9 · The expression of crustacean mating strategies

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CHAPTER SUMMARY

Three fundamental patterns of phenotypic expression exist for alternative mating strategies. These patterns include Mendelian strategies, developmental strategies, and behavioral strategies. Each pattern of expression is revealed by hormonal and neurological factors that regulate the timing and degree to which phenotypic differences appear; however, the nature of each regulatory mechanism depends fundamentally on its underlying mode of inheritance. The genetic architectures underlying such inheritance in turn depend on the circumstances in which mating opportunities arise, including the intensity of selection favoring distinct reproductive morphologies, and the predictability of mating opportunities within individual lifespans. This chapter concerns the nature of this variation and its possible causes, with illustrations from the Crustacea.

9.1 INTRODUCTION

Although crustaceans were among the first recorded examples of alternative mating strategies (*Orchestia darwinii*: Darwin 1874, p. 275; *Tanais* spp.: Darwin 1874, p. 262), there is currently no synthetic treatment of how such polymorphisms are expressed within this group. The apparent scarcity of reports of male polymorphism among crustaceans is unexpected given the frequency with which sexual selection has been demonstrated within this taxon (Holdich 1968, 1971, Manning 1975, Stein 1976, Thompson and Manning 1981, Knowlton 1980, Shuster 1981, Christy 1983, Hatziolos and Caldwell 1983, reviews in Salmon 1984, Koga *et al.* 1993). As explained below, when sexual selection occurs, alternative mating strategies are likely to evolve. This chapter provides an evolutionary framework for understanding the expression of alternative mating strategies, with illustrations from the Crustacea (Table 9.1). My goals are to show that in this fascinating collection of species, all known forms of alternative mating strategies are represented and opportunities for further research abound.

Several frameworks for understanding alternative mating strategies now exist (Gadgil 1972, Maynard Smith 1982, Austad 1984, Dominey 1984, Gross 1985, 1996, Lucas and Howard 1995, Gross and Repka 1998). Because these approaches have focused primarily on behavioral or developmental differences among individuals (that is, on "condition-dependent phenotypes" often called "tactics" (Box 9.1), and because such polymorphisms seldom conform to the simplifying assumptions required by game theory regarding inheritance and fitness, there has been little consensus about the theoretical and empirical approaches best suited for investigating alternative mating strategies and tactics, in the laboratory as well as in nature.

In response to this confusion, Shuster and Wade (2003; see also Hazel *et al.* 1990, Roff 1992, 1996, Sinervo 2000, 2001, Shuster 2002) explained how alternative mating strategies can be understood using conventional evolutionary genetic principles including game theory, provided that the average as well as the variance in fitness among the observed morphs is considered within quantitative analyses. This requirement is necessary because alternative mating strategies evolve in response to sexual selection, an evolutionary context in which fitness variance is often extreme. When fundamental principles are applied, the contexts in which alternative mating strategies evolve as well as the forms these adaptations assume become clear.

This chapter has three parts. First, I will explain the source of sexual selection and how it produces alternative mating strategies in the first place. Second, I will describe Levins' (1968) scheme for understanding polyphenism (the tendency for individuals to express variable phenotypes in response to environmental cues) to show why alternative mating strategies can be understood in this light (see Shuster and Wade 2003). Third, using crustacean examples, I will demonstrate how this approach predicts the

Alternative Reproductive Tactics, ed. Rui F. Oliveira, Michael Taborsky, and H. Jane Brockmann. Published by Cambridge University Press.

Table 9.1. *A preliminary taxonomic distribution of alternative mating strategies within the Crustacea*

Taxon	Species	Conventional morph	Alternative morph(s)	Mode of expression	References
Branchiopoda					
Anostraca	*Eubranchipus serratus*	Guard individual females in sequence	Usurper	Behavioral	Belk 1991
Notostraca	*Triops newberryi*	Hermaphrodite	Male	Mendelian	Sassaman 1991
Conchostraca	*Eulinmadia texana*	Hermaphrodite	Male	Mendelian	Sassaman 1989, Sassaman and Weeks 1993, Weeks and Zucker 1999
Maxillipoda					
Copepoda	*Euteropina acutifrons*	Large males	Small males	Mendelian/developmental	Haq 1965, 1972, 1973, D'Apolito and Stancyk 1979, Moreira *et al.* 1983, Moreira and McNamara 1984, Stancyk and Moreira 1988
Malacostraca					
Stomatopoda	*Pseudosquilla ciliata*	Guard individual females in sequence	Usurper	Behavioral	Hatziolos and Caldwell 1983
	Gonodactylus bredini	Guard individual females in sequence	Usurper	Behavioral	Shuster and Caldwell 1989
Decapoda					
Caridea	*Alpheus armatus*	Guard individual or groups of females	Usurper/sneaker?	Behavioral	Knowlton 1980
	Argis dentata	Protandrous hermaphrodites	Primary females	Developmental?	Fréchette *et al.* 1970
	Athanas spp.	Protandrous hermaphrodites	Primary males	Developmental?	Nakashima 1987, Gherardi and Calloni 1993
	Crangon crangon	Protandrous hermaphrodites	Primary females	Developmental?	Boddeke *et al.* 1991
	Exhippolysmata sp.	Protandrous simultaneous hermaphrodites		Developmental?	Bauer 2002
	Lysmata spp.	Protandrous simultaneous hermaphrodites		Developmental	Bauer 2000, Baeza and Bauer 2004
	Macrobrachium dayanum	Guard female groups	Female mimic, sneaker	Developmental	Kuris *et al.* 1987

Table 9.1 (*cont.*)

Taxon	Species	Conventional morph	Alternative morph(s)	Mode of expression	References
	Macrobrachium idea	Guard female groups	Female mimic, sneaker	Developmental	Kuris *et al.* 1987
	Macrobrachium malcolmsonii	Guard female groups	Female mimic, sneaker	Developmental	Kuris *et al.* 1987
	Macrobrachium rosenbergii	Guard female groups	Female mimic, sneaker	Developmental	Nagamine *et al.* 1980, Ra'anan and Sagi 1989, Kuris *et al.* 1987, Barki *et al.* 1992, Karplus *et al.* 2000, Kurup *et al.* 2000
	Macrobrachium rosenbergii	Large females	Small females	Unknown	Harikrishnan *et al.* 1999
	Macrobrachium scabriculum	Guard female groups	Female mimic, sneaker	Developmental	Kuris *et al.* 1987
	Pandalus spp.	Protandrous hermaphrodites	Primary females	Developmental?	Charnov 1979, 1982, Bergström 1997
	Processa edulis	Protandrous hermaphrodites	Primary females	Developmental?	Noël 1976
	Rhynchocinetes typus	Guard individual females in sequence (robustus, intermedius)	Sneaker (intermedius), sperm competitor (typus)	Behavioral	Correa *et al.* 2000, 2003, Correa and Thiel 2003
	Thor manningi	Protandrous hermaphrodites	Primary males	Developmental?	Chace 1972, Bauer 1986
Brachyura	*Callinectes sapidus*	Guard individual females in sequence	Usurper	Behavioral/developmental	Jivoff and Hines 1998
	Chionoecetes opilio	Smooth spermatophores	Wrinkled spermatophores	Unknown	Moriyasu and Benhalima 1998
	Inachus phalangium	Mate with many females in sequence	Sperm competitors	Behavioral	Diesel 1989
	Libinia emarginata	Guard individual females in sequence (large males)	Usurper (small males)	Developmental	Sagi *et al.* 1994, Ahl and Laufer 1996
	Pachygrapsus transversus	Guard female groups (large males)	Sneaker (small males)	Behavioral/developmental	Abele *et al.* 1986
	Scopimera globosa	Guard resources required by females (males occupy burrows)	Usurpers/wanderers (small males)	Behavioral/developmental	Wada 1986, Koga 1998
	Uca spp.	Guard resources required by females (males occupy burrows)	Usurpers/wanderers	Behavioral	Salmon and Hyatt 1983, Christy and

					Salmon 1991, Jennions and Backwell 1998
Palinura	*Jasus edwardsii*	Mate with many females in sequence	Sperm competitor	Behavioral	MacDiarmid and Butler 1999
Dendrobrachiata	*Sicyonia dorsalis*	Mate with many females in sequence	Sperm competitor?	Behavioral	Bauer 1992
Astacidea	*Homarus americanus*	Guard individual females in sequence	Usurper	Behavioral	Cowan and Atema 1990, Cowan 1991
Amphipoda	*Jassa falcata*	Guard individual females in sequence (thumbed males)	Sneaker (thumbless males)	Developmental	Borowsky 1985
	Jassa marmorata	Guard individual females in sequence (thumbed males)	Sneaker (thumbless males)	Developmental	Clark 1997, Kurdziel and Knowles 2002
	Microdeutopus gryllotalpa	Guard individual females in sequence (thumbed males)	Sneaker (thumbless males)	Developmental	Borowsky 1980, 1984, 1989
	Orchestia darwinii	Guard individual females in sequence (thumbed males)	Sneaker (thumbless males)	Developmental?	Darwin 1874
Isopoda	*Elaphognathia cornigera*	Guard female groups (large males)	Sneaker (small males)	Unknown	Tanaka and Aoki 1999, Tanaka 2003
	Idotea baltica	Guard individual females in sequence	Usurper	Behavioral	Jormalainen *et al.* 1994
	Jaera albifrons	Guard individual females in sequence (males with setose walking legs)	Unknown, males with nonsetose walking legs	Mendelian	Bocquet and Veuille 1973
	Paracerceis sculpta	Guard female groups (α-males)	Female mimic (β-males), sneaker (γ-males)	Mendelian	Shuster 1989, 1992, Shuster and Wade 1991, 2003, Shuster and Sassaman 1997, Shuster and Levy 1999, Shuster *et al.* 2001
	Thermosphaeroma spp.	Guard individual females in sequence	Usurper	Behavioral	Shuster 1981, Jormalainen and Shuster 1999
Tanadiacea	*Tanais* spp.	Guard individual females in sequence (large males with gnathopods)	Sneaker (small male with small gnathopods)	Developmental?	Darwin 1874

Box 9.1 Strategies and tactics

The term "strategy" as defined in evolutionary game theory describes a preprogrammed set of behavioral or life history characteristics (Maynard Smith 1982). Alternative mating strategies can thus be viewed as functional sets of behavior patterns or morphologies that are used by their bearers to acquire mates (Shuster 2002). An evolutionarily stable strategy (ESS: Maynard Smith 1982) is a strategy that persists in a population 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 have appeared in the population to date. If a strategy's average fitness is consistently *less* than that of other strategies, it will be removed from the population by selection (Darwin 1874, Maynard Smith 1982, Shuster and Wade 2003). *By definition*, individuals with fitness less than the population average are *selected against*. Thus, a *strategy* is an adaptation whose expression has been *shaped by selection*.

