

25

Alternative Mating Strategies

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In many animal populations, individuals exhibit discontinuous variation in their reproductive behavior and morphology (Gadgil 1972; Gross 1996; Shuster & Wade 2003). Although diversity may appear within either sex as well as within hermaphroditic populations, polymorphic mating phenotypes, also known as *alternative mating strategies*, are most commonly observed in species with separate sexes and are usually expressed among males. The staggering diversity and taxonomic breadth of mating polymorphisms have fascinated behavioral and evolutionary biologists since Darwin (1874; reviews in Gross 1996; Shuster & Wade 2003; Shuster 2007, 2008; Oliveira et al. 2008). In this chapter, I will briefly summarize this diversity and explain my view of why mating polymorphisms are biologically interesting. I will next discuss existing explanations for observed variation in mating polymorphisms, and then identify three fundamental questions that have persisted for over a quarter century in studies of alternative mating strategies. I provide answers to these questions using data from published literature as well as suggestions for new research.

DIVERSITY IN MATING STRATEGIES

Alternative male morphs appear in most major animal taxa (Shuster & Wade 2003; Oliveira et al.

2008). In certain squid, decapod crustaceans, and teleost fish, polymorphic male phenotypes are represented by small, nondescript yet fully mature individuals who lurk with bulging testes near massive harem masters, waiting for opportunities to flash into territories, steal a few matings, and then speed away unscathed (Hanlon 1998; Correa et al. 2003; Gross 1982; Taborsky 2008b). In isopod crustaceans, dung beetles, and ungulates, such “sneaker” or “satellite” males are often stealthy, insinuating themselves among females within the territories of combative males, and, again, mating when and with whom they can (Shuster 1989; Emlen 1997; Isvaran 2005). Alternative mating strategies may also include males who mimic females (isopods, Shuster 1992; sunfish, Dominey 1980; garter snakes, Shine et al. 2001; shorebirds, Delehanty et al. 1998), males who provide exceptional care to young (cichlid fish, Taborsky 1994; Awata et al. 2004), and males bearing two, three, or more distinct colors or display patterns that convey information to mates as well as to potential rivals (shorebirds, Lank et al. 1995; lizards, Sinervo & Lively 1996; fish, Taborsky 2008b). Adult male phenotypes may be determined from birth (mites, Radwan 1995; isopods, Shuster & Sassaman 1997) or they may be directed by a range of environmental influences (many species; Oliveira et al. 2008). Well-fed males in some species may delay maturation and become territorial (dung beetles, Moczek 1998), whereas rapid growth in other species leads

males to mature early, live fast, and die young (salmon, Hutchings & Myers 1994).

Polymorphic body forms are easiest to notice, but males may differ only in their behavioral phenotypes (Finke 1986; Waltz & Wolf 1988). Males may attempt to woo females with gifts, food, or shelter, but, lacking these enticements, will abandon chivalry and attempt to mate by force (scorpionflies, Thornhill 1981; ducks, Gowaty & Buschhaus 1998; primates, Smuts & Smuts 1993). Males may vary in their tendencies to seek multiple mating partners or to defend individual females for extended durations (horseshoe crabs, Brockmann & Penn 1991). Male phenotypes may also be age-related, with older males attempting to signal females, whereas younger males remain silent, waiting near signalers and occasionally, only occasionally it seems, securing a chance to mate (bullfrogs, Howard 1984; tree frogs, Gerhardt et al. 1987). Even when behavior alone is polymorphic, changes in phenotype may become permanent with age, but more often behavioral polymorphism is reversible, with males changing from searchers for females, to waiters for females, and back to searching again within a single afternoon (butterflies, Alcock 1994b).

The short explanation for observed diversity in male mating phenotype, within as well as among species, is this: opportunities for acquiring multiple mates tend to be greater for individuals in species with separate sexes, and, in such species, opportunities for polygamy occur most often for males (Shuster 2007; chapter 20). Sexual selection is especially strong when each female mates only once and when the sex ratio equals 1. Under these circumstances, if some males mate more than once, other males must be excluded from mating and sexual selection is the inevitable result (Darwin 1874; Shuster & Wade 2003). Regardless of the number of times females mate, sexual selection requires that some males reproduce at the expense of others, and although sexual selection can intensify when females mate more than once, these conditions are surprisingly restrictive. For sexual selection by sperm competition to occur, females who mate more than once must all tend to mate with the same subset of males within the population, and they must also all tend to fertilize their ova using sperm produced by particular males within that subset. If such a positive covariance between male mating success and male fertilization success does not exist, multiple mating by females will ameliorate rather than intensify sexual selection (Shuster & Wade 2003). In general,

sexual selection favors heritable traits that confer differential mating and fertilization success, including unconventional mating phenotypes. Stated differently, alternative mating strategies readily evolve when sexual selection is strong.

WHY STUDY ALTERNATIVE MATING STRATEGIES?

Why should we bother to study alternative mating strategies? There are at least three reasons, with the first reason described above. The diversity of alternative mating strategies is astonishing. It begs for explanation, and for this reason alone it has fueled the careers of many scientists. Yet alternative mating strategies also shed light on fundamental evolutionary processes, including a great paradox in evolutionary biology. That paradox is, how can sexual selection overcome the combined forces of natural selection on males and females that oppose it (Shuster & Wade 2003)? Highly modified male phenotypes are well known to impose great survival costs upon the males that possess them. How is it that these extreme male variants, as well as the females that mate with or produce them, are not simply eliminated by natural selection outright?

Thus a second compelling reason to study alternative mating strategies is, these traits show why sexual selection is among the most powerful evolutionary forces known (Shuster & Wade 2003). Sexual selection is well known for producing male displays, weaponry, and extreme female mate preferences (chapters 20 and 24), but it is also the primary evolutionary driver behind mating polymorphisms. As mentioned above, alternative mating strategies invade populations when relatively few conventional individuals secure mates (Gadgil 1972; Shuster 2007, 2008). As we will see, when the fraction of the population that is excluded from mating becomes large, sexual selection intensifies, increasing the likelihood that novel mating phenotypes will arise. Because alternative mating phenotypes allow their possessors to mate under these extreme circumstances and because some of these individuals mate with disproportionate success, unconventional male phenotypes experience intense sexual selection themselves. As a consequence, not only are alternative male morphs often the antithesis of conventional males in the species in which they appear (e.g., tiny, secretive sneakers coexist with huge, aggressive territory defenders) but their population frequency, as

well as the frequency of conventional mating phenotypes, can rapidly and dramatically change (Gross & Charnov 1980; Shuster 1989; Sinervo & Lively 1996).

Heritable phenotypes that are not under sexual selection, but instead which confer more subtle fitness costs or advantages to their possessors may also evolve, but natural selection on these traits leaves a less easily recognized signature than when sexual selection occurs. Why is this so? The reason lies in the magnitude of fitness variance generated by each form of selection (Shuster & Wade 2003). When differences in relative fitness among individuals are absolute, variance in fitness is large and selection becomes intense. In contrast, when differences in relative fitness are subtle, variance in fitness is small and selection is relatively weak.

Under sexual selection, when some males mate more than once and/or fertilize disproportionate numbers of ova, other males must be excluded from reproducing at all. This condition makes fitness variance very large (Darwin 1874; Shuster & Wade 2003; see below). Under natural selection, differential success by some individuals within the population may occur, but success by some individuals need not obliterate the fitness of other individuals outright, as sexual selection always does. This is not to say that natural selection is never sufficiently intense to cause rapid evolutionary change. Indeed, it can be. However, when natural selection is intense, new phenotypes often sweep through populations to fixation so quickly that evolutionary change goes unnoticed until after the fact (Wootton et al. 2002). Intense natural selection may also induce phenotypic cycles, but documented cases of this process appear to take years, decades, or even millennia to complete (Kettlewell 1955; Vermeji 1987; Hori 1993).

