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— JON SEGER AND FREDERICK R. ADLER

MATING STRATEGIES, ALTERNATIVE

In many animal populations, individuals adopt mating strategies that differ from the conventional strategy employed in the population. These *alternative mating strategies* are observed mainly in males, and they are widespread in species in which opportunities for multiple mating are greater for males than for females. Thus, there is little doubt that alternative mating strategies evolve when sexual selection is strong. Research is active on the degree to which the expression of alternative mating strategies depends upon discrete genetic differences among individuals, upon interactions between ge-

netic and environmental factors, or upon behavioral and developmental "choices," mediated by individual perceptions of social status. This article will explain the nature of this variation, identify its possible underlying causes, and describe the evolutionary forces that allow alternative mating strategies to persist in nature.

Sexual Selection and the Mating Niche. Charles Darwin, in *The Descent of Man and Selection in Relation to Sex,* (1874) considered the effects of sexual selection to be functionally similar to those that exist in populations with a surplus of males. He noted that "*if each male secures two or more females, many males cannot pair*" (p. 212). This elegant observation explains why sexual selection causes the divergence of male and female phenotypes, as well as why alternative mating strategies so readily evolve. When only a small number of males secure the majority of matings, male characteristics that promote polygamy are disproportionately transmitted to the next generation. Over time, males are expected to become more modified in their appearance than females. Consistent with this expectation, males show greater phenotypic diversity than females in related species, including a greater tendency to become polymorphic.

Why should alternative mating strategies evolve when some males mate and others do not? The answer lies in the *average* and *variance* in mating success among males, particularly among males expressing the most common—that is, the *conventional*—mating phenotype. Suppose, in a species with equal numbers of males and females, that males defend mating territories. If each such male acquires exactly one mate, sexual selection cannot exist because each male contributes equally to the next generation. However, if some territorial males acquire more than one mate, other males attempting to defend territories will be prevented from mating. When this occurs, the *average* harem size, as well as the *variance* in mate numbers among males, both will increase. Even in species that form pairs, when some males are excluded from mating, variance in male fitness will exist.

This condition not only causes sexual selection; it also creates a "mating niche" for males engaging in *unconventional* mating behaviors. Males who avoid direct combat with males defending territories can often invade breeding territories by indirect means. Once inside breeding territories, unconventional males may surreptitiously copulate with receptive females, as occurs in isopods (see Vignette), lizards, beetles, and ruffs. Alternatively, in species that spawn, unconventional males may position themselves near ovipositing females and spread their sperm over unfertilized ova, as occurs in horseshoe crabs, coral-reef fish, salmon, and midshipmen fish. Stolen matings may yield unconventional males only a fraction of the fertilization success gained by

males defending harems, but, if unconventional males sire even a few offspring, then on average they will have higher fitness than territorial males who secure no mates at all.

Game theory and population genetic analyses agree on the conditions necessary for the invasion and persistence of evolutionary stable strategies. For males employing alternative mating strategies, these conditions are most easily met when both the average harem size and the variance in mating success among conventional males are large. Increasing harem size among mating conventional males increases the fraction of conventional males who are excluded from mating altogether. Thus, the larger the average harem size becomes, the fewer fertilizations unconventional males need to acquire within harems in order for their average fitness to equal that of all conventional males combined. Although the fitness of unconventional males seems inferior to that of conventional males, in fact the average fertilization success of all unconventional males often equals or exceeds the average success of all conventional males (see Vignette).

Making the Best of a Bad Job. Note that the above description is distinct from the notion that unconventional males, often called *satellite* males, "make the best of a bad job." This latter hypothesis is often used to describe the relative fitnesses of males exhibiting unconventional phenotypes, and it is widely invoked to explain reports that satellite males are less successful at mating than territorial males. However, these apparent tests of the "best of a bad job" hypothesis consider only the mating success of males who actually mate. As explained above, when some territorial males are excluded from mating, average mating success, calculated only for mating territorial males, is certain to exceed the average mating success of satellite males. This is true because average harem size always overestimates the average mating success of all territorial males, unless every male in the population mates once. When mating males, as well as nonmating males, are included in calculations of average mating success, the fitnesses of territorial and nonterritorial males are expected to be, and have been shown to be, equivalent.