This definition implies that two further assumptions are met. First, genetic variation must 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; that is, if all individuals in the population are presumed to be genetically identical for a given trait (e.g., Eberhard 1979, 1982, Lucas and Howard 1995, Gross 1996), no evolutionary 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 eliminated by selection, more-fit trait variants reproduce, and over time, a trait's function becomes recognizable. Traits with uniformly inferior fitness are usually eliminated from populations *before* their phenotypes can become modified. And as mentioned above, no response to selection is possible unless genetic variation underlies the trait. Thus, stabilizing selection can operate only on *heritable* traits whose average fitness, relative to other similar traits, allows them to persist within the population over time. Stated differently, the average fitnesses of coexisting traits *must be equivalent*. If either of these assumptions is not met, discussions of trait evolution become meaningless.

Recent descriptions of discontinuous variation in mating phenotype have distinguished between genetically distinct "strategies" and phenotypes that represent condition-dependent "tactics" (Gross 1996, Gross and Repka 1998, Correa *et al.* 2003, Neff 2003, Howard *et al.* 2004). The term "tactic" is used to describe behavioral or morphological characteristics whose expression is contingent on environmental conditions or on the "status" of the individuals in which they appear. Status-dependent selection (SDS), the term now used to describe how selection may operate on such traits (Gross 1996, Gross and Repka 1998, Denoel *et al.* 2001, Hunt and Simmons 2001, Taru *et al.* 2002, Tomkins and Brown 2004), is presumed to allow individuals to assess their potential mating opportunities in terms of their physical condition, social status, or probability of success and then to make behavioral or developmental "decisions" that lead to greater mating success than if the choice had not been made.

According to the SDS hypothesis, dimorphic populations arise because *all* individuals choose one or another status-dependent phenotype. "Status" is presumed to translate into fitness according to a linearly increasing function, with the rate of increase greater for higher status individuals than for lower status individuals. The fitnesses of each phenotype are considered equal only at the intersection of their fitness functions, a location defined as the "switch point" (s^*) (Figure 9.1). Condition-dependent choices appear to cause much of the population to "make the best of a bad job"; that is, to experience inferior mating success compared to individuals of higher status (Eberhard 1979, 1982, Dawkins 1980). Furthermore, according to the SDS hypothesis, *all* individuals in the population are assumed to be genetically monomorphic with respect to their ability to make conditional choices (but see Gross and Repka 1998 and below). This part of the hypothesis salvages the lower fitness of males with apparently lower mating success (Y, Figure 9.1A) because, as stated above, a genetically uniform population *cannot* respond to selection. Thus, in spite of their inability to secure mates, the SDS hypothesis conveniently bends the principles of population genetics to allow inferior phenotypes to persist within populations over time.

Gross and Repka (1998) acknowledged that conditional strategies representing genetic monomorphisms are unlikely to exist due to overwhelming evidence that heritable factors influence trait expression. However, their revised model concluded that the assertions of Gross (1996) were still appropriate and that the SDS hypothesis is the best explanation for the appearance of behavioral polymorphism in nature (also Hunt and Simmons 2001, Forslund 2003, Tomkins and Brown 2004). But two problems remain with the revised SDS approach. The first difficulty is that it presumes *from the outset* that the average fitnesses of the two tactics considered (fighters and sneakers) are *unequal* (Repka and Gross 1995, p. 28; Gross 1996, p. 93; Gross and Repka 1998, p. 170). As stated above, this premise is evolutionarily untenable.

The assumption of unequal fitnesses among morphs prevents this and related theoretical methods (Repka and Gross 1995, Lucas and Howard 1995, Gross 1996) from considering situations in which the fitnesses of the different morphs *are* equal. It also places severe limits on the potential influence inheritance can have, both on trait expression as well as on how selection may influence trait frequency within the population. Furthermore, genetic monomorphism is still presumed to exist at the switch point (Gross 1996, Gross and Repka 1998), again removing any possibility that selection can influence its position. This issue is *not an assumption of models that consider condition-dependent phenotypes as quantitative genetic polymorphisms* (e.g., Hazel *et al.* 1990, Roff 1996, Flaxman 2000, Shuster and Wade 2003).

The fitnesses of the two tactics *are* considered equal at the switch point. However, this is merely a consequence of how tactic fitnesses are defined – as linear relationships between phenotype and fitness that happen to have different slopes (Figure 9.1B). The notion of the switch point as it is used in this theoretical approach is inappropriate because it assumes equal fitnesses to exist *only* at the population frequencies described at the switch point. This is contrary to the principles of game theory and population genetics, which state that for polymorphism to persist within a population, the relative fitnesses of the alternative morphs must be equal at *all* population frequencies, not just those occurring at the switch point (Shuster and Wade 2003). But again, assumption of equal fitnesses as the switch point is of little evolutionary consequence anyway because, as mentioned above, genetic variation is presumed to be absent for the polymorphism at this location (Gross and Repka 1998).

The second difficulty with the Gross and Repka (1998) approach is that relationships among the parameters used to estimate the frequency and fitness of the alternative tactics, as well as the proportion of progeny of each type that are transmitted to the next generation, are constrained by the authors *in advance* of the simulations they conduct. Thus, a higher existing frequency of one tactic imposes lower possible values for recruitment and heritability of the other tactic. The apparent goal of these interwoven constraints is to make the influences of each tactic on the other frequency dependent, and, indeed, measurable narrow-sense heritability of quantitative traits does depend on the frequency of the trait within the population (Falconer 1989). However, there is no population genetic precedent for the in heritability of traits to rely to such a large degree on their own population frequency, their own fitness, their own rate of recruitment into the population, or on the frequency, fitness, rate of recruitment, or mode of inheritance for another alternative trait.

Contrary to the predictions of the SDS model (Gross 1996, Gross and Repka 1998), considerable evidence already exists indicating that polymorphisms in mating phenotype with flexible expression represent mixturesof evolutionarily stable strategies (e.g., a normal distribution of genetically based reaction norms: Hazel *et al.* 1990, Roff 1992, 1996, Schlicting and Pigliucci 1998, Flaxman 2000, Shuster and Wade 2003). These results indicate that genetic architectures allowing phenotypic flexibility can persist in populations by frequency-dependent selection, a mechanism functionally identical to the way polymorphisms controlled by Mendelian factors persist in nature. In models of frequency-dependent selection, the inheritability of traits *does not* depend on their frequency in the population as in Gross and Repka (1998). If this condition were imposed, the salient feature of frequency-dependent selection (i.e., the tendency for alternative genotypes to have high relative fitness at low population frequency and low relative fitness at high population frequency) would cease to exist.

Thus, while the term "tactic" is indeed useful for describing phenotypes that are flexible in their expression, as opposed to those controlled by more rigid (e.g., Mendelian) rules, there is no need to distinguish a "strategy," as a phenotype that is *inheritable*, from a "tactic" as a phenotype for which genetic variation is *constrained* or *nonexistent*. Both traits clearly represent adaptations, that are underlain by genetic variation, and that are maintained in populations by selection. When viewed in this light, the term "strategy" is appropriate for *all* evolved polymorphisms in reproductive behavior, regardless of how their expression is controlled.

three fundamental ways in which alternative mating strategies are expressed, as well as the types of data that may be used for further hypothesis testing. My hope is that this framework will stimulate research on crustacean mating systems, particularly field studies that quantify the source and intensity of sexual selection, as well as laboratory studies that explore the genetic architectures underlying polymorphic mating phenotypes.

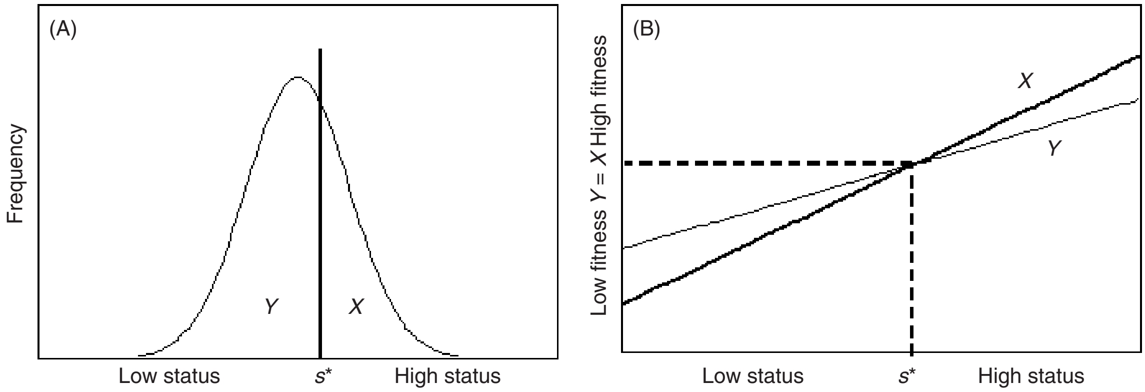

Figure 9.1 Intersection of the fitness functions of two phenotypes: the switch point.