Alternative mating strategies are different. They routinely involve multiple phenotypes that persist within populations, often with wide fluctuations in frequency. Why might this be so? The apparent answer is frequency dependent selection (Haldane & Jayakar 1963; Slatkin 1978; Crow 1986) and, in particular for mating polymorphisms, negative frequency dependent selection (see chapter 3). In this self-regulating evolutionary process, the frequency of one morph can increase, but as it becomes abundant relative to other morphs, its fitness advantage declines, progressively favoring a rarer morph whose frequency in turn increases until its own fitness decays. Fluctuating fitness differences among

morphs, as we will see, are a consequence of strong sexual selection, and under such circumstances, alternative mating strategies tend to oscillate within populations instead of rushing to fixation. Moreover, because selection on polymorphic phenotypes is so strong, these oscillations tend to be large and they tend to cycle fast.

Thus, a third reason for studying alternative mating strategies is, these polymorphisms show how sexual selection can cause rapid, recurring evolutionary changes over uncommonly short periods of time. Depending on the life span of the species involved, significant population cycles of conventional and alternative mating phenotypes may be observed within a few years (Sinervo & Lively 1996); some cycles are observed annually (Lank et al. 1995; Sinervo 2001); and in some cases, oscillations may occur within months or even weeks (Shuster et al. 2001). Alternative mating strategies reveal how negative frequency dependent selection is mediated by sexual selection, and because the currencies of sexual selection are mating success and variance in offspring numbers, investigations of alternative mating strategies allow the explicit quantification of both evolutionary processes, as we will see below (Wade 1979; Shuster & Wade 2003; Shuster 2007, 2008).

FUNDAMENTAL QUESTIONS

Several schemes now exist for describing the expression of alternative mating strategies. Each has a different emphasis, but all are based on the widely recognized tendency for mating polymorphisms to differ in the degree to which genotype and the environment may influence trait expression. Since Darwin (1874) described male polymorphism at length, several authors have proposed hypotheses about their expression and persistence (Morris 1951; Gadgil 1972; Dawkins 1980; Eberhard 1982; Maynard Smith 1982). Austad (1984), after reviewing these contributions, provided a synthetic description of the observed diversity, wherein he identified issues that have remained paramount in research on alternative mating strategies ever since.

Austad's dichotomously branching diagram (figure 25.1) distinguished (1) whether polymorphisms represented genotypic versus phenotypic alternatives, (2) whether the fitnesses of each morph were expected to be equal or unequal (*isogynous* versus *alogynous* phenotypes), and (3) whether

phenotypic alternatives were reversible or irreversible within individual lifetimes. Austad's (1984) diagram showed what researchers then and now have recognized: mating polymorphisms in which phenotypes show at least some flexibility in their expression are more common than those that do not. Austad (see also Dominey 1984) had begun to question whether game theory principles could be applied to the study of alternative mating strategies (or *alternative reproductive behaviors*, ARBs) because the assumptions required to find the evolutionary stable strategy (ESS; Maynard Smith 1982) did not always accord with data available for these polymorphisms. In particular, the average mating success of persistent phenotypes in many natural populations were not always found to be equivalent (Dawkins 1980; Thornhill 1981; Eberhard 1982). Then and now, equal fitnesses among morphs are a population genetic and game theory necessity if selection is to maintain genetically based polymorphism over time (Haldane & Jayakar 1963; Slatkin 1978, 1979a, 1979b; Maynard Smith 1982; Crow 1986). Nevertheless Austad (1984) explicitly identified a *genetic-nongenetic* dichotomy for alternative mating strategies consistent with Dawkins' (1980) hypothesis that fitnesses need not be equal among morphs when considering certain persistent alternative mating phenotypes (see below).

A second major development in the study of mating polymorphisms, and undeniably one of the most influential, was Gross's (1996) description of the status dependent selection (SDS) hypothesis. Gross, like Austad (1984) noticed the preponderance of mating phenotypes in nature with flexible expression, and proposed an evolutionary framework for considering them. He suggested that when the fitness consequences of alternative mating phenotypes depend on the relative competitive ability of the interactants, in other words, on their *status* relative to one another, then selection should be considered *status dependent*. Also, Gross (1996) proposed that when status did vary among individuals, this variation was primarily due to environmental influences.

Two central assumptions of the SDS hypothesis were that the distribution of status among individuals is normal within most populations, and that individuals always play the strategy that maximizes their fitness within the population given the particular local conditions of relative status. In this sense, the SDS model was conceptually linked to Dawkins' (1980) hypothesis that if sexual selection favored the most combative, showy, and vigorous males, then males unable to compete in this arena might adopt alternative sets of behaviors or morphologies that would still allow them to mate.

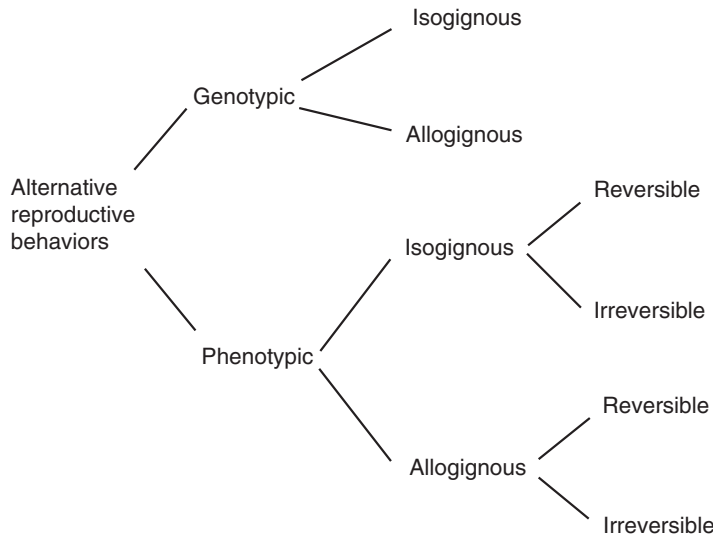


FIGURE 25.1 Austad's (1984, redrawn) diagram distinguishing whether (1) mating polymorphisms represented genotypic versus phenotypic alternatives, (2) the fitnesses of each morph were expected to be equal or unequal (*isogynous* versus *allogynous* phenotypes), and (3) phenotypic alternatives were reversible or irreversible within individual lifetimes.

These inferior males might be less successful than the dominant males in the population, but they would still do better than if they had secured no mates at all. That is, they could “make the best of a bad job,” and still persist within the population. Following the form of game theory models, Dawkins (1980) proposed that if all males possessed such flexibility, that is, if this form of plasticity were fixed within the population, there would be no need for the fitness of alternative variants of male mating behavior to be equal among all male phenotypes. Gross (1996) took this notion a step further to state that if all males were genetically identical, fitness differences among them of any kind would be of no evolutionary consequence.

Gross's (1996) hypothesis elegantly captured the central elements of most observations of polymorphic phenotypes to that date; it was obvious to everyone that flexible phenotypes were more common than inflexible ones. Also, many researchers had reported that the fitnesses of the different morphs were seldom equivalent (reviews in Austad 1984; Eberhard 1982). Thus, Gross's approach reconciled, too, the study of alternative mating strategies with game theory, which had identified conditional strategies as being *nongenetic*; that is, they were *bourgeois* phenotypes in which all individuals in the population were identical in their ability to express a flexible trait (Maynard Smith 1982; Taborsky 2008b). Gross (1996) also stated explicitly what Austad (1984) and game theory implied; that individuals within a species expressing conditional phenotypes were genetically *monomorphic*.

Taborsky (1998) provided the next seminal discussion on mating polymorphisms, identifying three different levels at which alternative male phenotypes could be assessed: (1) determination, the relative degree to which genetic or environmental variation influence phenotypes, (2) plasticity, the relative degree to which phenotypes are flexible or inflexible in their expression (chapter 6), and (3) selection, the way in which fitness differences might (or might not) lead to the persistence of phenotypes, as well as how variation in male phenotype within lifetimes influences overall mating success. Regarding determination, Taborsky (1998) moderated somewhat Gross's genetic monomorphism hypothesis (as did Gross himself; see Gross & Repka 1998). However, Taborsky reiterated the disproportionate representation of condition-dependent strategies in nature, and placed environmental influences in high relief, stating, “Reproductive phenotypes may be

either genetically or environmentally determined. It is highly unlikely, however, that only one of the mechanisms will be responsible for any important set of adaptive characters. Environmental modification, at least, should be ubiquitous.”