Alternative Mating Strategies in Males and Females. Why do alternative mating strategies appear more often in males than in females? The answer is once again found by considering the average and variance in mate numbers, and thus the average and variance in offspring numbers, within each sex. The average number of offspring produced by males who mate is equal to the average number of offspring per female, multiplied by the number of females with which each male mates. Thus, the average fitness of mating males can be many times greater than that of the average female. The fitness of the average unsuccessful male, on the other hand, is

zero, and is therefore less than that of the average female. The more females tend to mate only with certain males in the population, the more the average number of offspring sired by mating males increases, and the larger the variance in offspring numbers among all males becomes.

Even in species in which females routinely seek multiple mates, individual female fecundity tends to be more limited than individual male fertility. Thus, on a populational level, the variance in offspring numbers among females is seldom as large as it is among males. Moreover, unlike males, relatively few females are prevented from mating altogether. Smaller fitness variance among females, compared to that among males, limits the size of the "mating niche" available to females attempting to reproduce by unconventional means. Thus, it is only in species in which considerable variance in female fitness exists that alternative female mating strategies are expected to evolve (see below).

The Expression of Alternative Mating Strategies. Three fundamental patterns of phenotypic expression exist for alternative mating strategies: Mendelian strategies, developmental strategies, and behavioral strategies. Each pattern of expression depends, at the most proximate level, on hormonal and neurological factors that regulate the timing and degree with which phenotypic differences appear. The nature of each regulatory mechanism depends, in turn, on its underlying mode of inheritance. Ultimately, the genetic architectures responsible for each mode of inheritance depend on the circumstances in which mating opportunities arise — that is, on the intensity of selection favoring distinct reproductive morphologies, as well as on the predictability or unpredictability of mating opportunities relative to individual lifespan.

Mendelian strategies. Alternative mating strategies controlled by few loci of major effect, which segregate in populations according to Mendelian rules, are well documented in diverse animal species. Examples include marine isopods (Vignette), bulb mites, damselflies, fig wasps, several species of poeciliid fish, side-blotched lizards, and ruffs. In each of these cases, specific allelic combinations produce morphologically and behaviorally distinct male phenotypes.

Mendelian strategies are expected to arise when sexual selection favors specialized mating phenotypes, and when the relative mating success of each phenotype is unpredictable within male lifetimes. By chance, a morph is well or poorly suited for securing mates in a given environment, and accordingly, its relative fitness, as well as its relative population frequency, rises or falls. In such circumstances, genes of major effect are expected to exclude genetic architectures that allow a phenotypic response to environmental cues predicting mating success. When such cues are lacking, the benefits of being

STRATEGIES AND TACTICS

The term *strategy* comes from evolutionary game theory. In this sense, a strategy is a preprogrammed set of behavioral or life history characteristics. Alternative mating strategies can therefore be viewed as functional sets of behaviors or morphologies used by their possessors to acquire mates. An *evolutionary stable strategy* (ESS) is a strategy that persists in a population. Such persistence occurs for one of two reasons. Either the average fitness of individuals expressing the ESS *equals* that of all other strategies existing in the population, or the average fitness of individuals expressing the ESS *exceeds* that of other strategies that might invade the population. If a strategy's average fitness is consistently *less than* that of other strategies, it will be removed from the population by selection.

Strategies are *adaptive*. Implicit in this are two further assumptions. First, genetic variation is presumed to underlie such traits. Heritability is required for *any* trait to change in frequency or be removed from a population, as described above. If genetic variation is lacking, no response to selection is possible. Second, stabilizing selection is presumed to refine trait expression. This is the process by which less fit trait variants are culled, more fit trait variants reproduce, and over time, a trait's function becomes recognizable. Traits with uniformly inferior fitness seldom persist in populations long enough to be shaped by selection.