9.2 SEXUAL SELECTION AND THE MATING NICHE

Darwin (1874) considered sexual selection to have evolutionary effects 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" (Darwin 1874, p. 212). This observation is the primary reason why male and female phenotypes tend to diverge under the influence of sexual selection, and why in many sexual species, including a large number of crustaceans, males and females are sexually dimorphic in appearance.

When some males mate and others do not, a sex difference in fitness variance often appears. This occurs because of the necessary relationship between the mean and variance in male and female fitness in all sexual species (Wade 1979, Shuster and Wade 2003). Although many factors may contribute to "fitness," this concept is least confounded and most easily understood when considered in terms of offspring numbers (Wolf and Wade 2001). Because every offspring has a mother and a father (Fisher 1958), the average number of offspring per male must equal the average number of offspring per female when the sex ratio equals 1 (Wade and Shuster 2002, Shuster and Wade 2003). Also under this condition, the variance in offspring numbers for each sex, that is, the variance in fitness for each sex, will be equivalent if all males and females mate once.

However if some males mate and others do not, as is usually the case, then the average fitness of males who do not mate becomes less than the fitness of the average female, for obvious reasons. Simultaneously, the average fitness of males who do mate equals the average female fitness multiplied by the number of mates that male secures (Wade 1979, Shuster and Wade 2003). As matings by females become clustered with fewer and fewer males, the class of males with no mates and no fitness becomes increasingly larger. In contrast, the class of males who do mate becomes increasingly smaller, but these males secure an increasingly larger fraction of the total offspring produced. Whereas the total variance in female fitness remains unchanged by this process, the divergence of the male population into reproductive "haves" and "have-nots" causes the total variance in male fitness to become very large.

The magnitude of this sex difference in fitness variance provides an estimate of the strength of sexual selection ($V_{W\text{males} - W\text{females}}$: Shuster and Wade 2003). As the magnitude of this fitness difference becomes larger, sexual selection becomes increasingly intense and male characteristics that promote polygamy are transmitted disproportionately to the next generation. This is why, over evolutionary time, males within such populations become modified in their appearance to a greater degree than females. When fitness variance is greater in females than it is in males, as it is in sex-role-reversed species, it is also why females become modified in appearance to a greater degree than males (Shuster and Wade 2003, unpublished data). Among related species in which sexual selection occurs, this is why the sex in which selection is more intense shows greater phenotypic diversity than the sex in which selection is weaker. Also, within individual species, this is why the sex in which selection is strongest shows a greater tendency to express alternative mating strategies (Gadgil 1972, Shuster and Wade 2003).

Why does this last relationship exist? Why should alternative mating strategies appear within the sex in which sexual selection is strongest? The answer is that alternative mating strategies readily evolve when male mating success becomes uneven among males (or uneven among females in role-reversed species). The existence of uneven mating success among males not only causes sexual selection, as observed by Darwin (1874), it also creates a "mating niche" for males engaging in unconventional mating behavior (Shuster and Wade 1991, 2003).

For example, in many species, small males invade the breeding territories of larger males by avoiding direct competition altogether. Once inside breeding territories, these "sneaker" or "satellite" males surreptitiously mate with receptive females, as occurs in isopods (*Paracerceis sculpta*: Shuster 1992), amphipods (*Microdeutopus gryllotalpa*: Borowsky 1980; *Jassa marmorata*: Clark 1997, Kurdziel and Knowles 2002) and in many decapods (e.g., freshwater prawns, *Macrobrachium* spp.: Ra'anan and Sagi 1989; sand bubbler crabs, *Scopimera globosa*, Koga *et al.* 1993; spider crabs, *Libinia emarginata*: Sagi *et al.* 1994, Ahl and Laufer 1996; and rock shrimp, *Rhynchocinetes typus*: Correa *et al.* 2003). In each of these species, stolen matings appear to provide unconventional or satellite males with only a tiny fraction of the fertilization success gained by those males that defend harems. These satellite males appear to "make the best of a bad job" (Eberhard 1979, Gross 1996). Yet in each of these examples, because unconventional males take fertilizations away from males whose fertilization success is already disproportionately large, satellite males are more successful at siring offspring 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 evolutionarily stable strategies (Maynard Smith 1982, Crow 1986). These conditions are most easily met for males employing alternative strategies (Wade and Shuster 2004) (Box 9.2). The important relationship is this: The larger the average harem size is among conventional males, the larger the fraction of conventional males must be who cannot secure mates. Because the average fitness of conventional males includes the fitness of males who mate as well as the fitness of males who do not mate, the *larger* the average harem size is among conventional males, the *smaller* the fraction of the total fertilizations unconventional males need acquire within harems for their average fitness to equal the average fitness of *all* conventional males combined (Shuster and Wade 2003, Wade and Shuster 2004) (Box 9.2). Although the average fitness of unconventional males seems inferior to that of conventional males, in fact, the average fitness of unconventional males often *equals or exceeds* the average fitness of all conventional males (see also Shuster and Wade 2003).

9.3 THE EXPRESSION OF ALTERNATIVE MATING STRATEGIES

Levins (1968) proposed that polymorphism can persist in natural populations when selection acts in changing environments. When environments change little, selection is usually weak and phenotypic tolerance is allowed; however, when environments change frequently, selection is stronger, phenotypic tolerance is impermissible, and genetic polymorphism is expected to arise. Shuster and Wade (2003) argued that such conditions are especially likely when sexual selection occurs. Sexual selection is often extremely strong and circumstances favoring mating success are often highly variable. Thus, they proposed that sexual selection acting in variable environments will most often favor distinct phenotypes and genetic polymorphism. It is important to note that the term "genetic polymorphism" not only refers to single-locus polymorphisms with alleles that segregate according to Mendelian rules, but also describes the normal distribution of genetic factors that influence the expression of condition-dependent patterns in development or behavior (i.e., "tactics") Shuster and Wade 2003 (Box 9.1). The game-theory-inspired concepts of genetically "fixed" pure phenotypes versus genetically monomorphic "conditional" phenotypes, while useful as heuristic devices (Maynard Smith 1982, Gross 1996, Alcock 2005), make little evolutionary sense when considering how selection might shape phenotypic expression for one obvious reason: traits lacking underlying genetic variation cannot respond to selection and therefore cannot evolve (Shuster and Wade 2003).

Whether the genetic architecture underlying a phenotypic polymorphism will be Mendelian or polygenic depends on the "environmental grain"; that is, on the relative predictability of environmental change (Levins 1968) (Box 9.3). Shuster and Wade (2003) argued that mobile organisms like animals experience environmental grain primarily on a temporal rather than on a spatial scale. Furthermore, with respect to the evolution of alternative mating strategies, they proposed that environmental grain is perceived by males in terms of (1) the existence of cues that predict mating opportunities as well as (2) the timing of cue perception, relative to the lifespan of individual males.

Box 9.2 Jack-of-All-Harems

Shuster and Wade (2003) showed how to visualize the quantitative relationship between the intensity of sexual selection and the ease with which alternative mating strategies may evolve. If we assume that H is the average mating success of harem-holding males and that satellite males succeed in mating by invading the harems of such males, then the fitness of satellites, W_β, can be expressed as

$$W_\beta = Hs, \tag{B9.2.1}$$

where s equals the fertilization success of satellite males within the harems of territorial males. Although the fitness of territorial males who successfully secure mates equals H, the average number of mates per male is less than H. This happens because when territorial males acquire a harem containing k females, $k-1$, other territorial males will be unable to mate at all (Shuster and Wade 2003). To calculate the average success of territorial males *as a class*, it is necessary to consider the distribution of mates among *all* of the males in that class. Thus, the average success of *all* territorial males must be

$$W_a = R, \tag{B9.2.2}$$

where R, the sex ratio $(= N_♀/N_♂)$, is equal to the distribution of all females over all territorial males. As Shuster and Wade (2003) showed, the condition necessary for satellite males to invade a population of territorial males is

$$W_\beta < W_a. \tag{B9.2.3}$$

That is, the average fitness of satellite males,W_β, must exceed the fitness of territorial males, W_a. By substitution with Eqs. (1B9.2.1) and (2B9.2.2), this relationship can also be expressed as

$$Hs < R. \tag{B9.2.4}$$

If the sex ratio, R, equals 1 (i.e., $Hs > 1$), then by rearrangement, the condition necessary for the invasion of a polygynous male population by an alternative mating strategy becomes

$$s < 1/H. \tag{B9.2.5}$$

That is, to invade a population of territorial males, satellite males must obtain a fraction of the total fertilizations in harems, s, that exceeds the reciprocal of the average harem size of *successful* territorial males. To understand this relationship, we need only imagine that the average harem-holding male mates with three females, or $H = 3$. In such circumstances, Eq. (5B9.2.5) shows that satellite males need only secure mates one-third as successfully as territorial males to invade this mating system ($s = 0.333$). Thus, on average, satellite males would need only fertilize 1/3 of the clutch of each female, or sire the progeny of 1 of the 3 females in each harem, to invade the population. And, as harem size increases (as females become increasingly clustered around fewer territorial males), the invasion of alternative mating strategies becomes easier still – satellites can be even less successful within harems and still invade because the fraction, $1/H$, becomes smaller with increasing values of H (Figure 9.2).

Shuster and Wade (2003) showed that in a polygamous population, the fraction of nonmating males is $p_0 = 1 - (1/H)$. By rearrangement of this equation, we can see that $1/H = 1 - p_0$. Now, by substitution with Eq. (B9.2.5), it is clear that

$$s < 1 - p_0. \tag{B9.2.6}$$

This relationship shows the same result as Eq. (B9.2.5) but in a slightly different way. Here, as the fraction of territorial males excluded from mating, p_0, increases, the mating success necessary for satellites to invade this mating system, s, becomes increasingly small. At equilibrium (i.e., $s = 1 - p_0$), this relationship explicitly identifies the fraction of the territorial male population that is excluded from mating, p_0, when territorial and satellite males coexist.