Regarding plasticity, Taborsky (1998) covered similar issues as his predecessors, but he emphasized individual aspects of trait expression, particularly the tendency among individuals expressing conditional phenotypes to change or not change phenotypes within their own lifetimes. This emphasis specifically addressed Austad's (1984) third point. Taborsky (1998: 225) noted, “Reproductive phenotypes may be fixed for life, or be an expression of successive, ontogenetic stages, or be an adaptive response to momentary conditions. An important question to ask is whether behavioural plasticity exists at the population level only, or within individuals with either successive or simultaneous variation between tactics (which are not mutually exclusive).”

Regarding how selection might act on mating polymorphisms, Taborsky (1998: 225) considered both proximate and ultimate causation, and called attention to frequency dependent processes, although he allowed that inferior mating tactics might still appear within populations:

Alternative reproductive phenotypes may be stabilized by obtaining equivalent Darwinian fitnesses, or they may reflect a disparity in the quality of individuals. The former case is based on frequency-dependent pay-offs to reproductive competitors displaying either bourgeois or parasitic tactics. The latter case is based on the common fact that the ability to monopolize access to females differs greatly between individuals because of, for example, divergent growth histories, health or reproductive experiences. Individuals of inferior competitive ability may suffer from unavoidable constraints and maximize their lifetime reproductive success by adopting parasitic rather than bourgeois tactics, even if these do not provide similar fitness rewards.

Taborsky (1998) thus encapsulated many researchers' interest in individual variation in trait expression, apart from how such variation might be represented at the population level. In this context, Taborsky suggested that “any combination is possible between the alternatives existing at the levels

of determination, plasticity and selection of reproductive phenotypes” (225). He reiterated the possibility that environmental variation could lead to unequal fitnesses among phenotypes: within populations as well as within individual lifetimes. However, he also recommended that “these explanatory levels should be clearly separated from each other to avoid confusion.”

Shuster and Wade (2003) made this warning more explicit, and specifically addressed the conceptual and quantitative difficulties that arise when terminology used to describe individual and population variation become confused. They attacked the concept of genetic monomorphism in favor of the view that all traits include genetic and environmental influences on their expression. They did this to echo other researchers who had made this point (Austad 1984; Hazel et al. 1990; Gross & Repka 1998; Taborsky 1998), but rather because the assumption of genetic monomorphism seemed to be made whenever conditional strategies were discussed using game theory terminology (see Tomkins & Hazel 2007; Oliveira et al. 2008, pp. 6–13 for recent examples). Maynard Smith (1982, p. 4, 21–22) had emphasized that the genetic assumptions underlying mixed evolutionarily stable strategies were made for simplicity alone. However, the simplification of genetic monomorphism seemed repeatedly to be taken at face value as an accurate representation of the genetic architecture underlying phenotypic plasticity. Most results on the inheritance of conditional polymorphisms concur that it is not (reviews in Schlichting & Pigliucci 1998; Tomkins & Brown 2004; Rowland & Emlen 2009)

Shuster and Wade (2003) argued that although descriptions of individual variation may be interesting in their own right, whether a phenotype persists in a population will depend on its relative fitness: not when examined from one life stage to the next, but rather when considered relative to all other individuals within the population. Shuster and Wade restated the fundamental evolutionary principle that phenotypic variants with relative fitnesses below the population average will inevitably be removed by selection (Maynard Smith 1982; Crow 1986), even if that selection is slowed by environmental (i.e., conditional) influences on phenotype (Haldane & Jayakar 1963). Shuster and Wade (2003) also asserted that when mating and nonmating individuals were included in fitness calculations, average fitnesses among morphs were likely

to be equivalent (see below), even when phenotypic expression was condition dependent. They suggested therefore that Dawkins’ (1980) “bad job” may not be so bad after all.

Shuster and Wade (2003), like Austad (1984), cast doubt on the facile use of game theory terminology and assumptions for addressing population genetic and quantitative genetic variation. However, Shuster and Wade suggested, too, that with proper considerations of fitness variance within populations, specifically by including nonmating males in estimates of relative fitness (see below), solutions obtained using game theory would indeed conform to existing population genetic theory (Haldane & Jayakar 1963; Slatkin 1978). Lastly, Shuster and Wade advocated viewing conditional mating phenotypes within the existing quantitative genetic framework for threshold traits (Roff 1996; Schlichting & Pigliucci 1998), an approach that acknowledged the ubiquity of conditional mating polymorphisms and accorded with experimental results indicating that conditional phenotypes do have a genetic basis and do oscillate in apparent response to frequency dependent selection (reviewed in Tomkins & Brown 2004; Rowland & Emlen 2009).

Most recently, Taborsky et al. (2008b) and other contributors to the volume by Oliveira et al. (2008), in keeping with the predominance of conditional polymorphisms in nature, focused their discussion on *alternative reproductive tactics*, polymorphic behavioral or developmental phenotypes whose expression depends strongly on environmental conditions. These authors presented an extensive review of theoretical and experimental results and listed 12 questions they considered central to the future study of mating polymorphisms, particularly those with conditional expression. One question (#6) concerned possible mechanisms of trait expression; another (#8) concerned whether natural selection in other contexts might shape mating polymorphisms.

However, the remaining 10 questions concerned various aspects of what appear to be the three recurrent issues in this field. After more than a quarter century of concentrated research, two of Austad’s (1984) three central questions remain prominent: (1) to what degree are alternative phenotypes genetically or environmentally determined? and (2) under what circumstances must the fitnesses of alternative morphs be equal, within populations as well as within individual lifetimes? A different third question has now arisen to take the place of

Austad's, in part because the issue of reversibility seems solved (it happens, often), and also because an additional question seems more fundamental in light of recent research (Taborsky et al. 2008): (3) to what degree is frequency dependent selection responsible for maintaining mating polymorphisms within populations?

My goal for the remainder of this chapter will be to address these three issues. In my view, they are all closely linked to the same general phenomenon—sexual selection—and the controversy they incite can be reconciled by correcting a common experimental difficulty that arises when sexual selection is strong. I will first consider frequency dependent selection and explain why the operation of this evolutionary process tends to equalize fitnesses among morphs within populations (cf. Slatkin 1978). I will next provide an example of how frequency dependent selection can act on conditional mating polymorphisms such that the fitnesses of the morphs are equal over time. I will discuss, too, why the action of frequency dependent selection alone could be responsible for the preponderance of conditional mating polymorphisms. Following Shuster and Wade (2003) I will show how strong sexual selection generates a *mating niche* that can be invaded by alternative mating phenotypes, and after invasion occurs, how continued sexual selection generates frequency dependent selection that is sufficient to maintain mating polymorphism. Lastly, I will use a quantitative framework for documenting the intensity of sexual selection to show how data from existing studies claiming to verify Dawkin's (1980) "best of bad job" hypothesis are uniformly inadequate to address its central assumption.

FUNDAMENTAL CONCEPTS

Frequency Dependent Selection

Frequency dependent selection occurs when the fitness of a given phenotype depends on its frequency relative to other phenotypes within the population (see also chapter 3). The tendency for the frequencies of alternative mating phenotypes to fluctuate within populations (Shuster 1989; Lank et al. 1995) or even cycle over time (Sinervo & Lively 1996; Shuster et al. 2001) is well documented, for polymorphisms that are controlled by alleles of major effect, as well as for polymorphisms in which trait expression is contingent on environmental or

social conditions (Alcock 1994a; Taborsky et al. 2008). With few exceptions (Radwan & Klimas 2001), frequency dependent selection, and in particular, negative frequency dependent selection, in which rare morphs experience the highest fitness, is widely assumed to be the fundamental process by which alternative mating strategies are maintained within natural populations (Roff 1996; Gross 1996; Shuster & Wade 2003; Oliveira et al. 2008).

