species has to be induced and this is normally achieved by the male. In these cases, the female cannot ovulate unless coitus or copulation occurs. Included among

Table 1.1 *Oestrous periods and cycles*

Species	Length of oestrous cycle (days)	Length of oestrous period (days)
Mare	21 (polyoestrous)	7
Cow	21 (polyoestrous)	1 or <1
Sow	21 (polyoestrous)	2–3
Ewe	16 (polyoestrous)	1.5
Goat (Nanny)	16 (polyoestrous)	1
Bitch (Dog)	180–240 (monoestrous) (prolonged period of anoestrus – see text)	7–8
Queen (Cat)	21 (polyoestrous)	2–3

these 'induced' or 'non-spontaneous' ovulators are all the cats, including the lynx and jaguar, together with better-known wild cats such as the tiger, leopard and lion, as well as feral and domestic cats. Many smaller mammals such as rabbits, hares, minks, ferrets, raccoons, squirrels, field mice, voles and shrews are also induced ovulators, as are some larger mammals such as camels (including also llamas and alpacas). The females of these species need a copulating male to fire off the ovulatory hormone (luteinizing hormone or LH) from the pituitary gland at the base of the brain, and thus to bring about the release of their eggs. It is a very good way of making sure that the release of eggs and sperms is synchronized, even though egg release often does not occur for several hours after copulation has taken place.

Among the wild cats, lions copulate about every 15 minutes throughout a day. As will be seen later, it is possible that each mount, and apparent male orgasm, might not yield sperms. If this is the case, we cannot so far tell whether the first or first few mounts end in the ejaculation of sperms or whether it is the last or last few that do so. But there can be little doubt that copulation in induced ovulators is not solely concerned with the delivery of semen; the repeated coitus of lions might bring about a sort of staircase stimulus to the pituitary gland of the females.