Chapter 9: Alternative Reproductive Strategies

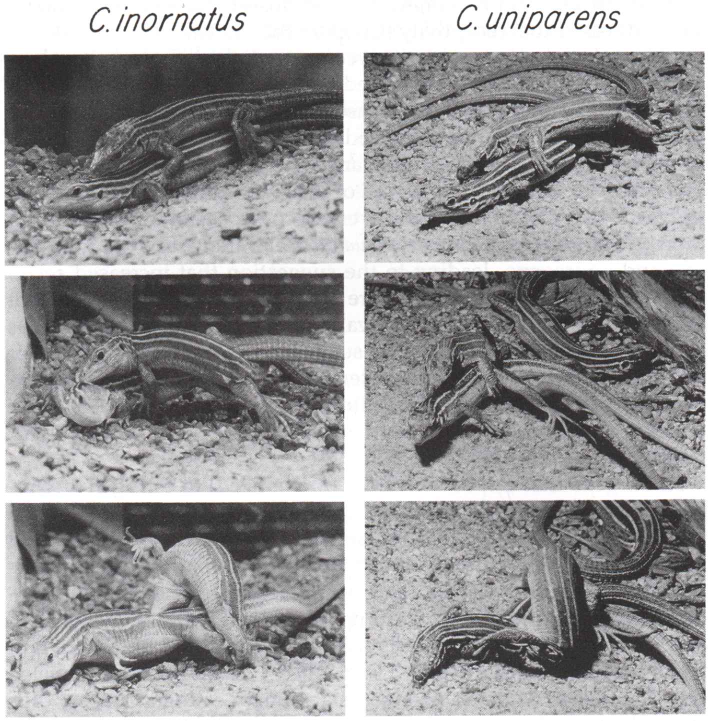
Why have sex?

The question of 'why have sex?' is amazingly one of the last unsolved problems of evolutionary biology (Maynard Smith 1982). Sex is so basic to life that it seems curious to question its existence. Most species of animals are **dioecious**, which literally translates into 'live in two houses' -- namely male and female. Many male and female behaviors revolve around the act of sex so it seems appropriate to get down to the root of the issue: why have sex? It is easier to think of the paradox of sex if we rephrase the question slightly and ask 'why have two sexes?' or let's get down to brass tacks and ask the question 'why bother producing males?'

Let's get outside of the realm of the esoteric theoretical issues of sex and think of a concrete example. *Cnemidorphorus* or whiptail lizards are common throughout western North America. Nearly all species of *Cnemidophorus* are sexual with males and females that produce male and female progeny. However, one "species" called *Cnemidophorus uniparens*, as its Linnean binomial implies, is uniparental; it has one-sexed parents. The species manages to propagate itself quite well without any males whatsoever (Crews et al. 1983).

Let's think of the advantages of an asexual existence, which highlights the disadvantage of males. Consider two females, one sexual the other asexual. Asexuals and sexuals produce an equal number of offspring. The sexual species must search out a mate, then copulate, then produce sons and daughters that go through the whole routine in the next generation. Asexuals produce only daughters. The sexual produces half the number of daughters because it must 'squander' half of its resources on the production of sons. Only daughters produce offspring -- males fertilize. The cost of sex is reflected in a decreased rate of population growth rate in a sexual population compared to the two-fold faster growth rate of an asexual population. In the next generation, sexual daughters are likewise disadvantaged in the reproduction game and contribute only half the number of females to the population compared to an asexual species. Get the picture? Asexual whiptail lizards could potential have two times the reproductive rate of its closely related sexual species. Such facts have led us to question the existence of sex. The planet earth should be completely populated by asexuals, given that they reproduce at double the exponential rate of sexuals.

Figure 9.1. *Cnemidophorus uniparens* in the act of 'pseudocopulation' in which one female grasps the other female by the nape of the neck in the fashion of a typical male-female sexual position found in closely related sexual *Cnemidophorus inornatus*. The individual that grasps from above also enters the copulation 'doughnut' posture (Crews et al. 1983).



To make matters worse for the male cause, asexual female whiptail lizards routinely pseudocopulate one another in laboratory colonies and in nature (Crews and Young 1991). During pseudocopulation one female engages the partner in the role of male (she's on top) while the other female plays the female (bottom). Of course, it is not possible for sperm to be transferred (no testicles are present), yet the female that is copulated produces a larger clutch than an asexual female that does not receive an 'isosexual' mounting. Males are not even required for the act of sex in this species and yet it seems that pseudocopulation stimulates and enhances reproductive output of asexual species.