For frequency dependent selection to operate, the frequency of an allele or phenotype must depend in a multiplicative way on its fitness, relative to other alleles or phenotypes within the population. In simple form, this relationship can be expressed as

$$p'_i = p_i (w_i / \bar{w}) = p_i \tilde{w}_i \quad (25.1)$$

where p'_i is the frequency of the i -th allele (or phenotype) after selection has occurred, p_i is the frequency of the i -th allele (or phenotype) before selection, w_i is the absolute fitness of the i -th allele (or phenotype) during selection (chapter 4), and the weighted sum of all alleles (or phenotypes) and their frequencies during the selective event, is the average fitness, \bar{w} , where $\bar{w} = \sum p_i w_i$. The relative fitness of the i -th allele (or phenotype), \tilde{w}_i , equals the absolute fitness of each allele (or phenotype), divided by the average fitness of all alleles or phenotypes ($= w_i / \bar{w}$). In a two allele system, it can be shown that when the frequencies of both alleles are equal ($p_1 = p_2 = 0.5$), and their relative fitnesses are equal ($\tilde{w}_1 = \tilde{w}_2 = 1$), both alleles will remain at equal frequency indefinitely. However, if the fitness of allele 1 decreases, say, to 0.4, the frequency of allele 2 will increase, and will eventually become fixed if its relative fitness remains greater than that of allele 1. If the relative fitness of an allele (or phenotype) decreases as it becomes common, then selection becomes negative frequency dependent and polymorphism is more likely to be maintained (Crow 1986).

The conditions necessary to maintain polymorphism have been explored extensively (reviews in Slatkin 1978, 1979a, 1979b; Fitzpatrick et al. 2007). Most researchers cite the maintenance of a 1:1 sex ratio by the equalization of fitnesses between the sexes (Fisher 1930) as the most intuitively clear example of how polymorphism can be maintained by negative frequency dependent selection (see box 20.2 and box 26.3). To visualize this process, one need only divide the total number of offspring in any generation, in turn, by the total number of individuals in each sex. Because

every offspring has a mother and a father, the ratio obtained for each sex provides an estimate of its absolute fitness, and because the minority sex always generates the larger fitness ratio, the minority sex in populations with biased sex ratios will always increase in frequency. By calculating the relative fitness for each sex as described above, the expected change in sex ratio per generation can be estimated explicitly.

In his considerations of frequency dependent selection, Slatkin (1978, 1979a, 1979b) discovered a fundamental relationship. He showed that when the number of phenotypic classes within a population is greater than 2, the number of heritable factors required to produce the possible phenotypes necessarily increases. He also showed that when relative fitness fluctuates, as it does under negative frequency dependent selection, the number of parameters requiring adjustment to equalize fitnesses among the phenotypes also increases. Slatkin (1979a, 1979b) argued that when relative fitness fluctuates, modifier alleles that cause the average fitnesses of the morphs to become more similar will be favored, thereby allowing polymorphism to be more easily maintained. He therefore proposed that when multiple morphs are favored within a population (cf. Levins 1968), alleles that modify the expression of genetic systems underlying polymorphic traits will rapidly accumulate. Under such circumstances, simple genetic mechanisms controlling the expression of each phenotype will become increasingly influenced by multiple genetic factors. Several authors, e.g., Charlesworth (1971), Roughgarden (1971), Strobeck (1975), and including Haldane and Jayakar (1963) and Slatkin (1979a, 1979b), described environmental conditions in which relative fitnesses among morphs might not be equalized. In general, however, Slatkin's (1978, 1979a, 1979b) overall results were robust, and under a wide range of circumstances, frequency dependent selection appears to equalize relative fitnesses among morphs via modifier loci, that equilibrate the fitnesses of phenotypic classes within populations at a rate dependent on the complexity of the genetic system underlying trait expression.

Frequency Dependent Selection and Alternative Mating Strategies

In most descriptions of negative frequency dependent selection as it relates to alternative mating strategies, the reciprocal relationship between

phenotype and fitness is represented in a bivariate plot showing two intersecting fitness functions representing alternative mating phenotypes (usually identified as α for males that sneak and β for males that fight), within the range of possible variation in a trait such as condition, age, or body size (figure 25.2). The point of intersection of the fitness functions is the switch point, at which the fitnesses of the two phenotypes are equal with respect to the character shown on the x-axis (Gross 1996). In representations of the SDS hypothesis, the distribution of a character (e.g., body size) is superimposed on the relationships between status and fitness (figure 25.3), suggesting that the population frequencies of this second trait are quantitatively related to the overlying fitness functions (Gross 1996; Tomkins & Brown 2004; Oliveira et al. 2008). However, in none of these examples is the distribution of population frequencies for the trait explicitly shown to have such a relationship to the fitness functions they accompany.

The relationships between the tactic fitness functions, the population variance in the position of the switch point, and the distribution of environmental

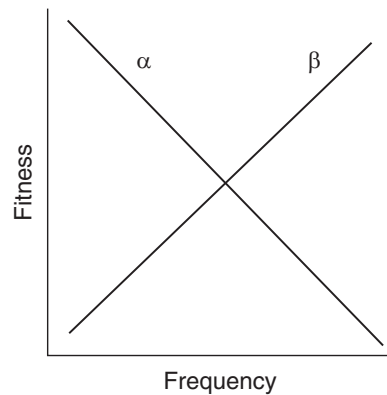


FIGURE 25.2 Bivariate plot showing reciprocal relationships between fitness and trait frequency for two mating phenotypes. α represents individuals who attempt to sneak matings, and β represents individuals who attempt to fight. The x-axis could be trait frequency (plotted), condition, age, or body size. Such descriptions are used to represent the action of negative frequency dependent selection on alternative mating strategies, but the distribution of population frequencies for traits are seldom shown to have a quantitative relationship to the fitness functions they accompany.

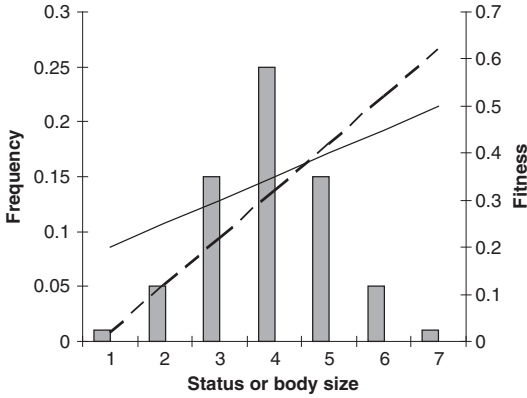


FIGURE 25.3 The status dependent selection (SDS) hypothesis (Gross 1996), in which the reciprocal relationship between status and fitness is represented in a bivariate plot showing two intersecting fitness functions within the range of possible variation in the trait; the point of intersection of the fitness functions is the switch point, at which the fitnesses of the two phenotypes are equal with respect to the character shown on the x-axis; the distribution of another trait (e.g., body size) is superimposed on the relationships between status and fitness, suggesting that the population frequencies of this second trait are somehow related to the overlying fitness functions, but such relationships are seldom explicitly shown.

cues inducing polyphenism are considered within the environmental threshold (ET) hypothesis described by Tomkins and Hazel (2007). This hypothesis explicitly combines known quantitative genetic principles and data with SDS and game theory frameworks to describe how conditional polymorphisms evolve. Tomkins and Hazel (2007) state that the combined effect of these factors on the selection differential acting on the switch point results in most cases in an equilibrium mean switch point that does not correspond to the intersection of the fitness functions. Also, Tomkins and Hazel report that the average fitness of the alternative tactics at this location will usually not be equal. Although their figures suggest that variation in status, cue reliability, and status-dependent fitness trade-offs can influence the distribution of reaction norms within a theoretical population (p. 524), the quantitative relationships among fitness, status, and traits influencing status (e.g., body size) are not clearly shown.