Box 9.3 Fitness sets and sexual selection

Levins' (1968) proposed that the fitness of each phenotype within a population changes as environmental conditions change and that the distribution of fitness for a specific phenotype can be characterized by the average and the variance in fitness. In these terms, environmentally "tolerant" phenotypes show a broader distribution of fitness in the face of environmental change than environmentally more "sensitive" phenotypes, i.e., the variance in the fitness of a tolerant phenotype, $V_{W(\text{tolerant})}$, is larger than that of a less more sensitive phenotype, $V_{W(\text{sensitive})}$ (Figure 9.3) or

$$V_{W(\text{tolerant})} V_{W(\text{sensitive})} \cdot \qquad \text{(B9.3.1)}$$

Because tolerance to variable environments is likely to impose fitness costs, the average fitness of the tolerant phenotype, W_{tolerant}, is less than for the sensitive type, $W_{\text{sensitive}}$ (Figure 9.3) or

$$W_{(\text{tolerant})} < W_{(\text{sensitive})} \cdot \qquad \text{(B9.3.2)}$$

Thus, a phenotype that maintains some fitness in marginal environments will be unable to achieve the highest fitness in the more common environment, whereas a phenotype that achieves low fitness in marginal environments will achieve higher fitness in the environment for which it is specialized (Figure 9.3).

A graphical means for identifying the optimal phenotype for a particular environment is obtained by holding environmental conditions fixed and examining performance as function of phenotype (Levins 1968, Shuster and Wade 2003). This procedure generates a curve describing the distribution of fitness for a given phenotype, i, across a limited range of environments, j. The peak of each curve identifies the optimal phenotype in each subset of environments, and because phenotypes deviating from this optimum have lower performance, fitness decreases symmetrically away from the phenotypic optimum toward zero (Figure 9.3). When the performance curves generated by the two most common environments are considered together (Figure 9.4), the phenotypic *tolerance* of a population can be quantified. Specifically, tolerance (T) is equal to $2d$, where d is the distance in phenotypic performance units from the peak of the distribution to its point of inflection.

The environmental range, E, is the difference in the average phenotypic performances in each environment ($s_2 - s_1$) (Figure 9.4). Approximately overlapping performance curves produced by each environment indicate a *tolerant* phenotype; that is, a phenotype whose ability to tolerate environmental change exceeds the range of conditions that usually appear within the environment. In such cases, $T > E$, and the optimal phenotype is approximately similar in each environment (Figure 9.4A). On the other hand, nonoverlapping curves (those in which $T < E$) indicate *intolerant* phenotypes. These phenotypes are favored when the range of environmental conditions is so great that a single phenotype is unable to tolerate all environmental circumstances. Thus, different phenotypes are optimal in each of the most common environments (Figure 9.4B).

When the values of the performance curve in environment 1 are plotted *against* those in environment 2, the familiar shapes of Levins' *fitness sets* appear (Figure 9.5). The similar performance curves of tolerant phenotypes generate *convex* fitness sets (Figure 9.5A), whereas nonoverlapping performance curves of intolerant phenotypes generate *concave* fitness sets (Figure 9.5B). Tolerant phenotypes can persist despite rapid changes in the environment, provided that the magnitude environmental variation, E, is small. These phenotypes experience environmental variation as an average of environment types (Levins 1968, Lloyd 1984). However, increasing the range of environmental fluctuation makes environmental tolerance more difficult. Thus, when the environmental range, E, becomes large, tolerant phenotypes, which achieve modest success across all environments, tend to go extinct and are replaced by specialists, which, while phenotypically inflexible compared to more tolerant phenotypes, can achieve higher average fitness due to their enhanced success in a particular environment.

In short, increasing the range of environmental variation intensifies selection in favor of phenotypes that are specialized for particular conditions. Given the postulated trade-off between fitness mean and variance, as selection intensity increases, specialization is favored and performance distributions must become narrower, more distinct, and therefore likely to generate concave fitness sets (Levins 1968). Thus, when environments fluctuate widely, more specialized phenotypes with higher average fitness are expected to invade populations consisting of tolerant, generalist phenotypes (Figure 9.3).

Box 9.3 (Cont.)

A wide range of environmental fluctuations alone can favor phenotypic specialization. However, Shuster and Wade (2003) argued that the *stronger* the selection in favor of a particular phenotype, the more *narrow* the distribution of performance in a particular environment. Thus, a concave fitness set will arise *whenever* selection becomes intense, even if the range of environmental fluctuation remains small. This occurs because under intense selection, the performance distributions within each environmental extreme will *contract* – the variance of the fitness distribution will be *reduced* (Figure 9.6). Thus, as selection becomes more intense, fitness sets will become increasingly concave and increasingly specialized phenotypes are expected to appear (see discussions in Bradshaw 1965, Lloyd 1984, Via and Lande 1985, Lively 1986, Moran 1992, Winn 1996, Schlicting and Pigliucci 1998).

But this is only part of the story. The optimum strategy for a given environment is not determined by the shape of the fitness set alone (Levins 1968, Shuster and Wade 2003). Rather, it is the *pattern* of environmental change impinging on each fitness set that determines (1) whether polymorphism will evolve and (2) the mechanism by which phenotypes will be expressed. When environmental changes occurs slowly, with periodicity *greater than* the average lifespan, individuals tend to experience their environments as alternative conditions with proportionately large, nonlinear effects on their fitness. Environmental changes occurring more rapidly, with periodicity *less than* the average lifespan, cause linear increases or decreases in the fitness of individuals because individuals experience the environment as a succession of different developmental conditions with their fitness averaged over them. The spatial and temporal scale of environmental change is the basis of Levins' (1968) concept of environmental *grain*.

Few or no changes within an individual's lifetime constitute *coarse* environmental grain, whereas rapid changes within an individual's lifetime cause the environment to be experienced as an average, and thereby constitute *fine* environmental grain. Phenotypes showing little variation are expected to evolve when environmental fluctuation is small in magnitude (Bradshaw 1965, Levins 1968). When the environment fluctuates, fitness sets become concave and polymorphic phenotypes of several kinds are expected to evolve, depending on how organisms perceive their environment.

If the arrival of change is unpredictable, environmental grain is coarse and Mendelian polymorphisms are expected to evolve. Under these conditions, the frequencies of genetically distinct phenotypes will depend on the probability with which each environment occurs and on the relative fitness that each phenotype obtains therein. Distinct genotypes persist when their fitnesses averaged across the environmental grain are equal (Bradshaw 1965, Levins 1968, Maynard Smith 1982, Lively 1986).

In fluctuating environments, if environmental grain is perceived as fine, then selection will favor *polyphenism* (Lloyd 1984). This variation differs from simple environmental tolerance because the fitness set is concave. That is, selection is so intense that even the most tolerant individuals cannot persist; only specialists can. Thus, selection favors individuals who are *developmentally* capable of generating more than one phenotype, over individuals developing only a single phenotype with broader tolerance (Bradshaw 1965, Levins 1968, Lively 1986, Moran 1992, Roff 1992). Polyphenism is a mechanism for tolerance of environmental variation and its existence is evidence of "adaptive plasticity" (Shuster and Wade 2003). A coarse-grained environment can be experienced as a fine-grained one by individuals who use environmental cues to predict when change will occur and adjust their developmental trajectories appropriately (Bradshaw 1965, Levins 1968, Lively 1986, Moran 1992, Roff 1992, Winn 1996).

The ability to respond to a change in one's environment represents a genotype-by-environment interaction (G×E) (Schlicting and Pigliucci 1998). The particular way in which this interaction is expressed – the way in which an individual responds to environmental change – is known as its *reaction norm*. Within populations, reaction norms tend to be normally distributed due to genetic differences among individuals (Hazel *et al*. 1990, Roff 1996). The level of adaptive plasticity is the average efficiency with which different individuals in the population respond to environmental change. Thus, the equilibrium distribution of genotypes in a population depends on the distribution of reaction norms, the distribution of environments, and the distributions of fitness for the different possible phenotypes within the population. As for any genetic polymorphism, stable phenotypic distributions (or in this case, stable distributions of reaction norms that allow plastic responses to changing environments) are expected to persist when the fitnesses of their underlying genotypes are *equal* (Hazel *et al*. 1990, Roff 1996, Flaxman 2000, Shuster and Wade 2003).

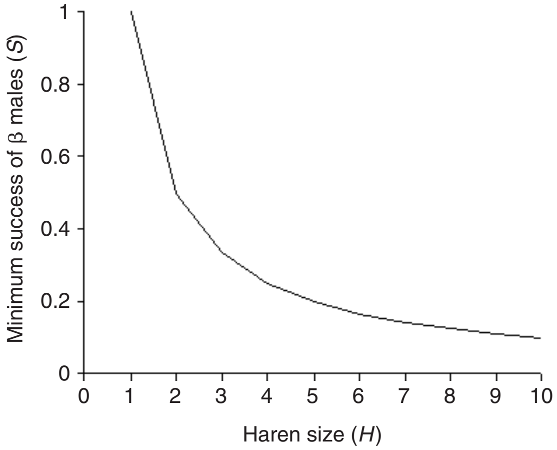

Figure 9.2 Success of satellite males in relation to harem size.

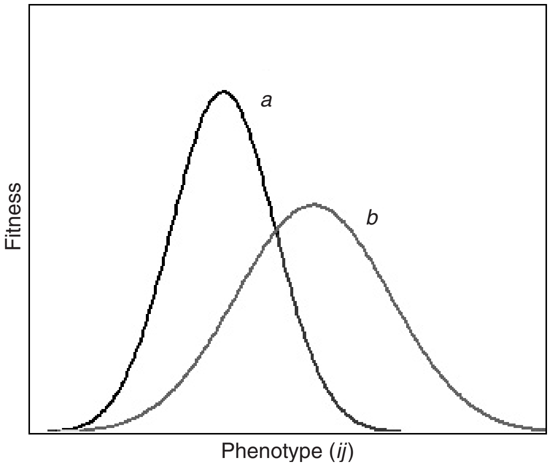

Figure 9.3 Fitness of "tolerant" and "sensitive" phenotypes.

