VII.6

Sexual Selection: Mate Choice
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The evolution of many extravagant traits and bizarre behaviors is attributed to sexual selection arising from mate choice. Mate choice occurs when individuals’ traits or behaviors (preferences) make them less likely to produce offspring when they encounter certain individuals of the opposite sex. It involves either some form of rejection of mating or fertilization opportunities, or mating multiply and selectively using the gametes from these mating partners to produce offspring. Such behaviors are expected to increase the interval between successive breeding events. All else being equal, slowing down breeding is costly; thus one expects some compensatory benefits of being choosy to explain its evolution. Choosiness can increase the mean number of offspring produced per breeding event and/or increase offspring quality (i.e., their reproductive value). The latter requires that potential mates vary in their effect on offspring fitness, either because of the genes they transfer or because of the direct benefits (e.g., parental effort) they offer. Females are generally choosier than males, although males often exhibit subtle forms of choice. Large differences in the relative availability of eggs and sperm and of sexually receptive males to females is key to understanding why the sexes differ in whether and how they engage in mate choice.

GLOSSARY

Direct Benefit. An increase in offspring number because preferred mates provide more resources than average, which are converted into additional offspring.

Direct Selection. Selection on traits that increase the bearer’s lifetime reproductive output (e.g., mating preferences that provide direct material benefits to the chooser).

Genetic Benefits. An increase in mean offspring fitness because their genotypes differ from those expected under random mating and fertilization.

Heterozygosity. The state in which each parent transfers a different version (allele) of a gene to offspring.

Homozygosity. The state in which both parents transfer the same version (allele) of a gene to offspring.

Indirect Selection. Selection on traits that increase the fitness of relatives rather than the number of offspring the bearer produces (e.g., selection on mating preferences that increase offspring quality through genetic benefits; offspring are relatives).

Operational Sex Ratio. The current ratio of males to females in the mating pool (i.e., adults that are ready to mate).

Polyandry. The propensity for females to mate with more than one male in a single reproductive cycle.

Sexual Conflict. The divergence in evolutionary interests of a male and a female. Conflict is removed only in strict lifetime monogamy.

Sperm Competition. Postejaculatory male-male competition to sire offspring when females mate polyandrously and where sperm compete to fertilize eggs; can cryptically be influenced by females.

1. WHY DOES MATE CHOICE FASCINATE EVOLUTIONARY BIOLOGISTS?

There is often an exquisite fit between organisms and their environment. The manner in which katydid crickets mimic leaves to camouflage themselves from insectivorous birds is just one example of the astonishing machinery organisms use to survive in a hostile world. Individuals detect predators or prey, acquire food, and maintain their bodies with such proficiency that it creates the illusion that they
were intelligently designed for survival in a hostile world. Ever since Darwin, natural selection has offered a biological explanation for such economical design.

Yet some characteristics of animals appear positively wasteful. Why, for example, do many birds and fish have gaudy colors and extravagant courtship displays that draw the attention of predators? Why do male fiddler crabs consume energy waving their massive claw to attract a female rather than simply waiting for one to approach? And why does mating involve features that reek of sexual conflict rather than harmonious union, like chemicals in the seminal fluid of fruit flies that manipulate the reproductive behavior of females, and the sharply barbed penises of certain beetles that damage females and shorten their life span?

The existence of characteristics that reduce longevity can be explained by evoking a trade-off between natural selection, which favors increased longevity, and sexual selection for characters that increase reproductive success. Evolutionary success ultimately depends not on how long an organism lives but on how many offspring it produces and, in turn, how successfully they breed. Sexual selection implies competition between members of one sex for access to gametes of the opposite sex. This is partly why females are usually choosier: there are many more sperm than unfertilized eggs available at any given time. The costs of choosing are usually larger for males, because the wait until the next available fertilization opportunity is longer.