Tomkins and Hazel (2007) suggest that their theoretical framework identifies conditions in which conditional phenotypes can persist within populations, even when their fitnesses are unequal. They state (pp. 523–525), “For the conditional strategy to be the ESS, cues must be more reliable than random and one of the alternative phenotypes must have greater fitness in one environment and vice versa. When these conditions are met, the fitness of the conditional strategists (which is a function of the average fitnesses of the two phenotypes they produce) is greater than that of competing unconditional strategists, but the average fitness of the two phenotypes produced by the conditional strategists can be equal or unequal.” It is not clear from this description whether Tomkins and Hazel envisioned fitness inequalities between conditional morphs occurring instantaneously *within* a particular environment, or if they considered fitness inequalities between morphs likely to persist over time. If frequency dependent selection indeed operates on the two phenotypes, the first condition is expected; the latter condition, however, is not.

The quantitative approach illustrated in equation 25.1 can be used to address uncertainty on this issue, as well as to verify that frequency dependent selection can indeed operate when environmental conditions have a strong influence on phenotypic expression (Taborsky et al. 2008). Following the framework of Tomkins and Hazel (2007; figure 25.4), let e_1 and e_2 represent the two possible environments in which mating contests may occur, let w_{α_1} and w_{α_2} represent the fitnesses of individuals (α_i) who attempt to sneak matings when small (α_1 in e_1) and large (α_2 in e_2), respectively, and let w_{β_1} and w_{β_2} be the fitnesses of individuals (β_i) who attempt to fight when small (β_1 in e_1) and large (morph β_2 in e_2), respectively. For simplicity, we will assume that each environment in which contests may occur appears with equal frequency, that each of the phenotypes in each environment occurs with equal frequency, and that only the fitness of one morph (β_i) differs in each environment.

Figure 25.4 shows that the fitness of β_2 is larger than the fitness of α_1 in environment 2; and that the fitness of α_2 is larger than the fitness of β_1 in environment 1. If the fitness of α_i is equal across the two environments, whereas the fitness of β_i is low in environment 1 and high in environment 2, then, indeed, within each environment, the average fitnesses of the two morphs are unequal (cf. Tomkins & Hazel 2007). However, because the

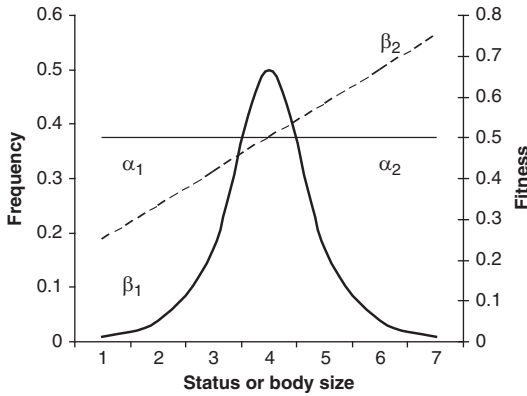


FIGURE 25.4 Frequency dependent selection on a condition-dependent mating polymorphism based on the assumptions of Tomkins and Hazel (2007); variables and relationships are described in the text.

overall frequencies of the two morphs are equal, and because the two environments appear with equal frequency, the average fitnesses of α and β across the two environments will also be equal. This can be shown as

$$[p_{\alpha_1}w_{\alpha_1}] + [p_{\alpha_2}w_{\alpha_2}] = [p_{\beta_1}w_{\beta_1}] + [p_{\beta_2}w_{\beta_2}] \quad (25.2)$$

where p_{α_1} and p_{α_2} , w_{α_1} and w_{α_2} , p_{β_1} and p_{β_2} , and w_{β_1} and w_{β_2} are the frequencies and fitnesses of the α and β phenotypes in environments 1 and 2, respectively. If the frequencies of the two morphs are indeed equal ($p_{\alpha_1} = p_{\beta_1} = p_{\alpha_2} = p_{\beta_2} = 0.25$), and if the fitnesses of α_i in each environment are also equal ($w_{\alpha_1} = w_{\alpha_2} = 0.5$), but the fitnesses of β_i are not equal ($w_{\beta_1} = 0.25$; $w_{\beta_2} = 0.75$), then by substituting these values, equation 25.2 becomes $[(0.25)(0.5)] + [(0.25)(0.5)] = [(0.25)(0.25)] + [(0.25)(0.75)]$, and clearly the fitnesses of each morph across environments are equivalent ($0.25 = 0.25$).

However, if we let the environments occur with unequal frequency, then each morph's fitness must be averaged over the two environments, and because the fitnesses of the morphs differ in each environment, the fitness of each morph must be considered relative to all other morphs in all other environments. The average fitness across all morphs can now be written as

$$W = \sum p_{ij}w_{ij}e_j \quad (25.3)$$

where p_{ij} is the frequency of the i -th morph in the j -th environment, w_{ij} is the absolute fitness of the i -th morph in the j -th environment, and e_j is the frequency with which the j -th environment occurs. Thus, the relative fitness of the i -th morph in the j -th environment is $\tilde{w}_{ij} = w_{ij}/W$.

We can now rewrite equation 25.2 as

$$[p_{\alpha_1}\tilde{w}_{\alpha_1}e_1] + [p_{\alpha_2}\tilde{w}_{\alpha_2}e_2] = [p_{\beta_1}\tilde{w}_{\beta_1}e_1] + [p_{\beta_2}\tilde{w}_{\beta_2}e_2] \quad (25.4)$$

If the different environments appear with unequal frequency (say, $e_1 = 0.6$ and $e_2 = 0.4$), then the relative fitnesses of the different morphs will also change, as will the frequencies of the reaction norms that produce the two morphs in each environment. It is certainly true that the average fitnesses of the morphs within each environment are unequal (cf. Tomkins & Hazel 2007), but under such conditions both morphs in the same environment will no longer persist. In this example, reaction norms that produce the β morph in environment 1 will become quite rare, as will reaction norms that produce the α morph in environment 2; moreover, the relative proportion of the population that consists of each morph will change.

This result appears similar to the SDS solution because it leads to a high frequency of reaction norms that make the right choice in each environment (Gross 1996). This result is also similar to the ET solution because it assumes that each phenotype is part of a distribution of heritable reaction norms whose frequency will change under selection (Tomkins & Hazel 2007). However, unlike both the SDS and the ET hypotheses (or so it appears anyway), the results illustrated in equations 25.2–25.4 do not assume that individuals with inferior fitness somehow persist within the population indefinitely. Individuals in the above example whose fitnesses are inferior, because their reaction norms fail to respond appropriately within a given environment (i.e., they express the wrong phenotype and so have lower fitness), are either reduced to low frequency to form the tails of the normal distribution of reaction norms (figure 25.3) or they are removed from the population entirely. The rate at which inferior phenotypes are lost from this population can be slowed if mechanisms underlying trait inheritance are complex (e.g., Slatkin 1978), if individuals do not always make the correct choice in each environment (Roff 1996), or if the frequency with which each environment appears is closer to 0.5 (Haldane & Jayakar 1963). It is also possible that when a

morph is common, it is less successful on average than it is when it is rare, that is, when negative frequency dependent selection occurs (Slatkin 1978, 1979a, 1979b).

What Happens When Sexual Selection Is Strong

When sexual selection occurs, two classes of males exist, males who mate and males who do not (Wade 1979; Shuster & Wade 2003, 2004). If we let p_s equal the fraction of males in the population who mate, and $p_0 (= 1 - p_s)$ equal the fraction of males that do not mate, we can express the average fitness of the mating males as $p_s(H)$, where H is the average number of mates per mating male. The average number of mates for all males is equal to the sex ratio, R , when it is expressed as $N_{females}/N_{males}$.

We can now identify three relationships (equations 25.5a–c). The first is the average fitness of all males, which equals the sex ratio, R , rewritten as

$$R = p_0(0) + p_s(H) \quad (25.5a)$$

Here, each term on the right side of the equation equals the fraction of males belonging to each mating class, multiplied by the average number of mates secured by members of that class. Rearranging equation 25.5a, we can see that $H = R/p_s$, indicating that the average mating success of *mating* males, H , is always greater than the average mating success of *all* males, R , except when each male mates only once.