With these two factors in mind, it is easy to see that the grain of the environment will be coarse if cues predicting male mating success do not exist. Such conditions may appear most often when male lifetimes are short. However, regardless of whether males are presented with few or many mating opportunities within their lifespans, when environments are unpredictable, specialists are favored and male mating behavior patterns are expected to represent Mendelian alternatives (Shuster and Wade 2003). The grain of the environment will be perceived by males as fine if environmental cues do predict the type of mating opportunities that will become available. Such conditions may exist most often when male lifetimes are long. But regardless of whether males are presented with few or many mating opportunities, strong sexual selection combined with fine-grained environments will favor the evolution of polygenic inheritance underlying the expression alternative mating strategies. In general, the expression of such traits is well explained by current models for threshold inheritance Shuster and Wade 2003) (Box 9.4).

When environmental cues perceived early in life predict mating opportunities later in life (when the interval between the perception of the cue and mating opportunities is long relative to total male lifespan), developmental processes will prevail. Thus, abundant food may enhance growth rate, increasing a male's body size as well as his likelihood of success in combat. Food shortages, on the other hand, may decrease the probability of such success in combat and instead lead to the expression of a noncombative, default phenotype. Males who respond to environmental cues with appropriate developmental trajectories are likely to outcompete males whose genotypes resist modification when environments change, as do Mendelian alternatives.

When environmental cues predicting mating success occur immediately before mating opportunities arise (when the interval between the perception of the cue and mating opportunities is short relative to total male lifespan), behavioral processes will prevail. Thus, a particular density of mating competitors may induce some individuals to become aggressive, whereas individuals insensitive to such cues will not engage actively in the commotion of direct mating competition. Or, a particular density of females may cause some males to associate themselves with individual females to await their impending receptivity, whereas individuals insensitive to such cues may continue searching for females more immediately receptive. The relative frequencies of sensitive and insensitive individuals in any population will depend on the relative success of these phenotypes over time (Box 9.3). Males who respond rapidly and appropriately to environmental cues that predict mating success in changing environments are likely to outcompete males whose genotypes resist environmental change, as well as males who cannot respond as rapidly to changes in conditions favoring mating success.

And yet, while it is widely acknowledged that genetic architectures sensitive to environmental cues can allow

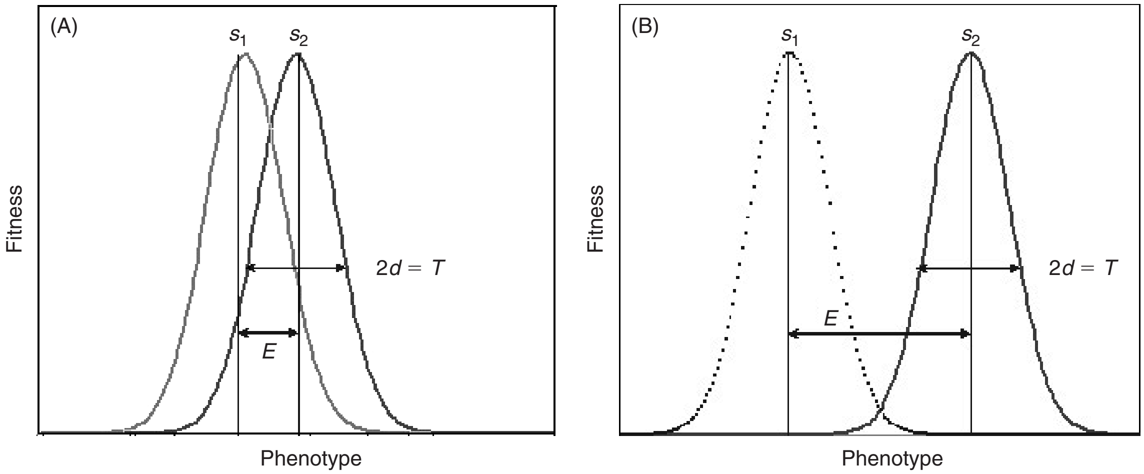

Figure 9.4 Phenotype tolerance of a population.

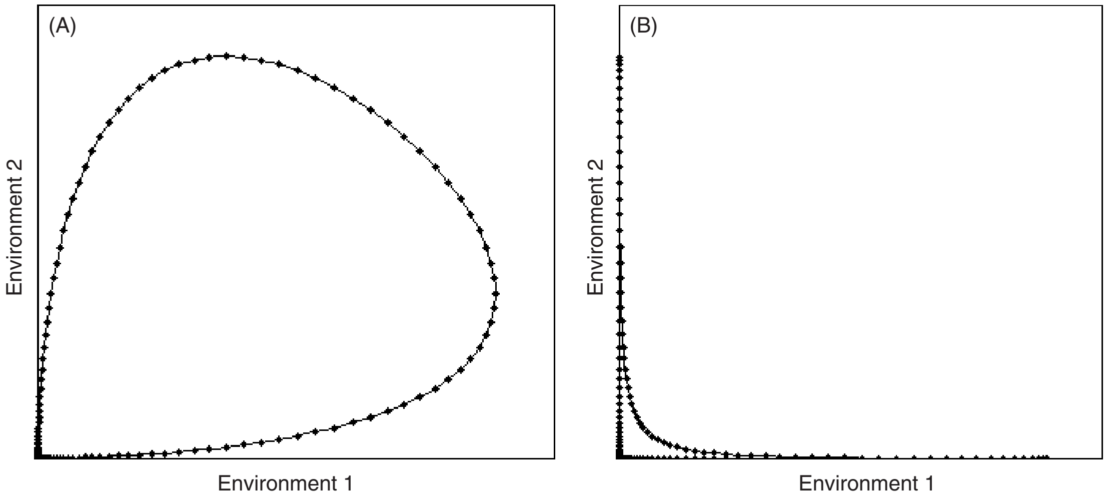

Figure 9.5 Levins' fitness sets (see Levins 1968).

males to express appropriate phenotypes in response to changing environments (Roff 1996, Schlicting and Pigliucci 1998), the evolutionary restrictions on phenotypic plasticity are seldom mentioned when variable phenotypes are observed (Shuster and Wade 2003). Phenotypic plasticity in development or in behavior is likely to evolve only if the following conditions exist:

(1) Genetic variation allowing a plastic response to changing environmental conditions must be present in the population – individuals must be genetically variable, not genetically identical.
(2) The cost of making the wrong developmental or behavioral "choice" must be high; that is, expressing an inappropriate phenotype in an environment in which it is not favored, leads to little, or more often, no reproduction at all.
(3) Circumstances favoring plasticity must occur frequently. Conditions in which a plastic response is required must be common, they must occur in a

consistent way, and they must not be contingent on special circumstances (such as a uniquely debilitating injury: West-Eberhard 2003; or the appearance of a uniquely compatible mate: Gowaty 1997, Tregenza and Wedell 2000).

(4) Conditions in which a plastic response is required must be experienced by a large fraction of the population.

All of these conditions must apply for phenotypic plasticity to evolve, because if they do not exist, either a response to selection will be impossible or selection on genetic factors allowing polyphenism will be weak. Clearly, phenotypic plasticity cannot evolve in the absence of genetic variation mediating a flexible developmental or behavioral response. However, phenotypic plasticity is also unlikely to evolve when circumstances favoring it are rare and highly contingent on the behavior of other individuals, or when they are experienced by only a few individuals in the

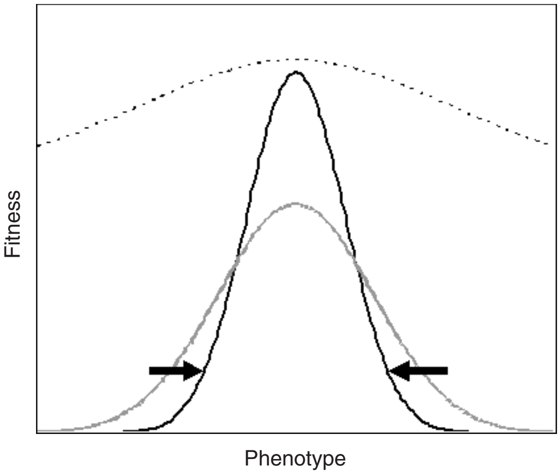

Figure 9.6 Change in fitness distribution under intense selection.

Box 9.4 Threshold characters

Discrete phenotypic classes within a population that fail to segregate according to Mendelian rules are often explained by threshold models of quantitative inheritance. As with most complex characters, continuous genetic variation appears to underlie threshold traits. However, a threshold of "lability" within this distribution also exists that makes trait expression discontinuous. Individuals with genotypes below the threshold express a default phenotype, whereas individuals with genotypes above the threshold express a modified phenotype (Figure 9.7).

The expression of threshold traits is not absolute. Depending on trait heritability, threshold position, and the environment, each genotype has its own probability of trait expression (Dempster and Lerner 1950, Gianola and Norton 1981). For this reason, environmental influences on threshold characters can be viewed in two ways. When the environment is constant, or reasonably so, as might exist over a period of maturation, trait expression appears as described above; genotypes above the threshold usually express the trait, trait expression becomes increasingly unlikely for genotypes below the threshold, and the population appears dimorphic. Alternative mating strategies involving distinct developmental trajectories are well described by this hypothesis.

When the environment changes over shorter timescales, few or no genotypes may express the trait at one environmental extreme, whereas at the other extreme, all or nearly all genotypes will become modified (Figure 9.8). The wider the environmental range, the greater is the proportion of the population that is likely to change. Although the probability of trait expression remains constant for each genotype, depending on the intensity of the environmental "cue" at any time, few, some, or all individuals in the population may express the trait. Alternative mating strategies involving behavioral polyphenism are well described by this hypothesis.