2. WHAT COUNTS AS MATE CHOICE?

Sexual selection is traditionally divided into two categories: contests among members of the same sex (intrasexual) and interactions between the sexes (interesexual). In this classification, mate choice belongs to the latter category. However, the importance of this distinction is easily overstated, and it is often difficult to consider one mechanism of mate choice without considering the influence of the other as well. Dividing sexual selection into purely intersexual and intrasexual mechanisms obscures the shared underlying structure when there is competition within a sex and the outcome of this contest is ultimately rewarded by access to gametes of the opposite sex. Victory in competition for mates is rewarded only because the eventual contest winner is more likely to be accepted as a mate (e.g., by virtue of being allowed to stay in the area). With mate choice there is likewise competition among rivals as individuals produce sounds, visual signals, chemicals, and tactile movements that increase the chances that they can induce a member of the opposite sex to mate and use their gametes. There is either a real war or a war contested by more diplomatic means. Nevertheless, to highlight the importance of these two topics to understanding the evolution and evolutionary consequences of behavior, competition between individuals of the same sex is dealt with in chapter VII.5. Here we consider intrasexual competition only in terms of its influence on mate choice.

While the dividing line between inter- and intrasexual selection is relatively irrelevant, it is important to note that sexual selection can occur without involving either mate choice or direct physical contact between rivals. Consider a situation in which individuals occur at low density, and members of one sex actively search for mates. Differences in the ability to locate the opposite sex—for example, variation in olfactory abilities required to find females—will create variation in mating success, even if no mating opportunity is ever rejected, every encounter leads immediately to fertilized eggs, and solitary individuals live at such low densities that no mating involves sperm competition. There is still competition among rivals analogous to that among treasured hunters: located trove is no longer available for rivals to find. Thus sexual selection can increase olfactory sensitivity (or any other trait that improves mate encounter rates, e.g., locomotor ability) beyond its naturally selected optimum, even if no mate choice occurs.

Reaching a clean definition of mate choice is challenging. First, and least controversially, conventional (precopulatory) mate choice occurs when individuals are more likely to mate with certain members of the opposite sex when they are encountered. Despite being uncontroversial, the definition strictly speaking states only that choosiness occurs—in practice it is surprisingly difficult to infer solely from an observed distribution of matings who is choosy. A male with a modest ornament may be accepted by some females but not by others. He is thus more likely to mate with some females than others, but this clearly does not imply that he himself was choosy. The correct interpretation relies on additional behavioral insight into which individuals “would have been willing” to mate. In practice, the definition is used in one of the following two ways. (1) When two or more potential mates are simultaneously encountered, a choosy individual is more likely to mate with one type than another. For example, female frogs generally prefer males with lower-pitched calls. (2) When mates are sequentially encountered, there is the additional requirement that some current mating opportunities will be rejected, even though the choosy individual has eggs or sperm available to produce offspring.

As a second category of mate choice, the potential for cryptic female choice occurs when females mate with more males than are required merely to fertilize all their eggs. Here, a female creates a situation in which there is competition not among males for a mating but among their sperm to fertilize her eggs. Such sperm competition
is often treated as analogous to males' fighting for access to mates. But as already noted, the distinction between intrasexual and intersexual selection is blurry: How should one take into account the various ways that a female's response to competing males (or their sperm) affects the males' eventual reproductive success? Sexual selection clearly occurs, but is it based on mate choice?

Some researchers argue that cryptic female choice occurs only when females actively engage in sperm selection, using the sperm of certain males disproportionately (more often than expected based purely on the relative numbers of sperm inseminated per male). For example, in field crickets, interactions between sperm and the female reproductive tract result in lower fertilization success for sperm from more closely related males. Similarly, in the beautiful Gouldian finch, there are two common head color morphs: red and black. If a female mates with males of both types, she is more likely to produce offspring sired by a male of her own color morph. This is an adaptive response from a female perspective, because offspring from genetically mismatched (different colored) parents are less viable. Females can sometimes also influence how many sperm are transferred by different males. Indeed, comparative studies have provided compelling evidence that the amazing diversity in both male genitalia (e.g., that were observed in similarly looking snakes) and behavior during and after copulation have partly evolved because these traits affect a female's propensity to accept, store, and use a male's sperm.