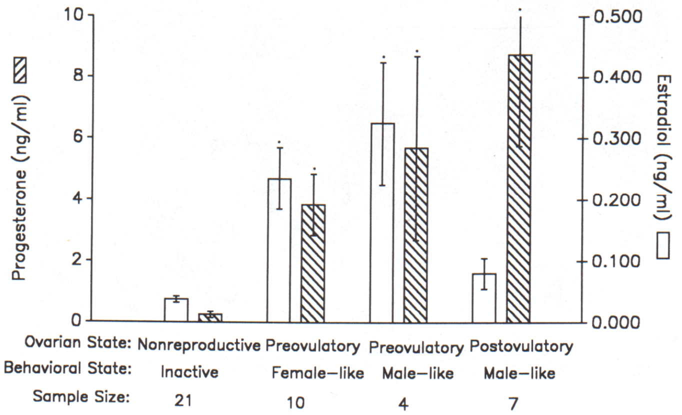


Figure 9.2 Reproductive cycle of *Cnemidophorus* lizards with regards to production of estrogen and progesterone and the cycle of egg production from (Moore et al. 1985).

The pseudocopulatory behaviors of asexual whiptail lizards have a proximate basis in the cycle of reproductive hormones. When any female vertebrate produces eggs, the eggs on the ovary produce the hormone estrogen, which is responsible for triggering the female behaviors that make her receptive to copulation (usually by males). When a female ovulates eggs, the copora lutea or scars from the developing eggs are left behind on the ovary. The copora lutea begin producing the hormone progesterone. In unisexual whiptail lizards, progesterone has been clearly linked to the expression of male-like behaviors such as mounting. The first asexual female has developing eggs and is 'receptive' to copulation because she has high levels of estrogen. The second male-like female that pseudocopulates the first female is exactly one-half cycle out of phase with her partner. The second female possesses corpora lutea and she has high levels of progesterone. The pseudocopulation by the second apparently stimulates the first female causing her to retain more eggs on the developing ovary, thereby increasing clutch size.

Certainly not all asexual species retain sexual behavior. If there is no benefit to sexual behavior among the female asexuals then sexual behavior should slowly decay away as mutations that control such behavior build up in the genes. This process has been verified in *Drosophila* that have been engineered to be asexual (Takenaka-Decanay and Carson 1991). In most asexuals, sexual behaviors no longer serve a function and mutations are not selected against. Slowly, over the course of several generations, sexual behavior will gradually fade away as deleterious mutations build. In contrast, asexual pseudocopulation in lizards increases clutch size so an asexual clone, which retains sexual behavior, might have higher fitness than one that lacks it because mutations have accumulated in the genes for sexual behavior.

Given the two-fold advantage of sex, and the lack of a need for males during the act anyway, why bother producing males lizards? The same reasoning that applies to sexual and asexual *Cnemidophorus* lizards applies to all animals. With impeccable logic, I have justified male utility out of existence. My wife, reading this over my shoulder, snickers in the background, goading me on to erase all advantage of males. If males are useless then why am I here? If males are useless then why do most animals produce by sexual reproduction?

If *Cnemidophorus uniparens* has such a tremendous advantage over the co-occurring sexual species, then why hasn't the asexual form replaced the sexual form? It is thought that *C. uniparens* has been derived relatively recently. This may be true for many asexual species. They are continually spawned from sexual species. In the long run most species remain sexual. Thus, the short-term two-fold advantage enjoyed by asexuals must be surmounted by some advantage to sexual reproduction.

We are Rescued from Asexuality by Parasites and Muller's Ratchet

The main advantage of sexual reproduction is that it creates tremendous variation within a species. The union of two distinctly different genomes can produce nearly unlimited variability (see Chapter 2). Recent work comparing sexual and asexual species suggest that asexual lineages have far higher rates of parasitism than closely related sexual lineages (Lively 1996). Parasites are continually evolving new resistance genes that allow them to break down the defenses of their hosts. The hosts are likewise evolving new defensive systems that allow them to attack their rapidly evolving parasites. Without new genetic variation and lots of it, an asexual organism really has no where to run and nowhere to hide from the attack of parasites. Asexuals are genetically uniform, and a parasite can eventually evolve a resistance gene that allows it specifically target one asexual lineage of clones. Given that the asexuals become quite common owing to the two-fold advantage, the parasite does quite well by zeroing in on the now quite common clone. The asexual gradually fades to low frequency. Sexual organisms win in the long run by having the ability to evolve parasite resistance. Meanwhile, yet another asexual arises to take the place of the first, having been spawned off as a new asexual mutation from its sexual parental species.