Because $p_s = (1 - p_0)$, we can rewrite equation 25.5a to show the second relationship as

$$p_0 = 1 - (R/H) \quad (25.5b)$$

This expression shows how p_0 , the fraction of males without mates (a parameter that often goes unmeasured because males who mate are more conspicuous than males who do not) is related to parameters we can measure, specifically, R , the overall ratio of males to females, as well as H , the average number of mates per mating male.

If the ratio of females to males, R , remains at 1, equation 25.5b simplifies to

$$p_0 = 1 - (1/H) \quad (25.5c)$$

an expression showing the fraction of males without mates, p_0 , in terms of H . Again, although the

fraction of nonmating males in the population, p_0 , can be difficult to measure, equation 25.5c shows that p_0 is a function of H , the average number mates per mating male. The value of H usually can be measured (and is what most researchers do measure) by simply observing the males who successfully mate.

As the value of H increases, the fraction of males without mates, p_0 , also must increase (figure 25.5). To place this relationship in more concrete terms, when the average number of mates per mating male, H , equals 5, as it can in African cichlids

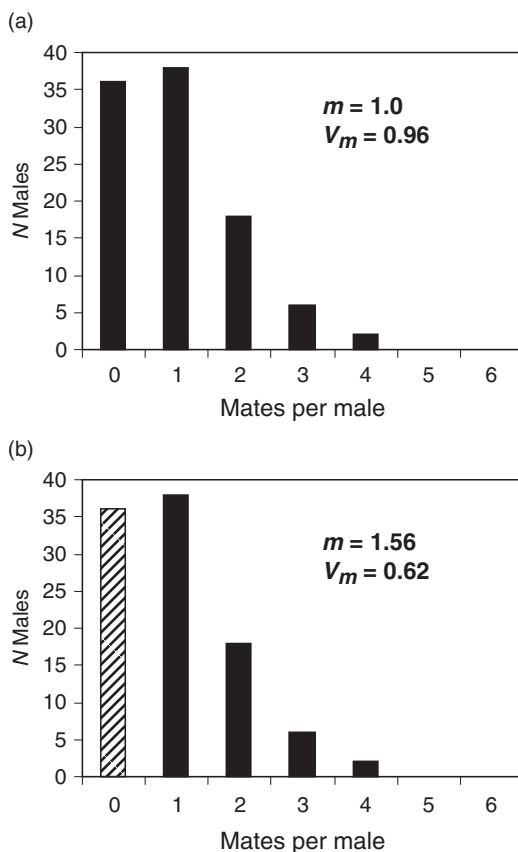


FIGURE 25.5 The mean, m , and variance, V_m , in mating success among 100 randomly mating males and females; females are assumed to mate only once; (a) when all males are included in parameter estimates; (b) when the zero class of males (hatched bars) is excluded from parameter estimates; the effect of omissions of nonmating individuals from fitness estimates tend to overestimate the average mating success and underestimate the variance in mating success for males.

(*Pelvicachromis pulcher*; E. Martin & Taborsky 1998), p_0 , the proportion of males who fail to mate equals 80%. Here disproportionate mating success by 20% of males obliterates utterly the fitness of the remaining four-fifths of the male population! Certainly, if sperm competition occurs or if females mate more than once, the actual value of H will be reduced and sexual selection will be eroded. Yet such conditions can be accommodated simply by recalculating the value of H after paternity data are considered.

Despite the possibility that sexual selection can be reduced in this way, sexual dimorphism and alternative mating strategies are widespread, revealing how often sexual selection occurs in nature. As we will see, the obliteration of the fitness of some males by the disproportionate mating success of others is the source of sexual selection and of frequency dependent selection on alternative mating strategies. It is also the source of what has become a central question in the study of this phenomenon; whether mating phenotypes achieving inferior mating success can persist within natural populations.

The Variance in Mating Success

To estimate the intensity of sexual selection in terms of the variance in mate numbers among males, we must again recognize that sexual selection creates two classes of males (or two classes of females in sex role reversed species). When mating and nonmating classes of males appear, the total variance in male fitness has two components: (1) the average variance in mating success within the class of males that mate and (2) the variance in the average mating success between the classes of mating and nonmating males (Wade 1979, 1995; Shuster & Wade 2003). Because the average number of mates for nonmating males is uniformly zero (Wade 1979, 1995), following the form of equation 25.5a, the average variance in mate number within each of the two male categories, mating and nonmating, can be written as

$$V_{within} = (p_0)(0) + (p_s)V_{harem} \quad (25.6)$$

where V_{harem} is the variance in mate numbers among the males who secure mates. By substitution from equation 25.5a, V_{within} can be rewritten as $(R/H)V_{harem}$, or, when the sex ratio, R , equals 1, $V_{within} = V_{harem}/H$. The median value of V_{harem} estimated from 27 studies of diverse animal taxa is 1.04,

suggesting that the distribution of females with males is approximately Poisson ($V_{harem} = H = 1$). However, if females tend to cluster within the harems of particular males, V_{harem} can become disproportionately large (Wade & Shuster 2004).

The second component of the variance in male fitness exists between the classes of successful and unsuccessful males, and equals the difference in average mating success, squared, or $(H - 0)^2$, multiplied by the variance between the mating categories, $(p_0)(1 - p_0)$, or

$$V_{between} = H^2(p_0)(p_s) \quad (25.7)$$

The total variance in male fitness in terms of male mating success, V_{mates} , is the sum of these two variance components, V_{within} and $V_{between}$, or

$$V_{mates} = (p_s)V_{harem} + H^2(p_0)(p_s) \quad (25.8)$$

When data are available on the average harem size, H , the proportion of nonmating males within the population, p_0 , can be estimated using equation 25.5b [i.e., $p_0 = 1 - (R/H)$]. When the variance in harem size, V_{harem} is available, equation 25.8 provides a means for estimating the total variance in male mating success, V_{mates} , even if researchers tend to focus on mating, rather than nonmating, males.

Why Alternative Mating Strategies Evolve

We can now answer more specifically why polymorphic mating strategies evolve when some males mate and other males do not. As explained above, differential mating success among males not only causes sexual selection among conventional males; it also creates a "mating niche" for males engaging in unconventional mating behaviors (Shuster & Wade 1991; 2003). By invading locations in which synchronously receptive females outnumber conventional males (i.e., *harems*), unconventional or satellite males may surreptitiously gain opportunities to mate without having to engage in combat.

To understand how such circumstances occur (cf. Shuster & Wade 2003), recall that R , the sex ratio ($= N_{females}/N_{males}$), is equal to the distribution of all females over all conventional males, mating and nonmating, and therefore equals the average fitness of conventional males, or

$$W_{\alpha} = R \quad (25.9)$$

When satellites invade breeding territories, they usually find mates among the harems of conventional males. We can express the fitness of satellites, W_β , as

$$W_\beta = Hs \quad (25.10)$$

where s equals the fraction of fertilizations satellite males obtain within the harems of conventional males and H equals the average harem size of conventional males. Stated differently, when satellite males mate with some of the females within the harems of conventional males, the average fitness of such males is reduced.

As Shuster and Wade (2003) showed, and as evolutionary theory (Slatkin 1978; Maynard Smith 1982) requires, for satellite males to invade a population of conventional males, the average fitness of satellite males, W_β , must exceed the average fitness of conventional males, W_α , or

$$W_\beta > W_\alpha \quad (25.11a)$$

Note that when $R = 1$, the average and relative fitnesses are equivalent. Because persistence of a polymorphism requires equivalent fitnesses among the different phenotypes (Slatkin 1978, 1979a, 1979b), when the average fitnesses of the phenotypes differ, their relative fitnesses will also differ, and the frequency of these phenotypes will change (equations 25.1 and 25.4). In this case, when satellite males invade a population of conventional males, their numbers are small. Nevertheless, the population frequency of satellites will increase because their relative fitness exceeds that of the average conventional male. This is how negative frequency dependent selection operates on alternative mating strategies.