Other researchers argue for a broader interpretation: female choice occurs whenever females set the "rules of engagement" that determine which males are more likely to gain fertilizations. For example, if females of internal fertilizers have a reproductive tract that increases the fertilization success of the last male to mate, this could be considered a cryptic form of choice that biases paternity toward more recent mates. Likewise, if a female's reproductive physiology makes male fertilization success directly proportional to the relative numbers of sperm inseminated, why not describe this as a mechanism of female choice favoring males that produce more sperm? Such forms of mate choice are rather "passive" compared with behaviors such as physically expelling or destroying sperm. The evolutionary outcome is, however, fundamentally the same: certain males gain more paternity owing to interaction between females and copulating males or the sperm they transfer. The case of direct proportionality could, however, also be viewed as the appropriate null model of reproductive tract design, so that it might be difficult to argue it evolved as a reproductive adaptation: From what simpler ancestral mechanism would it have evolved?

A third category of mate choice is often called cryptic male choice, though this refers to processes that are not necessarily specific to males. Even if an individual does not benefit from rejecting a mating, it might still benefit from adjusting its mating effort (courtship or gamete expenditure) depending on the types of opposite-sex individual it has encountered. For example, in Gouldian finches both sexes preferentially court mates of the same color morph. More generally, in many species males show a propensity to expend greater effort courting and to inseminate more sperm when they encounter larger, more fecund females. These behaviors qualify as choice, even if males never actually refused to mate with any female, because by courting one female more intensely than another males change the likelihood that they will produce offspring when they encounter different types of females. Likewise, when there is sperm competition, males that produce a larger ejaculate size usually have a greater likelihood of siring offspring. To qualify as choice, however, variation in ejaculate size is not sufficient; a male must adjust ejaculate size depending on female traits.

The description of some forms of mate choice as "cryptic" has its origin in cases in which the detection of choice requires information about sperm number and fertilization success inside a reproductive tract. As is clear from the preceding examples, however, not all "cryptic" choice is truly hidden from view; the terminology comes with some historical baggage. "Strategic adjustment influencing whom one has offspring with" is the common theme in all forms of choice.

**Male versus Female Cryptic Choice**

Male and female cryptic choice follows somewhat different evolutionary rules because the former depends crucially on the competitive behavior of rivals. The success of an ejaculate or the effectiveness of courtship depends on the intensity of sperm or mating competition for different females. Male-male competition means that sperm has to be produced in large numbers, or courtship has to be energetic, for a male to gain paternity. There is an upper limit to how much males can invest, so to maximize their returns they should strategically allocate their reproductive effort across the different females they encounter, depending on the value of each female as a potential mate (which includes considerations of how many of her eggs are likely to be fertilized by rivals). Thus, males engaging in sperm competition often exert choice through strategic allocation of sperm.

To be worthwhile, however, strategic allocation always requires that the savings accrued can be used fruitfully. This consideration points to a factor intrinsic to male-male competition that works against cryptic male choice. If female availability is low (e.g., if females reject most mating attempts and/or are usually unavailable to mate because they are providing maternal care),
male-male competition is intense, but males are also likely to have replenished their sperm supplies or re-energized themselves for courtship before they next encounter a female. There is then no reason not to invest maximally in each female. So, the lower the rate at which sexually receptive females are encountered, the less likely it is that males will exhibit cryptic or, indeed, conventional choice.