Threshold models may also explain age-dependent mating strategies, although contrary to current models of this phenomenon, a threshold view predicts that few males will perform both "young" and "old" mating strategies within their lifetimes (e.g., Correa *et al.* 2003). Instead, quantitative genetic variation is expected to predispose males to mate as satellites when young or as territorial males when old, with frequency-dependent selection maintaining the position of the threshold within the distribution of male maturation rates.

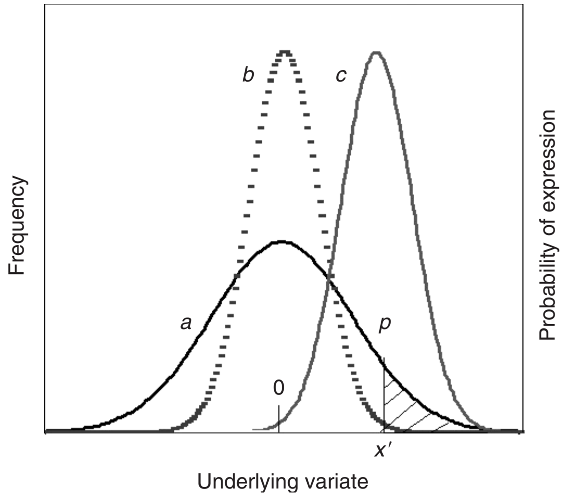

Figure 9.7 Phenotype expression of threshold characters.

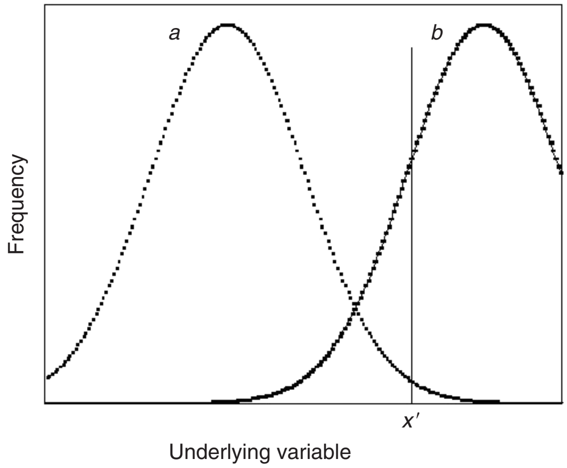

Figure 9.8 Modification of expression of a threshold character at environmental extremes.

population. Under these conditions, selection will be of low intensity, intermittent in its effects, and likely to influence only a small number of individuals in the population. In combination, these factors will weaken, if not obliterate entirely, the effects of directional selection favoring adaptive phenotypic plasticity (Shuster and Wade 2003).

9.4 MENDELIAN STRATEGIES

Among crustaceans, examples of Mendelian strategies include marine isopods (Shuster and Wade 1991, Shuster and Sassaman 1997, K. Tanaka, personal communication), freshwater isopods (Bocquet and Veuille 1973), androdioecious branchiopods (Sassaman 1991, Weeks and Zucker 1999), and sequentially hermaphroditic decapods in which primary males or primary females persist (Bauer 2000, 2002).

In *Paracerceis sculpta*, a marine isopod inhabiting the northern Gulf of California, three discrete male morphotypes coexist (Figure 9.9). Phenotypic differences among males are controlled primarily by an autosomal locus of major effect (*Ams* = alternative mating strategy), whose inheritance is Mendelian and whose alleles exhibit directional dominance ($Ams^{\beta} > Ams^{\gamma} > Ams^{\alpha}$). The different *Ams* alleles interact with alleles at other loci, switching on distinct developmental cascades that lead to discontinuous adult phenotypes. These interactions appear to influence male as well as female phenotypes. Alleles at *Ams*, and at an additional autosomal locus (*Tfr* = transformer), epistatically interact to radically distort family sex ratios (Shuster and Sassaman 1997, Shuster *et al.* 2001). This is accomplished when particular *Ams*–*Tfr* allelic combinations override the primary sex determination mechanism (WW = males; ZW = females: Shuster and Levy 1999) and cause individuals to mature as adults of the opposite sex (Shuster *et al.* 2001).

The dynamic nature of this mating system is consistent with the hypothesis that sexual selection is intense and

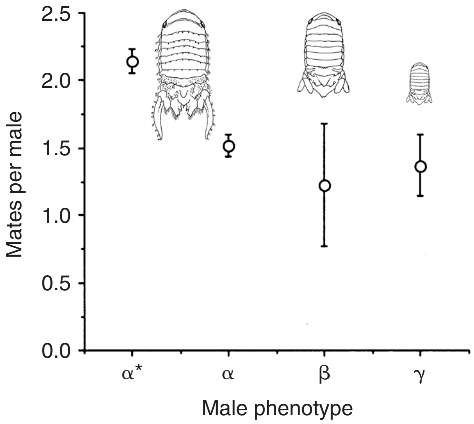

Figure 9.9 The mating success of *Paracerceis sculpta* α-, β-, and γ-males in *Leucetta lonangelensis* spongocoels between 1983 and 1985. The average harem size of mating α-males is represented by α*; α represents the average harem size of all α-males. (Redrawn from Shuster and Wade 2003.)

mating opportunities for males, as well as for females, are highly variable and unpredictable from one generation to the next. At breeding sites, mating success among the male morphs varies with the number of females, as well as with the number and type of other males (Shuster 1989, 1992, Shuster and Wade 1991). However, over time, the average fitnesses of α-, β-, and γ-males are equal (average ± 95% CI; α-males: 1.52 ± 0.16, $N = 452$; β-males: 1.25 ± 0.86, $N = 20$; γ-males: 1.37 ± 0.45, $N = 83$: Shuster and Wade 1991, 2003) In this species, α-males defend territories in sponges; thus mating as well as nonmating α-males are identifiable. Indeed, when only the average mating success of *mating* α-males (α*) is considered, this value is significantly larger than the average mating success for β- and γ-males (2.22 ± 0.17) (Figure 9.9). This example shows why satellite males in many animal species may appear to "make the best of a bad job" when unsuccessful males cannot be identified. In reality, satellite males usually experience average fitness equal to that of all territorial males, winners as well as losers.

A genetic polymorphism in male leg morphology exists in *Jaera albifrons*, a freshwater isopod in which males guard females before mating (Bocquet and Veuille 1973). In other isopods with similar precopulatory behavior (*Thermosphaeroma*: Shuster 1981, Jormalainen *et al.* 1999), the legs of males in several species are more setose than those of females and may be useful in retaining control of mates during usurpation attempts by other males. Unfortunately, in *J. albifrons*, environmental or social factors maintaining the polymorphism have not been examined nor has the possibility that males may employ different reproductive strategies in the context of mate guarding.

However, males in species with pre-copulatory guarding are widespread within the Crustacea (Ridley 1983, Conlan 1991, Jormalainen 1998), and individual males are known to switch between mate-guarding and mate-usurping behavior. It is likely that the inheritance of mate-guarding behavior is polygenic rather than Mendelian, consistent with behavioral polyphenism (see below). And yet, the existence of Mendelian phenotypes in *J. albifrons* suggests that such genetic architectures are more widespread than is currently recognized. In such species, more detailed experiments designed to identify genetic influences on morphology as well as behavior among males are clearly needed.

A Mendelian polymorphism may also exist in the gnathiid isopod *Elaphognathia cornigera*, a species inhabiting mud banks and coral rubble in coastal regions of the western Pacific (Tanaka and Aoki 1999, Tanaka 2003). In this species, males are larger than females and possess enormous mandibles that are used to defend breeding aggregations and to encourage females to enter breeding sites. In addition to large males, small, sexually mature males coexist with territorial males in these populations (K. Tanaka, personal communication). Although the inheritance of this polymorphism is currently unknown, like *P. sculpta*, gnathiid isopods are semelparous (Upton 1987, Tanaka 2003); thus, individual lifetimes are relatively short. In addition, the pelagic praniza larvae of gnathiids, which are parasitic on fish (Roberts and Janovy 2005), seem unlikely to have opportunities to detect cues predicting their mating success until they arrive at breeding sites as adults. Such conditions could favor Mendelian inheritance of the adult male phenotype (although a developmental polymorphism is also possible; see below). Experiments are currently under way to test this hypothesis (K. Tanaka, personal communication).

Although usually not considered in discussions of alternative mating strategies, mating systems in which males persist with hermaphrodites (androdioecy) or in which females persist with hermaphrodites (gynodioecy) often represent Mendelian polymorphisms controlling the expression of alternative mating strategies (Charlesworth 1984, Charlesworth and Charlesworth 1987). In the clam shrimp *Eulinmadia texana*, males coexist with two phenotypically similar, but genetically different, types of hermaphrodites that may self-fertilize or outcross. Sex in this species is controlled by a single genetic locus (Sassaman and Weeks 1993), in which a dominant allele codes for the hermaphroditic condition (S) and a recessive allele codes for males (s). Phenotypic males are homozygous recessives (ss) whereas hermaphrodites may be homozygous (SS = monogenic) or heterozygous (Ss = amphigenic). Monogenic hermaphrodites are homozygous dominants (SS) and produce 100% monogenic progeny when selfed (SS) or 100% amphigenic progeny when outcrossed (Ss). Amphigenic hermaphrodites produce mixtures of monogenic, amphigenic, and male progeny depending on whether they self or outcross (25% monogenics, 50% amphigenics, and 25% males when selfed; 50% amphigenics and 50% males when outcrossed). The composition and the relative fitness of each genotype within each population determine the observed genotype frequencies and, despite a high frequency of selfing for *E. texana* (inbreeding coefficients ranging from 0.20 to 0.97: Sassaman 1989, Weeks and Zucker 1999), androdioecy persists in nature.