Recent descriptions of discontinuous variation in mating phenotype distinguish between genetically distinct "strategies" and phenotypes that represent condition-dependent "tactics." The term *tactic* is used to describe behavioral or morphological characteristics whose expression is contingent, either on environmental conditions, or on the "status" of the individuals in which they appear. *Status-dependent selection* (SDS), the term used to describe how selection may operate on such traits, is presumed to allow individuals to assess their potential mating opportunities, and then make a behavioral or developmental "decision" that leads to greater mating success than if the choice had not been made. According to the SDS hypothesis, individuals in dimorphic populations are identical in their ability to choose one or another status-dependent phenotype.

The term *tactic* is clearly useful for describing phenotypes that are flexible in their expression, as opposed to those that segregate according to Mendelian rules. However, considerable evidence now indicates that polymorphisms in mating phenotype, which arise by phenotypic plasticity, in fact represent *mixtures* of evolutionary stable strategies. If this pattern is a general one, genetic architectures that allow phenotypic flexibility, like polymorphisms controlled by Mendelian factors, are expected to persist in populations by frequency-dependent selection. Thus, while "tactic" adequately describes reproductive phenotypes that vary with environmental conditions, "strategy" is appropriate for *all* evolved polymorphisms in reproductive behavior, regardless of how their expression is controlled.

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able to change phenotype are low or nonexistent. Because trait heritabilities of the genetically determined strategies approach unity, the frequencies of Mendelian strategies are expected to oscillate over brief intervals with changes in morph fitness. Over longer durations, different morphs are expected to persist in the population because their average fitnesses are equal.

Developmental strategies. Discontinuous phenotypes produced by distinct developmental trajectories, which *do not* segregate in a Mendelian manner, are also well documented among animals. Examples include earwigs, crickets, horned beetles (see below), amphipods, freshwater prawns, salmonids, coral-reef fish, midshipmen fish, and again, side-blotched lizards. Developmental strategies are expected to arise when sexual selection favors specialized mating phenotypes, *and* when environmental cues, detectable by males, predict the type of mating opportunities likely to become available. Genetic architectures sensitive to environmental cues allow males to tune their mating phenotypes in response to changing environments. Such architectures are expected to exclude major genes that do not permit phenotypic plasticity.

In many species, the environmental cue to which males respond appears to be their own growth rate. In certain species, males unable to reach some threshold size within a given duration tend to mature early as satellites, whereas males who cross this threshold continue to grow and mature later as territorials. In other species, rapidly growing males tend to mature as satellites, whereas slower growers tend to become territorial. Genetic variation controlling male growth rate, like most

traits influenced by numerous hereditary factors, appears to be normally distributed. Thus, the position of the body size threshold within the distribution of male growth rates determines the proportions of the population likely to consist of satellites and territorials. The relative success of satellites and territorials, in turn, appears to determine where the average male growth rate lies with respect to the body size threshold. Although circumstances favoring satellites or territorials can influence the population frequencies of each morph, directional selection can also change the position of the threshold itself.

For example, males in most species of *Onthophagus* beetles bear impressive horns. In all such species, horns are present only on large males and are used in contests for access to females. Horns vary in size, shape, and location on individual beetles, and a steplike relationship exists between horn length and body size in adult males. Small individuals possess rudimentary horns or lack them entirely, whereas large individuals possess well-developed weaponry. Although smaller males lack effective combat structures, these males are sexually mature and highly mobile and steal matings within the burrows of horned males. Horn size correlates with success in burrow defense, but small body size correlates with success in stealing matings. Thus, males that are intermediate in either of these characteristics are unlikely to mate at all.

Douglas Emlen and his colleagues have used controlled breeding designs and diet-manipulation experiments to explore the genetic basis of intraspecific variation in male horn length in several species of *Onthophagus*. Within lineages, morph frequencies do not segregate in a Mendelian manner. However, Emlen found that he could produce males with unusually large and unusually small horns by selecting in opposite directions on male horn length. This approach changed horn length, as well as the size within each lineage at which males developed horns. These results indicate not simply that horn length is heritable. They also demonstrate that a heritable "threshold" exists, which influences how males respond to their feeding history and thus to their own growth rate.