Another advantage to sexual reproduction is that it allows deleterious mutations to be purged from the genome. A substantial fraction of sexual offspring die every generation. Many of those deaths are directly related to genetic lesions or mutations that have recently and spontaneously shown up in a species. While sexuals lineages have deleterious mutations purged each generation, an asexual lineage is not so fortunate. If a mutation arises in a clone, all daughters will inherit the genetic lesion from that point on. In any population of asexuals, some possess many mutations while others possess few. Mutations cut into the reproductive rate of an asexual, particularly if progeny die because of mutations that disrupt early development. In any population of asexuals there will be the lucky "least-loaded clone", a clone that carries the fewest deleterious mutations. The mutational load of an asexual lineage cannot decrease below that of the least-loaded clones. The load of mutations will increase in all clones as they acquire new mutations.

Muller, a Nobel Prize winning geneticist, came up the following argument regarding clones (Muller 1932). The first premise of his argument is that all clones will eventually accumulate mutations. The second premise is that most mutations are deleterious and only a few, perhaps only one in a few thousand, are beneficial. **Muller's ratchet** clicks with each new mutation, and with each click of the ratchet the overall fitness of the asexual lineage declines ever so slightly. To be sure, this leads to an advantage in the least-loaded clone, but eventually that lineage will accumulate mutations or be wiped out by some unforeseen disaster. A full click of Muller's ratchet occurs when the least loaded clone is removed by chance death of some natural disaster, or when the least-loaded clone accumulates yet another mutation.

Figure 9.3. Given enough time, Muller's ratchet will eliminate the least loaded clone. When this happens, the ratchet clicks once, and the asexual species becomes slightly more disadvantaged by the total load of deleterious mutations that it harbors (in preparation).

Sex has evolved as a way to create diversity. Through the process of **recombination**, existing variation is scrambled between alleles that come from male and female parents. In addition, sex generates the raw material upon which natural selection acts to promote steady "improvements" in the species. Male's thus play an important and equal role with females in generating genetic variation, the raw material for evolutionary change. As we will see in chapter 10, a female's choice of mate may depend on more fine-scale perceptions of his genetic quality and perhaps ability to resist parasites.

Why sperm and why egg?

If two "sexes" are required for production of offspring, why does one sex produce macrogametes or large eggs, while the other produces microgametes or small sperm? Why don't the two sexes share equally by creating gametes of the same size that fuse to produce a big embryo? It seems as if males are cheating in that they produce a small wad of millions of tiny sperm relative to the enormous investment that females make in a few large eggs.

We can think of this problem in terms of yet another cost of sex, that of ensuring that each gamete successfully fuses with another gamete. The whole point of sex is mating with someone else to create variation, so you definitely do not want your gametes to fertilize with your own gametes. The challenge then is bringing together your own large gametes with those large gametes from a sexual partner. If gametes were equal in size, many gametes would not necessarily find a partner with which to fuse simply because of the limitations of search area (the gametes must search over a wide area), and because of the limitations of time (the gametes might exhaust or run out of reserves before fusion).

Figure 9.4. Drawing illustrating how a microgamete can invade a population of individuals that only produces large medium-sized eggs (in preparation).

Even in good mixture of gametes from the first parent and gametes from the second, it is tough to get each and every gamete to find a gamete from the other parental mating type. Some gametes go to waste unable to find a union. If all gametes are the same large size there would be considerable fitness loss for both parents. However, if one sex produced a few large macrogametes (what we call eggs), while the other sex produced a large number of small microgametes (what we call sperm), nearly all of the macrogametes would find a fusion partner (Parker 1982). Many of the microgametes would go to waste, but since they are so small and cheap to build it is inconsequential. While this waste of gametes is a 'cost of sex', the waste is minimized because one sex specializes in delivering a nucleus (valuable genetic variation) while the other sex specializes in delivering nutrition to the newly fused zygote.

In nearly all of the examples described below, it is invariably the case that more than one male participates in fertilizing a single female's brood, or clutch. In these cases, the males engage in sperm competition where depositing sperm is only the first step in successfully siring progeny. The sperm that a male delivers to a female can be thought of as an independent stage in the life cycle of the male. Whereas sperm do not feed, they are mobile, particularly in animals with external fertilization (e.g., salmon). Even if fertilization is internal (e.g., lizards, birds, mammals), the sperm must swim to fertilize the ova of the female. Males are strongly selected at two phases of the life cycle. The body of the male (soma) is selected for alternative behaviors that enhance the delivery of sperm to the female's eggs. Once there, the sperm (germ line) ejaculated by males is strongly selected for competing against the sperm delivered by a rival to the same female. It is a race of sorts, may the best sperm win. This is the essence of **sperm competition**. If two males fertilize the same female's eggs, there is sperm competition.