Sex determination also appears to be controlled by a simple mechanism in the notostracan *Triops newberryi*

(Sassaman 1991), in which female genotype at a single autosomal locus influences whether females produce families that are all-female or which consist of mixtures of males and females. *Triops* and *Eulimnadia* species, like many other branchiopods, inhabit temporary pools in arid regions (Sassaman 1991, Weeks and Zucker 1999). The dormant zygotes of these species can persist for years in a desiccated state and are dispersed by wind and floods. Thus, as predicted above, the lifetimes of these species are short, and conditions favoring males or hermaphrodites in newly colonized pools are likely to be unpredictable, with intense selection favoring selfing or outcrossing from one habitat to the next.

A bewildering array of mating systems appears to exist within the caridean decapods (Bauer and VanHoy 1996, Bauer 2000), and while many species appear to include some form of developmental sex change (see below), the persistence of individuals who do not change sex suggests the existence of a Mendelian polymorphism (Roff 1996, Lively *et al.* 2000). Caridean examples include protandrous mating systems with primary males (e.g., *Thor manningi*: Chace 1972, Bauer 1986; *Athanas* spp.: Nakashima 1987, Gherardi and Calloni 1993), mating systems with protandric simultaneous hermaphroditism (PSH) (e.g., *Lysmata* spp. and possibly *Exhippolysmata*: Bauer 2000, 2002), and protandrous mating systems with primary females (e.g., *Processa edulis*: Noël 1976; *Crangon crangon*: Boddeke *et al.* 1991; *Argis dentata*: Fréchette *et al.* 1970; *Pandalus*: Charnov 1979, 1982, Bergström 1997). The persistence of distinct, nonchanging adult phenotypes in each of these mating systems strongly suggests the existence of underlying genetic variation that is maintained within the population by equal fitnesses among the recognizable morphs.

9.5 DEVELOPMENTAL STRATEGIES

Examples of developmental strategies within the Crustacea appear to include certain copepods (Haq 1972, Stancyk and Moreira 1988), a large number of decapods (Carpenter 1978, Ra'anan and Sagi 1989, Kuris *et al.* 1987, Bauer 2000, Baeza and Bauer 2004), as well as numerous amphipods and tanaids (Darwin 1874, Borowsky 1980, 1984, Conlan 1991, Clark 1997, Kurdziel and Knowles 2002).

In the harpacticoid copepod *Euteropina acutifrons*, two distinct male morphs coexist with females (Haq 1965, 1972, 1973, D'Apolito and Stancyk 1979, Moreira *et al.* 1983, Moreira and McNamara 1984, Stancyk and Moreira 1988). While earlier descriptions suggested that the male morphs differed in their developmental rates (Haq 1972, 1973), later experiments that directly examined the possible effects of paternity and temperature on morph expression (Stancyk and Moreira 1988) suggested that a combination of Mendelian and developmental polymorphisms may exist in which primary males coexist with protandrous hermaphrodites, a situation similar to that observed in many caridean shrimp (Bauer 2000).

Ra'anan and Sagi (1989) described three male morphs representing successive growth stages in freshwater prawns (*Macrobrachium rosenbergii*) (see Nagamine *et al.* 1980). Also in this species, Kuris *et al.* (1987) demonstrated that developmental trajectories among the male morphs are determined by feeding schedule and social interactions among individuals. These authors suggested that, in fact, four morphs are identifiable (see also Barki *et al.* 1992, Kurup *et al.* 2000) and that dominance hierarchies among the morphs exist, wherein removal of larger individuals induces smaller individuals to grow and in some cases assume the morphology of the missing larger class. However, not all individuals responded equally to this stimulus, as expected if males vary in their responsiveness to social and nutritional cues (Kuris *et al.* 1987, Karplus *et al.* 2000). Such variation is characteristic of traits with threshold expression (Box 9.4).

Other *Macrobrachium* species also appear to exhibit male polymorphism (*M. dayanum*, *M. idae, M. malcolmsonii, M. scabriculum*; reviewed in Kuris *et al.* 1987), and it is likely that similar growth and social stimuli influence the fitness and frequencies of the different male morphs, and thus the means by which developmental switches are favored. In *M. rosenbergii*, females are dimorphic as well (Harikrishnan *et al.* 1999). In all of these populations, extreme sexual dimorphism involving large size and elongated chelae in males suggests that competition for mates is intense (Wade and Shuster 2004). Moreover, relatively long-lived individuals appear to obtain information and respond appropriately with respect to their future mating opportunities and to nutritional and social cues during development (Kuris *et al.* 1987). Populations of the same species appear to vary in the proportions of individuals exhibiting different male morphologies (Karplus *et al.* 2000, Kurup *et al.* 2000). All of these observations are consistent with quantitative genetic inheritance of threshold traits (Roff 1996) (Box 9.4). Given that freshwater prawns provide an important food source in many countries, there is likely to be continued commercial interest in studies identifying the degree to which developmental programs can be manipulated, either by altered environments or by selection on norms of reaction (Emlen 1996).

In the rock shrimp, *Rhynchocinetes typus*, males exhibit three phenotypes of increasing size that evidently represent increasing states of maturation (*typus, intermedius, robustus*; Correa *et al*. 2000, 2003). The *typus* morphotype is similar in morphology to the female. The *robustus* morphotype possesses powerful chelae and elongated third maxillipeds. During development, males undergo several intermediate molts between these two morphs. Such males are classified as *intermedius*. All three male types are sexually mature and all three exhibit similar behavior when allowed to mate with females in isolation. However, in competitive situations, males established size-based dominance hierarchies (*robustus* $>$ *intermedius* $>$ *typus*), and males differed in their rates of interaction with females and spermatophore deposition. Subordinate males engaged in these activities more rapidly than more dominant males.

It is unclear whether these morphs represent the same level of specialization that appears to exist in *Macrobrachium* spp. or in amphiopods with two developmentally distinct male morphs (Kurdziel and Knowles 2002). Because *typus* males appear to eventually grow into *intermedius* and *robustus* stages, Correa *et al*. (2000, 2003, Correa and Thiel 2003) consider the variation observed in *R. typus* to be entirely behavioral and consistent with models for condition-dependent switching of phenotypes (see below). However, populational variation in the tendency for *typus* males to follow this developmental trajectory is unknown, and unfortunately, like other marine decapods, the presence of planktonic larvae and prolonged juvenile development are likely to prevent the detailed breeding experiments necessary to identify genetic variation underlying different male phenotypes. The tendency for *typus* males to display highly specialized mating and sperm-transfer behavior associated with their small size (Correa *et al*. 2003) suggests that selection favoring this morphotype is strong. Also, the tendency for the population frequencies of the three male morphs to remain constant within populations and to be variable among populations suggests an underlying developmental mechanism involving threshold inheritance (Correa *et al*. 2003).

Darwin (1874) identified a male polymorphism in the Brazilian amphipod *Orchestia darwinii*. In this species, adult males possess gnathopods (chelae) that are either enlarged or reduced in size. Darwin added "the two male forms probably originated by some having varied in one manner and some in another; both forms having derived certain special, but nearly equal advantages, from their differently shaped organs." He also mentioned a dimorphism in *Tanais* "in which the male is represented by two distinct forms, which never graduate into each other. In the one form the male is furnished with more numerous smelling-threads, and in the other form with more powerful and more elongated chelae or pincers, which serve to hold the female" (Darwin 1874, p. 262).

Whether these dimorphisms are developmental in their expression is unclear. However, the possibility that they are is made credible by the detailed work of Borowsky (1984, 1985, 1989), Clark (1997), and Kurdziel and Knowles (2002), who have documented two sexually mature male morphs representing different growth stages in the marine amphipods *Microdeutopus gryllotalpa*, *Jassa falcata*, and *J. marmorata*. In each of these species, larger males ("majors" or "thumbed" males) possess enlarged gnathopods that are lacking in smaller males ("minors or "thumbless" males). Majors vigorously defend tubes inhabited by receptive females against other majors, whereas minors tend to travel among tubes and avoid conflict. Similar mating systems are evidently widespread within the Amphipoda, and sexual dimorphism involving enlarged male gnathopods is common in taxa in which males defend females in burrows or other cavities (Conlan 1991).

Kurdziel and Knowles (2002) demonstrated that in *J. marmorata*, the polymorphism is indeed developmental, and their results are consistent with threshold models of quantitative trait inheritance (Roff 1996, Shuster and Wade 2003) (Box 9.4). Well-fed males tend to grow to large size and develop enlarged gnathopods, whereas poorly fed males do not. However, Kurdziel and Knowles' (2002) initial interpretation of their results ("Heritability analyses indicated the reproductive phenotypes do not reflect genetic differences between dimorphic males," p. 1749) is suspect given their application of a standard full-sib breeding design to investigate broad sense heritability for male phenotype (Falconer 1989). The probabilistic nature of threshold trait expression (Box 9.4) makes this approach less likely to identify a genetic component underlying male differences than the method specifically designed to detect the heritability of threshold traits (Falconer 1989, p. 300). A reanalysis of the data of Kurdziel and Knowles (2002), or a breeding design conducted using methodology appropriate for such traits, could determine whether male polymorphism in these and other amphipods involves threshold inheritance.

Tendencies for individuals within populations to undergo sex change are likely to represent a developmental strategy that evolves when individuals regularly encounter distortions in population sex ratio (Shuster and Wade 2003). The dynamics of sex change are well known in *Pandalus* shrimp, for which much of sex allocation theory was developed (Charnov 1979, 1982). Also, in the caridean shrimp *Lysmata wurdemanni* (Bauer 2000, Baeza and Bauer 2004), individuals mature as male-phase (MP) individuals and later change to female-phase (FP) individuals, which possess female external morphology but retain both male and female reproductive capacity (another example of protandric simultaneous hermaphroditism).