By substituting values from equations 25.6 and 25.7, we see that equation 25.8a can be expressed as

$$Hs > R \quad (25.11b)$$

When the sex ratio, R , equals 1, equation 25.11b becomes $Hs > 1$, and by solving for s , we can see the minimum fertilization success that satellite males must obtain to invade a population of harem holding, conventional males is

$$s > 1/H \quad (25.11c)$$

Thus, when the average harem size, H , equals 5 (e.g., Martin & Taborsky 1997), the fitness of

satellites need only slightly exceed 20% of the fitness of the average conventional male, to satisfy the conditions required for successful invasion ($s > 1/H = 0.20$). As harem size increases, females become increasingly clustered around fewer conventional males and the invasion of alternative mating strategies becomes easier still (Shuster & Wade 2003).

By rearranging equation 25.5c, we can see that $1/H = (1 - p_0)$, and substituting from equation 25.11c, we see that the proportional success of satellite males need only exceed the proportion of mating males in the population or

$$s > 1 - p_0 \quad (25.12)$$

We can now see why failures by conventional males to successfully defend harems provide mating opportunities for unconventional males. As p_0 increases, the mating success necessary for satellite males to successfully invade harems, s , becomes increasingly small, and negative frequency dependent selection favoring satellite males becomes increasingly intense. At evolutionary equilibrium, equation 25.12 identifies the condition necessary for both conventional males and satellite males to coexist within the same population. In effect, satellite males replace the nonmating males in the conventional male population (see below).

Why Alternative Mating Strategies Persist

After invasion occurs, how rapidly will the frequency of alternative mating strategies increase? The answer depends on how strong selection is on males of each mating phenotype. Recall that the intensity of sexual selection depends on the magnitude of fitness variance that exists among males. We have seen above how sexual selection provides a mating niche for satellite males. We can use the same framework to understand the relative intensity of selection on alternative mating strategies after invasion has occurred. Because we can partition the mating success of males into mating and nonmating classes, as well as into conventional and satellite male phenotypes, we can also use our estimates of fitness variance to determine whether the average fitnesses among male morphs are distinct. Stated differently, we can quantitatively address whether or not males “make the best of a bad job” (Dawkins 1980; Austad 1984; Gross 1996; Tomkins & Hazel 2007; Oliveira et al. 2008).

Again, when sexual selection occurs, two classes of males appear, conventional males who mate, $p_{s\alpha}$, and conventional males who do not mate, $p_{0\alpha}$ where, among conventional males $(p_{0\alpha} + p_{s\alpha}) = 1$. The fraction of conventional males in the population at any time equals $p_{\cdot\alpha}$, where the “.” indicates that all mating classes of conventional males are included. When alternative mating strategies invade conventional male populations, an additional class of males appears, $p_{s\beta}$, the successfully mating satellites, whose population frequency among all males equals $p_{s\beta} = (1 - p_{\cdot\alpha})$. As invasion proceeds and $p_{s\beta}$ increases, as it must because the average fitness of satellite males exceeds that of conventional males, satellite males will soon exhaust the supply of uninherited harems. When this condition arises, $p_{s\beta}$ must itself divide into two classes: satellite males that mate, $p_{s\beta}$, and satellite males that fail to mate, $p_{0\beta}$, where within the satellite males $p_{0\beta} = (1 - p_{s\beta})$ and $(p_{0\beta} + p_{s\beta}) = 1$. The fraction of satellite males in the population at any time equals $p_{\cdot\beta}$, where the “.” indicates that all mating classes of satellite males are included. For all males, $[p_{\cdot\alpha} + p_{\cdot\beta}] = 1$.

With the appearance of the latter two male classes, it is now possible to partition the variance in mate numbers within each of the male phenotypes, into within- and among-male components. Then, using these variance subtotals for each morph, estimate the grand total variance in male mating success, V_{mates} , by partitioning the variance in mate numbers within and among the male morphs (Shuster & Wade 2003). This procedure is straightforward when the proportions of mating and non-mating males of each mating phenotype, as well as the average and variance number of mates per male for each of the mating classes, are available (Shuster & Wade 1991; Shuster 2007, 2008). The method becomes more difficult when field researchers focus only on mating males (table 25.1; see below), but quantification of V_{mates} is still possible provided that average number of mates per mating male, H , and the variance around that average V_{harem} , are reported. Here is how this can be done.

When multiple male phenotypes exist in the same population, we can estimate the variance in mating success, $V_{mates(i)}$, for each of the i -th mating phenotypes using equation 25.8. Note that in calculating $V_{mates(i)}$ the fractions of mating and non-mating males within each morphotype will each sum to 1 as described above. Next, we can estimate the total variance in mating success for all of the males in the population, $V_{mates(total)}$, as the sum of

two components: (1) the average variance in mating success for conventional and satellite males, $V_{within(morphs)}$ and (2) the variance in the average mating success for conventional and satellite males, $V_{among(morphs)}$. The within-morph variance in mating success equals

$$V_{within(morphs)} = p_{\cdot\alpha} [V_{mates(\alpha)}] p_{\cdot\beta} [V_{mates(\beta)}] \quad (25.13)$$

where $p_{\cdot i}$ is the proportion of the male population comprised of each i -th male phenotype and $\sum p_{\cdot i} = 1$. The among morph variance in mating success equals

$$V_{among(morphs)} = p_{\cdot\alpha} (R - H_{\alpha})^2 + p_{\cdot\beta} (R - H_{\beta})^2 \quad (25.14)$$

where H_j is the average mating success of males achieved by mating males of each j -th male phenotype. Note that the proportion of males belonging to each male phenotype, $p_{\cdot j}$, the average mating success of mating males within each male phenotype, H_j , and the sex ratio, R , are often (but not always) available from field studies of alternative mating strategies.

CASE STUDIES

In the nearly 3 decades since Dawkins (1980) articulated his “best of a bad job” (BOBJ) hypothesis, an impressive number of researchers claim to have substantiated it, theoretically (Gross 1996; Gross & Repka 1998; Tomkins & Hazel 2007) as well as empirically (Fincke 1986; Møller & Birkhead 1993; Johnsen et al. 1998; Alcock 1996a, 1996b, 1996c; Low 2005; Beveridge et al. 2006; reviews in Oliveira et al. 2008). In contrast, Shuster and Wade (2003; Wade & Shuster 2004; Shuster 2008) have maintained that such conclusions are premature, either because the theoretical assumptions are unrealistic (see above), or because field results have inadequately accounted for the class of non-mating individuals. When clear genetic differences exist among males, there has been little dispute over whether fitnesses among morphs must be equivalent for polymorphism to be maintained (Gross 1996; Taborsky 1998; Taborsky et al. 2008). However, among conditional polymorphisms, despite considerable data suggesting that such polymorphisms represent quantitative traits with threshold inheritance (review in Rowland & Emlen 2008), uncertainty still persists (Oliveira et al. 2008).

Because the assumptions underlying theoretical analyses often require specific examination before they can be rigorously tested, there is little chance of addressing them here. However, Shuster and Wade's (2003) hypothesis regarding omission of the zero class of males in field studies generates clear predictions that are testable by combining the above framework with published results. Shuster and Wade (2003) predicted that omissions of nonmating individuals from fitness estimates would overestimate the average fitness, underestimate the variance in fitness for conventional males (figure 25.5), and cause the mating success of conventional males to appear to be significantly greater than that of satellite males. They confirmed this prediction using published data on male mating success in the marine isopod, *Paracerceis sculpta* (Shuster & Wade 1991; Shuster 2008). Unfortunately, these predictions cannot be specifically tested for other species except when information on the population frequencies, the average and variance in mating success, and the sex ratio of the species studied is available (Wade & Shuster 2004; see below).

Nevertheless, Shuster and Wade's (2003) assertion does suggest an additional, more easily testable hypothesis for any field study of a conditional mating polymorphism claiming to substantiate the BOBJ hypothesis. This prediction has two parts: (1) in studies claiming to support the BOBJ hypothesis, the zero class of males, p_0 , will either be unidentified or unreported; in contrast, (2) when the zero class of males has been reported for conditional polymorphisms, equal fitnesses among male morphs will be found. The results of this analysis can be compared using Fisher's exact test.

