4.9: Sexual dimorphism

What, biologically, defines whether an organism is female or male, and why does it matter? The question is largely irrelevant in unicellular organisms with multiple mating types. For example, the microbe *Tetrahymena* has seven different mating types, all of which appear morphologically identical. An individual *Tetrahymena* cell can mate with another individual of a different mating type but not with an individual of the same mating type as itself. Mating involves fusion and so the identity of the parents is lost; the four cells that result are of one or the other of the original mating types.

In multicellular organisms, the parents do not themselves fuse with one another. Rather they produce cells, known as gametes, which do. Also, instead of two or more mating types, there are usually only two sexes, male and female. This, of course, leads to the question, how do we define male and female? The answer is superficially simple but its implications are profound. Which sex is which is defined by the relative size of the fusing cells the organisms produce. The larger fusing cell is termed the egg and an organism that produces eggs it is termed a female. The smaller fusing cell, which is often motile (while eggs are generally immotile), is termed a sperm and organisms that produce sperm are termed a male. At this point, we should note the limits of these definitions. There are organisms that can change their sex, which is known generically as sequential hermaphroditism. For example, in a number of fish it is common for all individuals to originally develop as males; based on environmental cues, the largest of these males changes its sex to become female. Alternatively, one organism can produce both eggs and sperm; such an organism is known as a hermaphrodite.

The size difference between male and female gametes changes the reproductive stakes for the two sexes. Simply because of the larger size of the egg, the female invests more energy in its production (per egg) than a male invests in the production of a sperm cell. It is therefore relatively more important, from the perspective of reproductive success, that each egg produce a viable and fertile offspring. As the cost to the female of generating an egg increases, the more important the egg’s reproductive success becomes. Because sperm are relatively cheap to produce, the selection
pressure associated with their production is significantly less than that associated with producing an egg. The end result is that there emerges a conflict of interest between females and males. This conflict of interest increases as the disparity in the relative investment per gamete or offspring increases.

This is the beginning of an evolutionary economics, cost-benefit analysis. First there is what is known as the two-fold cost of sex, which is associated with the fact that each asexual organism can produce offspring but that two sexually reproducing individuals must cooperate to produce offspring. Other, more specific factors influence an individual’s reproductive costs. For example, the cost to a large female laying a small number of small eggs that develop independently is less than that of a small female laying a large number of large eggs. Similarly, the cost to an organism that feeds and defends its young for some period of time after they are born (that is, leave the body of the female) is larger than the cost to an organism that lays eggs and leaves them to fend for themselves. Similarly, the investment of a female that raises its young on its own is different from that of the male that simply supplies sperm and leaves. As you can imagine, there are many different reproductive strategies (many more than we can consider here), and they all have distinct implications. For example, a contributing factor in social evolution is that where raising offspring is particularly biologically expensive, cooperation between the sexes or within groups of organisms in child rearing can improve reproductive success and increase the return on the investment of the organisms involved. It is important to remember (and be able to apply in specific situations) that the reproductive investments, and so evolutionary interests, of the two sexes can diverge dramatically from one another, and that such divergence has evolutionary and behavioral implications.

Consider, for example, the situation in placental mammals, in which fertilization occurs within the female and relatively few new organisms are born from any one female. The female must commit resources to supporting the new organisms from the period from fertilization to birth. In addition, female mammals both protect their young and feed them with milk, using specialized mammary glands. Depending on the species, the young are born at various stages of development, from the active and frisky (such as goats) to the relatively helpless (humans). During the period when the female feeds and protects its offspring, the female is more stressed and vulnerable than other times. Under specific conditions, cooperation with other females can occur (as often happens in pack animals) or with a specific male (typically the father) can greatly increase the rate of survival of both mother and offspring, as well as the reproductive success of the male. But consider this: how does a cooperating male know that the offspring he is helping to protect and nurture are his? Spending time protecting and gathering food for unrelated offspring is time and energy diverted from the male’s search for a new mate; it will reduce the male’s overall reproductive success, and so is a behavior likely to be selected against. Carrying this logic out to its conclusion can lead to behaviors such as males guarding of females from interactions with other males.