Intrasexual versus Intersexual Selection and Alternative Behaviors

We will explore the strategies of the two sexes over the course of the next three chapters. While much of the discussion in this chapter is related to male reproductive strategies, a few examples of female strategies are also discussed. The rationale for separating a discussion of the two kinds of sexual selection is that intrasexual selection (between individuals of the same sex) is distinctly different from intersexual selection (attracting a mate of the opposite sex). Intersexual selection involves male-male competition or female-female competition. We have treated some of the aggressive strategies used in male-male contests in Chapter 8. In contrast, intersexual selection or aspects of mate choice by definition occur between the sexes, and many of the decisions of mate choice rest with females (see chapter 10). Males evolve ornaments of attraction under intersexual selection and weapons of conflict under intrasexual selection. Here, I focus on specific behavioral strategies used by males to deliver sperm to the female. We begin with a discussion of the middle ground, individuals that can be male and female -- **hermaphrodites**. A consideration of hermaphrodite strategies will show that the selective pressures on a male's physiology, anatomy, and behavior are quite distinct from those experienced by females.

Males, females, and hermaphroditic strategies

The evolution of a distinction between male and female gametes does not necessarily mean that individuals have to be only male or only female. Many species of invertebrates and some species of fish are hermaphrodites. There are two kinds of hermaphrodites: simultaneous hermaphrodites and sequential hermaphrodites. **Simultaneous hermaphrodites** have both male and female gonads in the same body at the same time. **Sequential hermaphrodites** start out as one sex, and then transform into the other sex later in life. Interesting behavioral situations arise when there are not strict divisions between maleness and femaleness within individuals.

The Behavior of Flatworms that is Simultaneously Male and Female

Many lower invertebrates are not exactly endowed with great intellect. Indeed, few have considered the flatworm a candidate for a very discriminating nervous system, let alone exciting behaviors. Nevertheless, *Dugesia gonocephala* is a flatworm that exhibits discriminating taste for a mate as well as an interesting behavior for assessing mate quality. *Dugesia gonocephala* engages in a peculiar precopulatory behavior in which one partner glides over the other and then each partner flattens out to the limits of their ability (Vreys and Michiels 1997). It is thought that by performing this odd behavior, flatworms assess each other's size.

In flatworms, female fecundity is a function of body size. Flatworms are also simultaneous hermaphrodites and each individual couples with a partner to transfer sperm and receive sperm. If copulations are costly, then flatworms would be expected to favor a large partner, at least the male part of the flatworm should prefer a large female partner. On the other side of life, the flatworm being assessed should try to stretch and become as large as possible so that they can assess the other flatworm as well as show-off their size. Because the feeling is mutual, flatworms should mate with others who are the same size. Vreys and Michiels (1997) have found that *D. gonocephala* do mate assortatively by size in the wild. Moreover, in laboratory tests, pairs of flatworms that differed in size exhibited twice as many mating attempts for the first copulation than did partners of the same size. This suggests that the first partner that they encountered was unacceptable and they were waiting for a better choice of mate, one that is the right size.

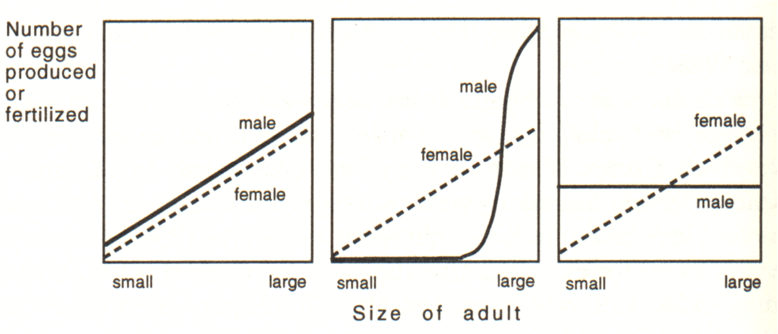
The Causes of Sequential Hermaprhoditism in Reef fish

The simultaneously hermaphroditic polychaete worm has a mixed strategy for gender during its life exhibiting a **protandrous** phase in which it is only male. The worm goes through a phase in which it only has male gonads because individuals benefit most from being male when small. However, the worm benefits from being a simultaneous hermaphrodite when large because it can attract a quality mate through egg-trading. Many reef fish have a **protogynous** phase where they are female early in life and then change into a male later in life. Deciding on whether to be a protandrous versus protogynous hermaphrodite depends on the size-dependent advantages of maleness or femaleness (Charnov 1982). If success at being a male requires large size then individuals should be protandrous. If success at being a female requires large size then individuals should protogynous (Fig 9.5).