Cryptic female choice is more likely to be driven by variation in the genetic benefits of being fertilized by certain males. As with cryptic male choice, there is strategic investment: a female "spends more eggs" with some males than with others (exactly symmetrically to the situation in which males spend more sperm with some females than with others). But this is not because the female could not otherwise gain access to enough of the chosen male's sperm. Unlike eggs for males, sperm is only rarely limiting for females, so the presence and behavior of other females is less likely to be a significant factor in shaping egg expenditure. The decisive factor is again mate availability: strategic adjustment of egg expenditure per potential mate becomes more beneficial when rejecting one potential mate does not imply a long wait for the next mate. Similarly, for males, strategic adjustment of sperm is more likely in situations with a short wait for the next female.

Previously, we noted that within-sex competition for opposite-sex gametes generally selects against strategic allocation (cryptic choice) of any kind; competition means opportunities are scarce, so existing ones should be neither rejected nor exploited only partially. There are two exceptions, however. First, strong competition can create a situation in which some individuals benefit by pursuing options that at face value offer lower fitness benefits—for example, preferring females with poor fecundity—but become better options by virtue of being ignored by others. This option has been called prudent choice and can happen in male-male competition (e.g., in some fish, individuals of low competitive ability preferentially court small females) as well as in the relatively rare situations where females are sperm limited. For example, attractive male ungulates can become temporarily sperm depleted, which can lead to direct female-female competition for access to preferred males. Some females are more likely to win contests for access to these males, so less competitive females consequently decide to mate elsewhere.

Second, intense sperm competition can create conditions in which mating opportunities are abundant for males, but each opportunity offers meager fitness gains. To see why male-male competition can now select for (cryptic) male choice, recall that sperm competition can reach intense levels only if females mate multiply. Consider an extreme case in which all females in the local population mate with all males. Mating opportunities are no longer scarce for males, and males should use sperm relatively sparingly: each mating brings about only modest paternity, and future mating opportunities are likely to occur soon. Even though future mating opportunities, too, yield meager benefits, it remains true that saving sperm now is likely to pay off in the near future, because opportunities arise regularly. In this setting, male-male competition can select for strategic sperm allocation because it does not coincide with the low availability of mating opportunities. To qualify as choice, however, variation in male responses to different females (e.g., based on her fecundity or mating status—virgin or otherwise) is still required.

3. CHOOSEINESS LOWERS THE BREEDING RATE, AND THERE ARE OTHER COSTS

The fundamental cost of conventional mate choice is that all else being equal, it lowers an individual's lifetime reproductive output by reducing how often it breeds. This cost can, however, become negligible when many potential mates are simultaneously available. In general, the cost rises when potential mates are encountered rarely.

The simple time delay caused by searching or waiting for an acceptable mate is not necessarily the most significant cost of being choosy. Spending time in other activities before breeding commences can also increase the risk of dying. This risk is present when simply waiting for potential mates, but if mate sampling involves greater mobility, then risks and energetic costs (including less time left to forage) can become even more pronounced, again strengthening the expectation that the lifetime number of offspring produced will decline. Another commonly incurred cost, most relevant in the context of conventional female choice, is that attempts to reject a mate can be costly. Such costs can be substantial despite being subtle. For example, female puppies choose to forage in suboptimal areas to avoid the sexual attention of males. Or costs might be of a more dramatic nature: females that decline to mate run the risk of being injured or even killed by sexually coercive males. Lack of female choosiness in such cases is described as convenience polyandry. By contrast, there are very few species in which males that try to reject a mating are damaged by females.

The concept of convenience polyandry predicts that multiple mating is sometimes the least costly option for a female when there is sexual conflict over mating rates (it minimizes the costs of resisting). However, because multiple mating is a prerequisite for cryptic female choice, it is also worth recalling the costs of multiple mating that would be minimized with monogamy. The most obvious costs include acquiring sexually transmitted diseases, being damaged by the male during
copulation, being killed by a predator while copulating, and losing male contributions to parental care (in cases in which only one social mate helps with feeding the young; this can be reversed to become a benefit of multiple mating if several male mates are willing to feed).