Table 25.1 summarizes the results presented in 13 studies of conditional male polymorphisms reported since 1985. This is not an exhaustive list, but it does include prominent studies. These studies include four species of insects (four studies on the same species), one species of fish, one species of frog, and five species of birds. Eight of these 13 studies conclude that satellite males make the best of a bad job. The remaining five of the 13 studies find the fitnesses of the different male morphs to be equivalent. Consistent with the above predictions, of the 8 studies concluding that satellite males make the best of a bad job none (0/8) reported the size of the class of nonmating males in their studies. In contrast, all of the studies (5/5) in which males were found to have equal fitnesses either identified or included the class of nonmating males in their calculations of average mating success (Fisher's exact test, $P < 0.001$).

A classic study of *Hyla cinerea* by Gerhardt et al. (1987) provides another useful example for comparison. These authors recorded the mating success of calling, satellite, and noncalling males over 3 years. Of the 57 males who mated, 50 were callers and 7 males were satellites, suggesting that the average success of callers was greater than for satellites. However, because Gerhardt et al. (1987) identified mating as well as nonmating males in their analysis, they were also able to show that 416 of the 466 calling males (89%) were unsuccessful at mating, and that 50 of the 57 satellite males (88%) were also unsuccessful. Gerhardt et al. (1987) concluded that the fitnesses of the two male phenotypes were equal because nearly equal proportions of each population were successful in mating (11–12%).

TABLE 25.1 Research articles addressing Dawkins' "best of a bad job" hypothesis

Author and Date	Taxon	Zero Class Quantified?	Average Fitness among Morphs
Fincke 1986	Damselflies	No	Unequal
Gerhardt et al. 1987	Tree frogs	Yes	Equal
Waltz and Wolf 1988	Dragonflies	Yes	Equal
Møller and Birkhead 1993	Birds	No	Unequal
Koprowski 1993	Birds	Yes	Equal
Alcock 1994a	Butterflies	Yes	Equal
Johnsen et al. 1998	Birds	No	Unequal (but not significant)
Alcock 1996a	Solitary bees	No	Unequal
Alcock 1996b	Solitary bees	No	Unequal
Alcock 1996c	Solitary bees	No	Unequal
Low 2005	Birds	No	Unequal
Beveridge et al. 2006	Solitary bees	No	Unequal
Rios Cardenas and Webster 2008	Pumpkinseed fish	Yes	Equal

These authors did not report the variance in mating success within the classes of mating males, so it is not possible to accurately estimate variance in mating success within and among calling and noncalling males using equation 25.8. However, it is still possible to determine whether the observed success of satellite males was sufficient for these males to persist within the population. Using equation 25.3c, we can see that if $p_{0\text{calling}}$ equalled 0.89, then the average harem size of calling males, H_{calling} equalled 9.32 (not reported by Gerhardt et al.). If s represents the success satellites had to obtain by stealing mates from calling males to persist within the population, then from equation 25.12, $s > 1 - p_{0\text{calling}}$ or 0.11; indeed this value is approximately equal to the fraction of the total matings satellite males actually obtained ($7/57 = 0.12$).

FUTURE DIRECTIONS

There is now little doubt that both genetic and environmental factors influence the expression of alternative mating strategies (Shuster & Wade 2003; Tomkins & Hazel 2007; Oliveira et al. 2008). Thus, Austad's (1984) first question, whether behavioral differences between individuals stem from genetic differences, is for the most part solved. Slatkin's (1978, 1979a, 1979b) theoretical results indicate that the relative influences of genetic and environmental variation on trait expression mainly affect how fast, rather than whether, morph frequencies will respond to frequency dependent selection. His results also provide a simple evolutionary hypothesis for why mating polymorphisms with polygenic inheritance are overwhelmingly more common among species than mating polymorphisms with Mendelian inheritance (Austad 1984; Gross 1996; Shuster & Wade 2003; Oliveira et al. 2008). If strong negative frequency dependent selection favors the evolution of modifier alleles that equalize fitnesses among distinct phenotypes, then initially simple inheritance mechanisms underlying such traits will rapidly become polygenic. The observed rarity of simple inheritance mechanisms underlying mating polymorphisms may therefore simply reveal the lower end of the distribution of all such polymorphisms, which inevitably proceed toward greater underlying genetic complexity over time.

Whether it is possible for mating polymorphisms to persist in populations when the fitnesses of the morphs are unequal remains uncertain. However,

this question, too, seems near resolution provided that researchers can agree on appropriate terminology and methods for addressing this problem. Most researchers appear to agree that frequency dependent selection operates on most if not all populations exhibiting mating polymorphism. This finding is consistent with the hypothesis that frequency dependent selection acts relentlessly to equalize fitnesses in natural populations (Slatkin 1978, 1979a, 1979b), and suggests that situations in which morph fitnesses are unequal, although plausible, may in fact be transitory. There can be little doubt that claims of unequal fitnesses among morphs are premature if based on data that excludes the zero class of males, that is, focuses only on the average success of mating males. Future research that quantifies the zero class of males and/or includes estimates of the mean and variance in mate numbers among the mating class of males will place this conclusion on firmer ground.

The central prediction that frequency-dependent selection will act on all phenotypes whose frequencies and fitnesses may vary, suggests that future research on alternative mating strategies in the following areas will be productive: (1) detailed analysis of genetic architectures underlying alternative mating phenotypes to establish whether the expression of any variable phenotype is not influenced in some way by underlying genetic variation; (2) accurate documentation of the fitnesses of mating and non-mating individuals in populations to further test the hypothesis that over time, the average fitnesses of alternative morphs will be equal; (3) investigations of how flexible phenotypes are expressed and how rapidly such traits respond to selection; (4) investigation of alternative mating phenotypes in females: if such polymorphisms are expected to appear within the sex in which fitness variance exists, females, as well as males, should express alternative strategies when fitness is variable within that sex (e.g., Berglund et al. 1989; Delehanty et al. 1998). Such variation is likely to exist in species in which males defend breeding sites and such sites become limited (e.g., pipefish, sea horses, sea spiders, shorebirds) as well as when females defend resources crucial to reproduction and these resources become limited (e.g., social insects, hyenas, primates).

Despite its appeal for devotees, the importance of alternative mating strategies in evolutionary biology is currently underappreciated and often misunderstood. Polymorphic mating phenotypes do not merely provide amusing examples of bizarre animal sex: they provide quantifiable examples of intense

frequency dependent sexual selection and its rapid evolutionary consequences. Few other evolutionary phenomena are likely to be as common among species, or provide such a detailed look at how evolution proceeds. There is much exciting work to be done.

SUGGESTIONS FOR FURTHER READING

Interested readers have a wide range of possibilities for further reading on alternative mating strategies. Darwin (1874) was first to describe such variation in detail and examples abound within the second edition of *The Descent of Man and Selection in Relation to Sex*. A review of these considerations, with speculation on why Darwin found female mimicry uninteresting can be found in Shuster and Wade (2003, chapter 10). For masterful presentations of multiyear data, start either with Sinervo and Lively's (1996) account of the

rock-paper-scissors polymorphism in side blotched lizards (see also chapter 3 of this volume), or Tomkins and Brown's (2004) report of earwig forcep dimorphism on Scottish islands. Lastly, the entire 2008 volume by Oliveira et al. (2008) offers unprecedented detail on how alternative mating strategies are expressed and can evolve as alternative reproductive tactics.

- Darwin CR (1874) *The Descent of Man and Selection in Relation to Sex*, 2nd ed. Rand, McNally, New York.
- Oliveira R, Taborsky M & Brockmann HJ (2008) *Alternative Reproductive Tactics*. Cambridge Univ Press, Cambridge, UK.
- Shuster SM & Wade MJ (2003) *Mating Systems and Strategies*. Princeton University Press, Princeton, NJ.
- Sinervo B & Lively CM (1996) The rock-paper-scissors game and the evolution of alternative male strategies. *Nature* 380: 40–243.
- Tomkins JL & Brown GS (2004) Population density drives the local evolution of a threshold dimorphism. *Nature* 431: 1099–1103.