Threshold models for phenotypic plasticity require that individuals are genetically variable, *not* genetically identical. This is a reasonable assumption, given what is known about genetic variation in natural populations. In the case of growth rate polymorphisms, individuals either commit to an accelerated developmental trajectory or not, depending on the position of their genotype relative to the population threshold. Thus, only *part* of the population, not the *entire* population, must respond to an environmental cue for male polymorphism to appear. Threshold inheritance explains much about variation in male phenotype within and among populations. As the

frequency of circumstances favoring one or another male phenotype changes, the proportion of a population likely to respond to environmental cues is also expected to change. Interpopulational variation in the proportion of males exhibiting each phenotype is expected to exist, and it does. Such variation is *not* expected if males are genetically monomorphic with respect to their ability to express one or another mating phenotype.

Behavioral strategies. The most commonly observed alternative mating strategies appear to be those involving discontinuous shifts in mating behavior. Behavioral strategies are expected to evolve when environmental changes influencing mating success occur often within individual lifetimes, *as well as* when the circumstances in which successful matings occur are highly variable. Thus, mobile species that breed more than once are most likely to exhibit behavioral polyphenism in the context of mating. Examples of such variation in mating behavior include dungflies, solitary bees, scorpionflies, many amphibians, songbirds (see below), ruffs, rodents, ungulates, felids, and primates. In each of these cases, males, and often females as well, rapidly change their behavior in ways that allow them to exploit mating opportunities as they arise.

An excellent example of such variation exists in cases of extrapair mating and egg dumping in songbirds. Darwin was intrigued by sexual dimorphism in group-nesting, apparently monogamous birds. He reasoned that sexual selection could operate in such species if females in superior condition nested early with the most attractive males. Elaborate male characters could thus be favored through the enhanced fecundity of their mates. However, an alternative, more powerful hypothesis exists, now that DNA fingerprinting has shown that males and females in a large number of "socially monogamous" species engage in extrapair copulations (EPCs). If multiple females sneak matings with the most attractive males and then rear the resulting offspring with cuckolded males, variance in offspring numbers among males will increase, and sexual dimorphism can evolve.

A surprising number of non-dimorphic, "socially monogamous" animals also engage in EPCs. In these species, both sexes routinely seek multiple mates, although particular individuals do not appear to be favored. Paternity in most nests is mixed, and mixed maternity also exists because females "dump" eggs in other females' nests. If EPCs and egg dumping increase the variance in offspring numbers in either sex, sexual dimorphism could evolve. However, if most individuals tend to mate more than once, although the average and the variance in mate numbers may increase in both sexes, the sex difference in the variance in offspring numbers will be small. In such cases, the species will remain monomorphic.

The underlying genetic architectures responsible for

behavioral variability are not well understood, but they appear to be similar to those described above for developmental strategies. That is, genetic variation underlying quantitative traits is expected to influence the likelihood that individuals will express a particular mating behavior. In a given situation, individuals with phenotypes below the liability threshold express a default set of mating behaviors, whereas individuals with phenotypes above this threshold express another behavioral set. Genetically variable characters influencing behavioral liability are known to include individual sensitivities to crowding and to circulating hormone levels. Other characters likely to influence mating behavior may include heritable sensitivities to pheromones, or to observations of multiple mating by other individuals. In the presence of a strong environmental cue, many individuals are expected to adjust their phenotype, whereas weaker cue intensity may induce few or no individuals to change. Thus, the same female distributions that induce some males to assume satellite behavior are expected to cause other males to persist as territorial males, as is widely observed.

Satellite Males on Leks in Ruffs. Delicate sandpipers known as ruffs (*Philomachus pugnax*) inhabit marshy regions in northern Europe and Asia. Ruffs are named for the mane of feathers borne by adult males. Ruffs breed on clusters of mating courts (leks), and in most populations, males exhibit two color morphs. About 85 percent of males consist of territorial residents, who bear darker plumage and defend mating courts against other court residents. Nonterritorial, satellite males, bearing lighter plumage, make up the remainder of male populations. Satellites are recruited onto residents' courts, where pairs of males form temporary breeding alliances.