Multiple mating can also intensify sexual conflict when selection favors male traits that elevate a female's immediate rate of offspring production, which is not always congruent with maximizing her lifetime reproductive output. For example, male seminal fluid can contain chemicals that elevate female egg production at the price of decreasing her life span. Males are selected to speed up their mates' reproduction because a male's likelihood of paternity is highest shortly after the mating; later, his sperm might have died, and the female will more likely have had time to remate.

4. THE REWARDS OF BEING CHOOSY

All the preceding factors create a baseline expectation that choosiness has a negative effect on fitness, albeit with some significant complications. If, for instance, multiple mating is costly, then conventional choice can have a positive effect on female fitness by minimizing such costs. However, if conventional choice leads to monogamy, then the prospects for cryptic female choice are erased. By and large, though, the described costs confirm that choosiness should offer compensatory benefits to overcome its negative expected effect on the rate of offspring production.

What form do these rewards take? A common requirement for both sexes is that choosiness is beneficial only when potential mates vary in the benefits they provide. Although some benefits apply to both sexes, it is easiest to first consider females.

Direct Selection for Material Benefits

The least controversial explanation for female preference for certain males is that this increases the number of offspring produced per breeding event or, more generally, over a female's lifetime. Although rarely explicitly discussed, a female might benefit by choosing a male who helps with parental duties or offers some other kind of material resources to the extent that she can now work less hard to raise young; offspring production per brood might not be elevated, but the female now lives longer. All such positive effects on female fitness result in direct selection on female mating preferences. Males do not have to provide material resources actively (e.g., in the form of parental care or nuptial gifts) for direct benefits to occur. They can also elevate a female's fitness by providing her with access to food or other essential resources. This benefit is common in species in which males defend breeding territories that also contain food. Alternatively, females can use mate choice to avoid males that reduce their life span, such as those infected with transmissible diseases.

Although direct benefits are typically considered to be uncontroversial, the evolution of preferences for them offers intriguing challenges. One caveat is that to benefit from material contributions, females must somehow detect males that offer superior resources. This is straightforward when females can reliably assess the quality of the resources before they mate. It is more difficult to gauge how much parental care a male will provide in the future. Although some sexual traits do appear to predict how much care a male will provide, it is unclear what maintains the honesty of these signals. What prevents a male from promising to be a good father and then reneging on the deal? Early theory about parental care and mate choice asked whether "coyness" of females could evolve as a means to make sure a mate is committed enough to stay, but this idea has scarcely been followed up. On the male side of the equation, the fact that material benefits can rarely be divided among several females without reducing the benefit that each gains means that there are interesting courtship and allocation questions still awaiting study.

Indirect Selection for Genetic Benefits

Females can compensate for costly choosiness if it increases offspring fitness. This is a quality-quantity trade-off, so that even if a choosy female has fewer offspring than a randomly mating female, she could still end up with more grandoffspring.

There are two main ways that offspring fitness can be elevated. First, as noted earlier, females might choose males that provide more resources, and these are used to nourish each offspring better instead of increasing the total number of offspring produced. Better-nourished juveniles tend to become more fecund adult females or sexually competitive males. This is not a genetic benefit of mate choice. Second, and far more controversially, preferred males might transfer genes that elevate offspring fitness above that of randomly mating females. If this process is strong enough, it could account for both conventional and cryptic female choice. For the process to work, females have to identify males with desirable genes and then preferentially use their sperm, whether by precopulatory (conventional) or postcopulatory (cryptic) choice.

The quality-quantity trade-off raises a major problem with mate choice for genetic benefits. Females often show an open-ended (directional) preference for certain male traits such as brighter colors or more complex songs. Indeed, directional female choice (not to be confused
with direct benefits!) provides the main explanation for selection on males to produce ever more elaborate sexual traits to increase their mating success. Male success comes not from being, say, bright; it comes from being brighter than rivals. If females choose males based on the expression of traits that do not simply signal information about material resources, this implies that these traits signal heritable variation in fitness ("good genes"). But to overcome the costs of choice, females must identify males who are genetically superior to a randomly chosen male. This must become an increasingly difficult task over time, given that previous female generations have already been selecting males for these same traits. A randomly chosen male of the current generation is expected to have already inherited "good genes." Relentless selection for genes that increase sexual trait expression should eliminate the very variation in "good genes" needed to maintain female.