Why should successful males be large? Males of many reef-fish species defend a territory that is used by females to deposit eggs. It makes sense for many reef fish to be males later in life rather than earlier because the advantage of large size is greater for males than for females. A large male is better able to defend a good territory where females deposit eggs. Several females will deposit their eggs on the male's territory. Whereas a large male can readily defend the territory, a small male would have very little chance of defending his eggs from **depredation,** which are the losses of eggs from the nest due to predators.

The pattern of sequential hermaphroditism in reef fish exemplifies the utility of adopting a proximate and ultimate perspective toward understanding developmental versus evolutionary causes of behavioral change during an animal's life. The proximate approach serves to uncover the mechanistic causes of behavior, while the ultimate approach serves to elucidate the selective causes of behaviors. In the case of hermaphroditic sex determination, the proximate cause is associated with the endocrine factors governing sex and sex-specific behaviors. Noteworthy in this regard is the gonadal steroids that govern aggression in males, the androgens, and how such aggression contributes to the maintenance of territoriality (see Chapter 8). The ultimate causes arise from the selective advantages of such aggression such as how body size influences a fish's RHP, or resource holding power. Thus, in hermaphroditic reef fish, the proximate and ultimate causes truly provide a complete picture of the evolution of behavior that would not be afforded by a more narrow study of just the hormonal system or by studying just behavior and fitness.

Figure 9.5. A graphical model for the size threshold at which a sequential hermaphrodite should sex change. When the fitness gain as a function of size is the same for males and females there is no selection favoring sex change (left). If size-dependent gains in fitness are greater for males then hermaphrodites should be protandrous and start life as a female. If size-dependent gains in fitness favor large females then hermaphrodites should be protogynous and start life as a male (right) (from Andersson 1994) after (Warner 1984).

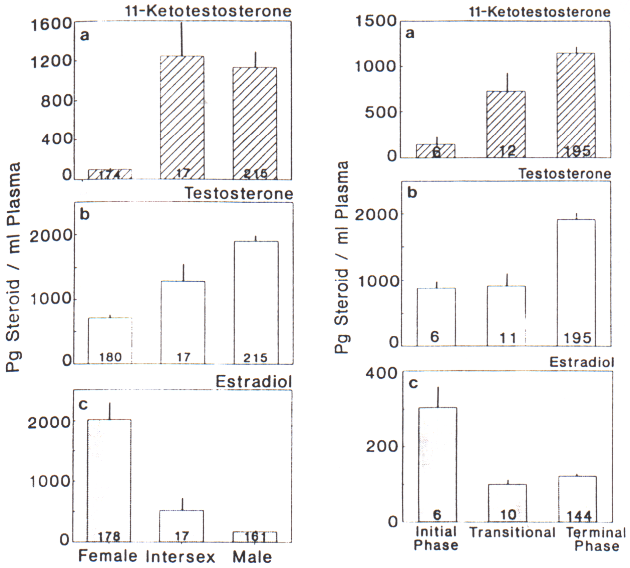


The stoplight parrotfish (*Sparisoma viride*) undergoes a protogynous sex change (Charnov 1982; Warner 1984). Individuals start out as females and transform into males. The twist in this story is that some females transform into terminal-phase territorial males near the end of life. Terminal phase (TP) males defend a territory and are quite aggressive. Other females transform into intermediate phase males first, then later in life they might transform into TP males. Intermediate phase (IP) males adopt an alternative pattern of behavior during the middle of life. IP males are functionally male in that they deliver sperm and do not have ovaries. However, IP males look like females and behave like a female. By behaving like females, IP males are able to 'sneak' copulations with females on a TP male's territory. While the TP male is preoccupied with fertilizing a female on his territory, the IP males dash in and squirt their sperm into the mix of the TP's sperm and female's eggs. IP males are also capable of transforming into a TP male later in life.