As we look at the natural world, we see a wide range of sexual behaviors, from males who sexually monopolize multiple females (polygyny) to polyandry, where the female has multiple male “partners.” In some situations, no pair bond forms between male and female, whereas in others male and female pairs are stable and (largely) exclusive. In some cases these pairs last for extremely long times; in others there is what has been called serial monogamy, pairs form for a while, break up, and new pairs form (this seems relatively common among performing arts celebrities). Sometimes females will mate with multiple males, a behavior that is thought to confuse males (they cannot know which offspring are theirs) and so reduces infanticide by males.

It is common that while caring for their young, females are reproductively inactive. Where a male monopolizes a female, the arrival of a new male who displaces the previous male can lead to behaviors such as infanticide. By killing the
young, the female becomes reproductively active and able to produce offspring related to the new male. There are situations, for example in some spiders, in which the male will allow itself to be eaten during the course of sexual intercourse as a type of nuptial gift, which both blocks other males from mating with a female (who is busy eating) and increases the number of offspring that result from the mating. This is an effective reproductive strategy for the male if its odds of mating with a female are low: better (evolutionarily) to mate and die than never to have mated at all. An interesting variation on this behavior is described in a paper by Albo et al\textsuperscript{134}. Male Pisaura mirabilis spiders offer females nuptial gifts, in part perhaps to avoid being eaten during intercourse. Of course, where there is a strategy, there are counter strategies. In some cases, instead of an insect wrapped in silk, the males offer a worthless gift, an inedible object wrapped in silk. Females cannot initially tell that the gift is worthless but quickly terminate mating if they discover that it is. This reduces the odds of a male’s reproductive success. As deceptive male strategies become common, females are likely to display counter strategies. For example, a number of female organisms store sperm from a mating and can eject that sperm and replace it with that of another male (or multiple males) obtained from subsequent mating events\textsuperscript{135}. There is even evidence that in some organisms, such as the wild fowl \textit{Gallus gallus}, females can bias against fertilization by certain males, a situation known as cryptic female choice, cryptic since it is not overtly visible in terms of who the female does or does not mate with\textsuperscript{136}. And so it goes, each reproductive strategy leads, over time, to counter measures\textsuperscript{137}. For example, in species in which a male guards a set of females (its harem), groups of males can work together to distract the guarding male, allowing members of their group to mate with the females. These are only a few of the mating and reproductive strategies that exist in the living world\textsuperscript{138}. Molecular studies that can distinguish an offspring’s parents suggest that cheating by both males and females is not unknown even among highly monogamous species. The extent of cheating will, of course, depend on the stakes. The more negative the effects on reproductive success, the more evolutionary processes will select against it.

In humans, a female can have at most one pregnancy a year, while a totally irresponsible male could, in theory at least, make a rather large number of females pregnant during a similar time period. Moreover, the biological cost of generating offspring is substantially greater for the female, compared to the male\textsuperscript{139}. There is a low but real danger of the death of the mother during pregnancy, whereas males are not so vulnerable, at least in this context. So, if the female is going to have offspring, it would be in her evolutionary interest that those offspring be as robust as possible, meaning that they are likely to survive and reproduce. How can the female influence that outcome? One approach is to control fertility, that is, the probability that a “reproductive encounter” results in pregnancy. This is accomplished physiologically, so that the odds of pregnancy increase when the female has enough resources to successfully carry the pregnancy to term. It should be noted that these are not conscious decisions on the part of the female but physiological responses to various cues. There are a number of examples within the biological world where females can control whether a particular mating is successful, i.e., produces offspring. For example, female wild fowl are able to bias the success of a mating event in favor of dominant males by actively ejecting the sperm of subdominant males following mating with a more dominant male, a mating event likely to result in more robust offspring, that is, off-spring more likely to survive and reproduce\textsuperscript{140}. One might argue that the development of various forms of contraception are yet another facet of this type of behavior, but one in which females (and males) consciously control reproductive outcomes.

Contributors and Attributions

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