This is a specific example of a general problem in evolutionary genetics: What maintains heritable variation in traits that strongly affect fitness and, ultimately, in fitness itself? A process unique to the maintenance of heritable genetic variation for preferred sexual traits is that these are assumed to reflect the net effect of all the genes that influence a male's ability to assimilate energy and nutrients and maintain his "condition." This measure of condition is an abstraction that equates to fitness prior to the effect of sexual selection on reproductive success. If sexual signals are condition dependent, then they are more likely to signal heritable differences in fitness. Because innumerable genes affect condition, and because condition can also depend on local adaptation (genotype-by-environment interactions), any mutations or minor temporal or spatial changes in the environment will generate variation in genes that improve condition.

Even with condition dependence and genotype-by-environment interactions, the genetic differences between "average" and "good" males might remain slight. This factor predicts, simply, that female choice for indirect benefits is most commonly found where choice is relatively cheap. For example, when male frogs gather to lek in a pond, and males in the best condition have the highest stamina, then a female that simply arrives when it suits her and prefers the most persistently calling male is effectively choosing for male stamina. The female pays a minimal cost (a randomly choosing female would be nearly identical), but her preference for calls has a great effect on male trait evolution and on which genes are passed on to future generations.

Importantly, some genetic benefits of mate choice can persist without the need for "good genes." Females might benefit by mating with males with more compatible genes, so that the specific genes maximizing fitness vary among females. An obvious example of mate choice for genetic compatibility is inbreeding avoidance. Rejecting mating with close relatives reduces the level of homozygosity in offspring (because relatives more often share the same versions of genes). This choice tends to increase offspring fitness because heterozygotes are better than homozygotes in a range of activities such as immune defense and physiological performance. Given that inbreeding also has a significant beneficial side (it elevates the number of gene copies identical by descent that are transmitted to future generations), inbreeding avoidance implies that genetic compatibility is a very important fitness consideration. It is, however, harder to explain how this kind of preference can lead to directional selection for elaborate mate traits, simply because it is difficult for a male to signal his compatibility to the majority of females in a population unless his heterozygosity, leading to good condition, implies that he is the son of a recent immigrant to the local population (if this is the case, then most females will find that breeding with this male will lead to avoidance of inbreeding).

What about the Benefits of Male Choice, and How Do the Sexes Differ?

Conventional male choice can be favored for the same reasons as female choice. Some females accrue more resources and end up being more fecund than others or produce higher-quality offspring that have been better provisioned. There can, therefore, be direct benefits of male mate choice. To see why conventional mate choice can be rare, though, consider a polygynous species. A choosy male can increase the number of eggs he fertilizes when he mates if rejecting other females allows him to have a maximally large ejaculate on encountering a highly fecund one. This strategy clearly assumes, however, that mating with the other females would have compromised his sperm stores to a significant degree. But if mating opportunities are rare, the likelihood of becoming sperm depleted is probably too small for a male to benefit by rejecting any mating opportunities that arise.

Other potential benefits of male choice follow similar rules to those for females. Some females will have better or more compatible mates than others, so that males can choose mates for genetic benefits, and indirect selection can favor the evolution of male choice, or even cryptic male choice. In reality, cryptic male choice seems to have evolved to maximize the mean rate of offspring production for a given level of male reproductive investment. Effectively, males strategically allocate limited resources (sperm or courtship effort) to maximize the total number of fertilizations across all mating encounters.