During early life, as females change into a male (either IP or TP), estradiol levels decrease and levels of testosterone increase. Some species of reef fish appear to use two kinds of testosterone, the standard form and 11-ketotestosterone (Cardwell and Liley 1991). Females that have just transformed into TP males have very high levels of 11-ketotestosterone, whereas females that have transformed into IP males maintain moderate levels of testosterone, and high levels of estradiol. Notice that IP males have the same steroid concentrations as the females (Fig. 9.7), however, during the transition from female to male, the 'intersex' individuals show a temporary increase in testosterone and 11-ketotestosterone, which is necessary to induce the change in morphology from female to male (really it is only needed to change the gonad from ovary to testis). However, IP males need a female-like profile of steroids to elicit female-like behaviors necessary for success as a sneaky IP male.

Injections of androgens into hermaphroditic fish cause females to transform into males (Stoll 1955; Reinboth 1972). High plasma levels of 11-ketotestosterone in fish are linked to aggressive territorial behavior in TP males. Aggressive behavior and territory defense allow the TP male to fearlessly drive away any and all intruders, irrespective of size. The specific form of androgen that is used in stoplight parrotfish for eliciting the aggressive behavior, 11-ketotestosterone, is commonly used in other species of fish that have male-based parental care of eggs.

Figure 9.7. Plasma concentrations of three steroids in stoplight parrotfish, *Sparsoma viride*, in a) females, transforming females (intersex), and terminal phase males (TP), and b) initial phase males (IP), transforming IP males, and terminal phase males (TP) (Cardwell and Liley 1991).

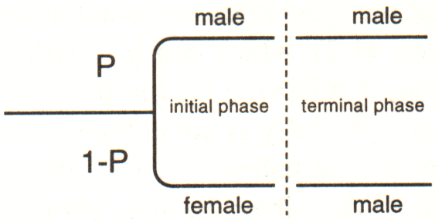


The **proximate control** of sex transformation in reef fish resides at the level of gonadotropins that are produced by the pituitary which then promote growth of the testes and production of androgens (those same hormones involved in male contests, see Chapter 8). Additional enzymes are responsible for converting androgens among the various kinds of steroids (e.g., testosterone versus 11-ketotestosterone). However, the **proximate environmental cue** that triggers the transformation from female to TP male in many protogynous reef fish appears to be the disappearance of a dominant TP male. When the dominant phase male disappears, a female will transform to take his place.

The **ultimate reason** for a sex transformation in reef fish is due to the fitness advantages from large size (Figure 9.5). Warner and Hoffman (1980) have studied the size threshold for sex change in the blue-headed wrasse, *Thalassoma bifasciatum*, another protandrous hermaphroditic reef fish. In the blue-headed wrasse, some fish skip the usual female phase and mature as an IP male, while other fish begin life as a female. Each of these two types can then mature into a TP male later in life (Fig. 9.8). Why not skip both phases and become a TP male straight away?

Theory predicts that females should change to the TP male phase when success as a female as a function of size equals male success as a function of size. A small juvenile is nowhere near the size required to be a territory-holding TP male, so they should start out life as a female or perhaps an IP male. The size threshold of switch occurs when TP males are large enough to spawn about 1.5 times per day, compared to a single spawning per day for females. TP males grow to be quite large they can spawn up to 40 times per day.

Figure 9.8. Life history pathways for blue-headed wrasse, *Thalasomma bifasciatum*. Juveniles can mature into either IP males or females with probability p and 1-p respectively. Later in life IP males and females can also transform into TP males. (from Andersson 1994, after Charnov 1982).



Why do some juveniles mature into IP males while other juveniles mature into females? We have to consider the relative success of IP males in terms of their resource, the TP males. Because IP males are sneakers, they parasitize copulations with females that are spawning on a territory defended by TP males. If too many females turn into sneaky IP males, there won't be enough females in the harems to be profitable as a sneaker male. Conversely, if too few females transform into sneaker males, then the harems of TP males are somewhat underexploited by the now rare sneakers. Thus, the frequency (p_{IP}) of IP males should be a function of the proportion of TP males (p_{TP}) and the average number of females spawning on a TP male's territory (F). A simple equation for the frequency of IP males is given by:

$$p_{IP} \approx (1 - p_{TP} \times F).$$

The empirical estimates of p_{IP} based on values of p_{TP} and F are in close agreement with the predictions of ESS theory. This is an example of **frequency dependent selection** in which the frequency of IP males depends on the frequency of TP males, and the frequency of females on a TP males territory. In general, alternative reproductive strategies in males and females are likely to be governed by frequency dependent selection. There is usually a unique frequency of each type, which allows each kind of sex or male strategy to obtain roughly an equal number of fertilizations. All types persist in the population because in the long run each strategy has a fitness that is equal to that of the alternative strategies.