David Lank and his colleagues (1999) have shown that plumage differences between residents and satellites are controlled by a single Mendelian locus, or perhaps by a chromosomal inversion that segregates within families. Females do not exhibit plumage variation like males, although females treated with testosterone implants develop male characters. When a female arrives on a mating territory, both males of the pair court her, but the resident often drives the satellite away. However, if a neighboring resident challenges the courting resident, the satellite may return and mate with the female while the residents fight. Females visiting mating courts routinely mate with both males, particularly on smaller leks. The combined displays of residents and satellites on small leks may be more attractive than larger leks containing only residents. Despite temporal variation in ruff behavior on leks, the average fitnesses of resident and satellite males appear to be equal.

Developmental Polymorphism in Pacific Salmon. Two male morphs coexist in southern populations of

coho salmon (*Oncorhynchus kisutch*). Fry of this species leave their natal streams and mature in the Pacfic Ocean. Larger, *hooknose* males return to spawn after three or more years. Smaller males, or *jacks*, mature early and return after only two years. Each hooknose defends a gravel nest on the stream bottom where females spawn. Hooknoses usually fertilize the ova in their nests. However, jacks lurking nearby may steal fertilizations by darting in and ejaculating when spawning begins. The male closest to the spawning female is most likely to sire young. Large hooknoses do best against other hooknoses, small jacks do best against other jacks, and most males of intermediate size are excluded from mating altogether.

Because jacks must be rare to mate successfully, the relative fitnesses of hooknoses and jacks appear to be frequency-dependent. Mart Gross (1996) demonstrated this relationship by considering the simultaneous influences of survival probability, reproductive tenure, and frequency-dependent spawning efficiency for males of each type. To standardize the units of these diverse fitness measures, Gross estimated the ratio of each jack-to-hooknose fitness estimate, then calculated the product of the three ratios. His result, .95, while not bounded by confidence limits, suggested that hooknoses and jacks experience approximately equal fitness. Such conditions are necessary and sufficient to maintain a genetic polymorphism in male phenotype by frequency dependent selection.

[*See also* Frequency-Dependent Selection; Sexual Selection, *article on* Bowerbirds.]

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— STEPHEN M. SHUSTER

MATING SYSTEMS

[*This entry comprises two articles. The first article provides a discussion of plant mating systems; the second article is an overview of the major kinds of animal mating systems with a discussion of their implications for mate choice. For related discussions, see* Male–Male Competition: *and* Mate Choice.]

Plant Mating Systems

Mating systems of flowering plants are highly diverse. Part of the reason for this diversity is simple: plants can repeatedly make new reproductive organs throughout their lives. Hence, different plants can, depending on the species, vary whether a flower contains only male reproductive organs (pollen grains—the male gametophytes), only female reproductive organs (ovules—the female gametophytes), or both, and they can even vary this from year to year. Mating systems range from one in which seeds can be produced without fertilization by an asexual process (apomixis), to those in which pollen needs to be transferred from one individual to another in a process known as pollination.

If you look at most flowers, you will see both male and female reproductive organs (or parts) in the same flower ("perfect" flowers). This mating system, hermaphroditism, is the most widespread one in flowering plants. Look even closer and you may notice that the male and female parts actually touch each other or can easily be brought into contact. This proximity makes it possible for plants to fertilize themselves (selfing). The most extreme case of selfing occurs in flowers that never open, but instead always self inside the bud. These are called cleistogamous flowers. However, not all hermaphroditic plant species self or are even capable of selfing. Selfing can lead to inbreeding depression, which occurs when seeds produced from selfing are not as vigorous or die more often than those produced from nonselfing (outcrossed). Hence, mechanisms for reducing or avoiding selfing exist in many hermaphroditic species with perfect flowers. These outcrossing mechanisms include separation of the male and female parts in time (dichogamy), separation of the parts in space (herkogamy), and genetic prevention of selfing (self-incompatibility). Finally, some plants have evolved unisexuality (separation of the sex parts into different flowers or individuals) as a way of reducing or preventing selfing.

As mentioned, even if a plant makes perfect flowers, it can reduce selfing by presenting male and female parts