To examine social mediation of sex change, Baeza and Bauer (2004) reared MP individuals in both large and small social groups with different sexual and size composition. As expected, if the availability of mating opportunities for members of each sex influenced the intensity of sexual selection (Shuster and Wade 2003), these authors found that the speed of sex change was inversely related to the abundance of FP individuals in the "large group" experiment but the trait was less obvious in smaller groups. Baeza and Bauer (2004) suggested that a more rapid change to the female phase may occur when male mating opportunities are low because the simultaneous-hermaphrodite FPs can immediately reproduce as a female while maintaining male mating capacity.

While sex allocation theory is consistent with the observations above, the theoretical framework for sex ratio equalization almost without exception involves family selection (review: Wade *et al.* 2003). That is, the primary source of selection on sex ratio derives from the fitness of females who bias their family sex ratios toward the minority sex, relative to that of females who either bias their family sex ratios toward the majority sex or do not bias their family sex ratios at all. This evolutionary process is extremely slow and is unlikely by itself to explain the observed dynamics in sex ratio in natural populations. Shuster and Wade (2003; see also Wade *et al.* 2003) proposed that in many species undergoing sex change, genetic polymorphisms may exist that mediate individual abilities to either change sex or remain unchanged, as evidently occurs in the isopod *Paracerceis sculpta* (Shuster and Sassaman 1997, Shuster *et al.* 2001)

A simple method for investigating this possibility involves estimating the frequency of the population that exists as a single sex. If this fraction represents an alternative mating strategy, then as explained above (see Eq. (6B9.2.6), Box 9.2), their fitness relative to that of hermaprodites, s, may be used to approximate the fraction of the hermaphroditic population that is *unsuccessful* in reproducing as that sex, p_0. Thus, primary males would represent the alternative phenotype in androdioecy and in protandrous and protandric simultaneous hermaphroditic mating systems with primary males. Similarly, females would represent the alternative phenotype in gynodioecy and in protandrous mating systems with primary females.

9.6 BEHAVIORAL STRATEGIES

Within the Crustacea, examples of polymorphism in mating behavior appear, as predicted, in long-lived taxa such as stomatopods (*Pseudosquilla ciliata*: Hatziolos and Caldwell 1983; *Gonodactylus bredini*: Shuster and Caldwell 1989) and decapods (*Alpheus armatus*: Knowlton 1980; *Pachygrapsus transversus*: Abele *et al.* 1986; *Homarus americanus*: Cowan 1991, Cowan and Atema 1990; *Uca* spp.: Salmon and Hyatt 1983, Christy and Salmon 1991, Jennions and Backwell 1998; *Sicyonia dorsalis*: Bauer 1992; *Callinectes sapidus*: Jivoff and Hines 1998; *Scopimera globosa*: Wada 1986, Koga 1998; *Chionoecetes opilio*: Moriyasu and Benhalima 1998; *Jasus edwardsii*: MacDiarmid and Butler 1999; *Rhynchocinetes typus*: Correa and Thiel 2003, Correa *et al.* 2000, 2003).

Howevever, they also appear in shorter-lived taxa including amphipods (*Microdeutopus gryllotalpa*: Borowsky 1984; *Gammarus duebeni*: Dick and Elmwood 1995; *Jassa marmorata*: Clark 1997) and isopods (*Thermosphaeroma* spp.: Shuster 1981, Jormalainen and Shuster 1999; *Paracerceis sculpta*: Shuster 1992, S.M. Shuster and X. Y. Arnold, unpublished data; *Idotea baltica*: Jormalainen *et al.* 1994). In each of these cases, males, and often females as well, are highly mobile, have multiple mating opportunities within their lifetimes, and individuals can rapidly change their behavior in ways that allow them to exploit mating opportunities as they arise.

The underlying genetic architectures responsible for such variability appear to be similar to those described above for developmental strategies (Hazel *et al.* 1990, Shuster and Wade 2003). 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 one set of mating behavior, whereas individuals with phenotypes above this threshold express another behavioral set (Box 9.4). In variable situations, weak stimuli will induce few individuals to perform mate-acquiring behavior. Strong stimuli, however, will cause most individuals to attempt to mate (Box 9.4; see also Shuster and Wade 2003). This "behavioral threshold" hypothesis predicts differential responsiveness to the same environmental cues among individuals within populations due to genetic differences among males. This hypothesis also predicts differential responses to different cue intensities among individuals within populations, again, due to genetic differences among males.

Behavioral strategies are expected to arise when sexual selection favors specialized mating phenotypes, as in all of the cases previously considered. In these polymorphisms the relative mating success of each phenotype is predictable within male lifetimes and the timescale for change is short; so short, in fact, that environments may change dramatically within minutes or seconds. Behavioral plasticity is expected to exclude major genes and developmental plasticity as modes of phenotypic expression when reliable cues predicting mating success are available and mating opportunities change quickly.

Pre-copulatory mate guarding is widespread among crustaceans (Ridley 1983, Jormalainen 1998). The explanation for this tendency in many species is that molting initiates female receptivity and chemical cues present in female urine or present on females themselves prior to this molt allow males to locate, guard, and inseminate females as soon as they become receptive. Mate guarding reduces the ability of females to mate more than once; thus, a male who guards a female successfully fertilizes all of her ova. If a male unsuccessfully guards his mate, or if he leaves her in search of other females before her receptivity is complete, the male's fertilization success with that female will be eroded due to matings by other males. Sperm competition as an alternative mating strategy in crustaceans and in other taxa is discussed in more detail in Shuster and Wade (2003; see also Diesel 1989, Koga *et al.* 1993, Orensanz *et al.* 1995, Jormalainen 1998).

Males in a wide range of crustacean species that engage in mate guarding exhibit flexibility in guarding duration in response to local sex ratios, as well as in their responses to female body size, reproductive condition, parasitemia, and resistance to male guarding attempts (reviews: Shuster 1981, Ridley 1983, Jormalainen 1998, Plaistow *et al.* 2001). Variability in guarding duration in response to sex ratio shows a consistent pattern in several peracarids (Jormalainen 1998). In at least five species, males tend to shorten their average guarding durations when exposed to operational sex ratios that are female biased ($R_0 = N_{\text{males}}/N_{\text{females}} < 1$) and to lengthen their average guarding durations when sex ratios are male biased ($R_0 > 1$). Such behavioral flexibility is consistent with the hypothesis that mate guarding evolves as an adaptation to prevent multiple mating. Flexibility in mate-guarding behavior is evidently under strong sexual selection because males who guard ineffectively lose fertilizations to other males. Thus, the expression of this behavioral trait is consistent with the predictions of threshold inheritance of behavioral phenotypes (Shuster and Wade 2003).

Genetically variable characters likely to influence behavioral lability include individual sensitivities to crowding and to circulating hormone levels (Sagi *et al.* 1994, Briceno and Eberhard 1998, Borash *et al.* 2000, Peckol *et al.* 2001, Nephew and Romero 2003). Other characters likely to influence mating behavior may include heritable sensitivities to pheromone concentrations (Ferveur 1997, Giorgi and Rouquier 2002), to the density of mating competitors (Haig and Bergstrom 1995), or to the perception of mating behavior by other individuals (Shuster 1981). In the presence of a strong environmental cue, all but a few individuals are expected to express a modified behavioral phenotype. Weaker cue intensity, on the other hand, may induce few or no individuals toward behavioral change (e.g., Lively *et al.* 2000). The behavioral threshold hypothesis, like the developmental threshold hypothesis, predicts differential responsiveness to the same environmental cues among individuals within populations. 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.

Among populations, the tendency for males to exhibit one behavior or another is also likely to vary, leading to the likelihood that different proportions of each population will express the modified behavioral phenotype at any given time. Such interpopulational variation in behavioral expression is known to anyone studying behavior in multiple populations. The explanation for this variation is the same as for developmental polymorphisms. The underlying genetic basis for behavioral expression is similar to that of most threshold characters. Moreover, observed proportions of different morphotypes within a population depend multiplicatively on the frequency and relative fitness of each type. Thus, as with Mendelian and developmental polymorphisms, behavioral polymorphism is maintained within a population because the average fitnesses of each phenotype are equal.

9.7 CONCLUSIONS

The expression, inheritance, dynamics, and persistence of alternative mating strategies in natural populations of crustaceans, like other strategies discussed in an evolutionary context, can be investigated following well-established principles from population genetics and, given certain assumptions, evolutionary game theory. Alternative mating strategies clearly evolve under intense sexual selection. Contrary to current hypotheses regarding the importance of male genetic quality or sexual conflict (review: Shuster and Wade 2003), this condition minimizes the potential influence of viability selection on morph fitness, making investigation of life-history differences among males less important for understanding the persistence of polymorphism than investigation of the intensity of sexual selection within and among morphs (Gross 1996).

In species in which sexual selection is strong, not only are alternative mating strategies expected to evolve, but the evolutionary effects of sexual selection on alternative mating phenotypes are likely to be more easily documented than for phenotypes evolving in response to natural selection. Because population sizes may be large and generation times long, students of natural selection may fail to observe the effects of selection within their own lifetimes. In contrast, students of alternative mating strategies, because sexual selection acts so intensely on these traits, are usually able to observe the evolutionary effects of sexual selection in real time in many species.

How is this possible? Characters evolving under sexual selection, particularly polymorphic male phenotypes, are often easily recognizable. The signature of evolutionary change, as revealed by changes in morph frequency resulting from differential mating success, can be readily observed in some cases over a few days or weeks. Crustaceans are second only to the insects in their abundance and diversity among arthropods. They include economically and ecologically important species. In many major taxa, the majority of the scientific literature addresses newly described species (Brusca and Brusca 2004). If sexual selection is indeed one of the most powerful evolutionary forces known, then studies of adaptations evolving in this context are likely to reward investigators with abundant data and important new insights. The future is bright for continued studies in the evolution, persistence, and expression of mating strategies, particularly among the Crustacea.

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