The Fisherian 50:50 sex ratio

Why aren't all animals simultaneous or sequential hermaphrodites? Most species are dioecious and they have separate sexes. An adaptive explanation for the male and female dichotomy could always be couched in terms of the gains in fitness that arises from size (e.g., Fig. 9.5). However, there are many examples in the animal kingdom where large size is favored in one sex, and yet the animals are born male and female. Mountain gorillas, *Gorilla gorilla,* would benefit from being a protandrous hermaphrodite, being female first and then becoming male. In a gorilla troop only the dominant male gets copulations and the dominant is usually quite old, large, and powerful (Andersson 1994). The answer to this issue may be because of stringent 'developmental constraints'. Many mammals, birds, and reptiles which have internal fertilization have radically different reproductive systems for developing eggs or organs for exchanging sperm. Changes in morphology between males and females may be prohibited by such complexity. Fish have simple differentiation into male versus female gonads and the same opening that delivers eggs can be readily modified developmentally to deliver sperm. The dichotomy of the sexes may arise from such constraints of development and the architecture of primary sexual traits.

Given a separation of the sexes, we will consider one final problem in our discussion of 'why have sex?' Why do animals typically have a 50:50 sex ratio in their offspring? Ronald Fisher (1930) came up with a frequency dependent explanation that for the evolution of a 50:50 sex ratio in most animals. Consider a population with a male-biased sex ratio. In this population, many males will have trouble finding mates. A mutant female that produces a slightly female bias to her offspring will have an advantage because her offspring will all find males. In contrast, the more common females that produce a male-biased sex ratio will have some sons that get zero fitness in the next generation because there aren't enough females to mate.

The same problem arises for a population in which females produce a female-biased sex ratio. Once their progeny come to dominate the population, the population becomes more and more female-biased. The daughters of these females will face a shortage of males. A mutant that evolves to produce excess sons would have an advantage. The advantage then shifts to the mothers that produce a male-biased sex ratio. Evolution does not see-saw back and forth, but rather the evolutionary stable sex ratio is one where an equal number of male and female progeny are produced.

An important caveat to the simple Fisherian sex ratio of 50:50 males and females relates to the relative cost of parental investment in offspring. If additional effort is required to raise male young to maturity we might expect that females alter energy allotted to sons versus (Trivers and Willard 1981). We will explore many interesting adjustments of the Fisherian sex ratio in upcoming chapters, but the basic 50:50 rule is an intuitively appealing idea that is also grounded in ESS theory.

Alternative Male Reproductive Strategies

Males and females clearly have very different ways of achieving reproductive success and we see striking dimorphisms between the sexes. Males often evolve large size relative to females, because they tend to become engaged in conflicts over females. This generality is invalidated by some notable exceptions in which females compete for males (see Chapter 10). It is however, generally true that males commonly compete for females. Males have more time and energy to compete because of their lower level of investment in gametes. Females either spend more time accruing the resources necessary for provisioning gametes, and in some species females care for the eggs after they are fertilized.

Because males compete, some males inevitably come to control a greater share of females. This variation in reproductive success between males leads to strong sexual selection for behaviors and morphology directly related to success in competition against other males. It is useful to think of males and females as two kinds of morphs within one species that solve the job of successful reproduction. In the same vein, males have evolved spectacular variation in morphologies and behaviors as alternative ways of getting copulations. The male mating strategies that are described below represent relatively discrete male morphs. When two or more discrete types occur in the same population we refer to the collection of types as a **polymorphism** (for many morphologies).

What kinds of male types are you likely to encounter if you head out into the wild? Alternative males strategies are usually broken down into several categories. Males that have more than one female as a mate are **polygynous**. Polygynous males also tend to be aggressive. Other males are **monogamous**, just mating with one female. While the strategy of a monogamous male may seem staid and pedestrian compared to polygynous males, their strategy has some advantages. Monogamous males can easily mate-guard a single female and ensure that no other males gain access and copulate with her. There is a third type of male that does not obtain copulations by defending a harem or guarding a single female. Rather, they sneak in and attempt to gain furtive copulations. For this reason they are referred to as **sneaker** males. In addition, because they often skulk around the edges of the more dominant males in the population, they are also called **satellite males**. However, a distinction is often made between sneakers and satellites. Sneaker males do not benefit the territory holder, while satellite males may provide some benefit to the male. For example, a satellite male may resembles a female and the presence of a satellite on a dominant males territory, may attract other females to the territory. If so, the losses that a dominant male experiences to the satellite in sperm competition may be offset by the gains the satellite provides by attracting females.