Whether one considers cryptic or conventional mate choice, male choice for female traits is expected to be
strongest when mate availability (for males) is high, and each mating and any allied consequences require a large investment. The potential exception is prudent choice that can evolve as a response to a highly competitive situation in which some males opt out and ignore the most highly competed-for females. The prediction that choosiness occurs when mate availability is high follows from the fact that a male should reduce his mating effort (or actually reject a female) only if savings in the form of time, energy, or sperm are likely to be useful in the near future. This clearly requires that future potential mates are readily available.

5. WHY DO THE SEXES DIFFER IN CHOOSINESS?

Both sexes can be choosy, but females tend to be choosier. This conclusion is most obvious when surveying the occurrence of elaborate male and female sexual traits that have evolved owing to mate choice. There are few female equivalents to the peacock's train or the male nightingale's song. However, this is primarily a statement about conventional mate choice. If we take into account cryptic choice, there is abundant evidence that, for example, males in many species strategically adjust the size of the ejaculates they transfer to different females.

One potential explanation for greater female choosiness is that males may be more variable than females in terms of the benefits they provide as potential mates. Data do not, however, support this idea. Females can differ greatly in fecundity, while in many species without male parental care the only benefit of female choice is variation in heritable male fitness, which is likely to be modest in scope.

The most general explanation for the greater prevalence of strong female than male choice in nature is based not on the benefits of choice but its costs. Males, in general, pay a larger cost if they are choosy. To see why, we must consider the total investment (tallying up the number and size of gametes, the effort expended on courtship, and the subsequent investment in caring for offspring) per mating. This investment is often much greater for females than for males. The largest source of this asymmetry can usually be found in parental care, although in external fertilizers lacking care it can be a consequence solely of eggs being larger than sperm. The net result is that after each mating, females take longer to return to a state in which they can again mate (“recovery time”), or in some cases they may be at risk of dying while performing costly care, so they never return to the pool of potential mates. In either case the result is often a male-biased operational sex ratio, reflecting a situation in which there are many more males than females seeking to mate at any given time (see chapter VII.4).

This asymmetry has considerable consequences for mate availability. When the rate at which a female encounters males is far higher than the rate at which a male encounters females, the delay caused by rejecting a potential mate has very different outcomes for each sex. If a female rejects a male, the next potential mate is never far away. (A Helsinki saying is that one should never run for a tram or a man.) In contrast, a male may have to wait a long time until he encounters another female. Consequently, a male should not reject a less profitable than average mate encounter based on the (rare enough to be irrelevant) prospect of taking advantage of a better one soon. This effect is magnified if females have embarked on an evolutionary trajectory toward being choosy. This means that the relevant mate encounter rates for males drop further: ignoring coercive copulations, only females that accept a particular male usefully qualify as potential mates, so mate availability from a male perspective is now even lower.

Of course, there are situations in which males can choose between two or more simultaneously available females. If the situation excludes mating with both, males effectively have to choose: males will reject one for the other, and nonrandom choice is favored. Similarly, conventional male choice is more likely in systems with biparental care or when males otherwise make a substantial postzygotic investment and cannot care for a limitless number of young. Cryptic mate choice can be even more widespread. Multiple mating by females tends to shorten the interval between matings for males, so that prudent sperm usage can become favored as future mating opportunities become more likely for males. Intriguingly, the complexity of male strategic allocation decisions argues against the stereotype that male mating behavior is indiscriminate. Nevertheless, a large asymmetry between the sexes remains: cryptic male choice only rarely leaves females without offspring, whereas female choice (cryptic or otherwise) often creates a large subset of males without genetic descendants. This imbalance has obvious consequences for the overall level of mating effort by each sex seen in nature.

FURTHER READING


Slatyer, R. A., B. S. Mautz, P.R.Y. Backwell, and M. D. Jennions. 2011. Estimating genetics benefits of polyandry from experimental studies: A meta-analysis. Biological Reviews 87: 1–33. The empirical evidence from experimental studies that females mate multiply because they can bias fertilization toward males that elevate offspring performance (fitness) (i.e., for genetic benefits) is quantitatively summarized.