Alternative Behaviors versus Alternative Morphologies in Wasps

Many of the species described in this chapter have relatively discrete male morphologies that also correspond to discrete behavioral phenotypes. However, it is quite likely that males of many species display alternative behaviors, without any major differences in morphology among the males of the population. We have our own perceptual biases about what we are likely to recognize as different. When male types are quite distinct, the behavioral strategies are readily apparent. However, it takes careful study of the behaviors in a species with monomorphic males to discover the alternative behaviors. Alternative behaviors in males of monomorphic species serve the same function as the behavioral and morphological specializations observed in males of another species. The behaviors are shaped by natural and sexual selection for maximizing the number of progeny a male is likely to sire.

For example, Field and Keller (1993) describe two behavioral strategies that male wasps use in courting females. If two rivals are on the same leaf courting a female and one male initiates a mating signal to the female by pulsing his wings, the second male has two options. He can choose to pulse his wings in a male-like fashion, but given that the other male already may have the female's attention, this strategy would be ineffective. Alternatively, the male could adopt a 'deceptive' female receptive position in response to the pulsing by the first male. The first male, deceived by the female-mimicking behavior of the second male, attempts to copulate with him. The female-mimicking male then darts towards the female and copulates with the female, while the first male is left behind to resume his typical male-like courtship.

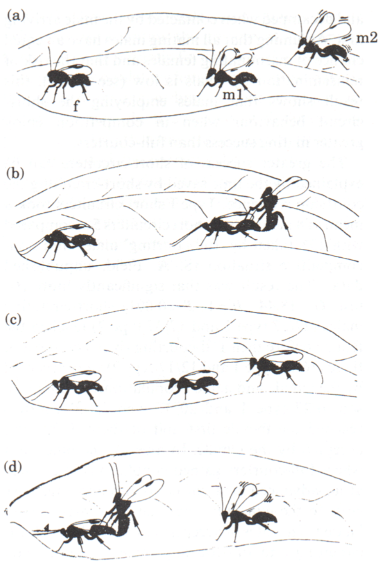
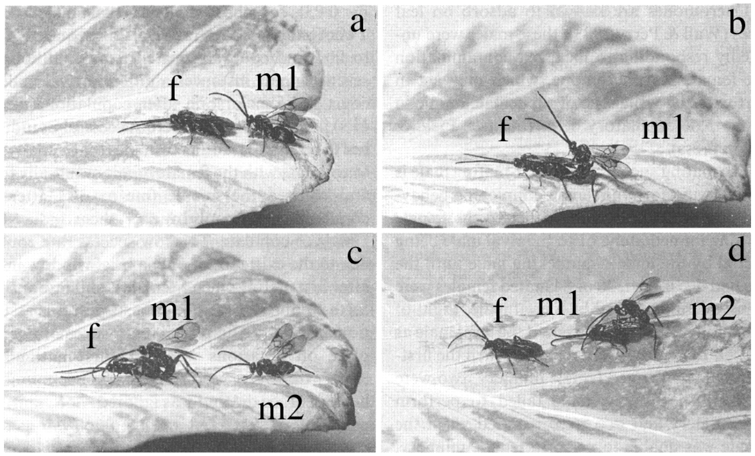


Figure 9.9. Males of the parasitic wasp *Cotesia rubecula* use alternative male behaviors to deceive rivals during courtship. a) Two males land on a leaf to court female (f). Male m2 pulses his wings to court the female. Male m1 assumes a female receptive posture. (b) Male m2 advances and begins to copulate male m1. (c) Male m1 moves on to copulate with the female. (d) Male m2 continues his courtship while m1 successfully transfers sperm to the female (from Field and Keller 1993).

Males of the parasitic wasp species *Cotesia rubecula* also adopt a post-copulatory alternative mating tactic that leaves a potential rival deceived. If a rival male lands while a male and female are copulating, the copulating male will finish copulating, disengage, and immediately assume a female receptive position. This lures the intruding male and the intruder begins copulating with the first male. By engaging in pseudocopulation with the intruder, the first male lowers the probability that the intruder will copulate with the female. The act of pseudocopulation circumvents a situation of sperm competition that would arise if both males copulated with the female.

Figure 9.10. Post-copulatory female-mimicking behavior in *Cotesis rubecula*. a) Male wasp m1 approaches female f and they begin copulating in panel b). c) A second male approaches the pair. d) The first male finishes copulation, and then immediately assumes a female receptive position and the intruder male m2 engages the male m1 in copulation (from Field and Keller 1993).

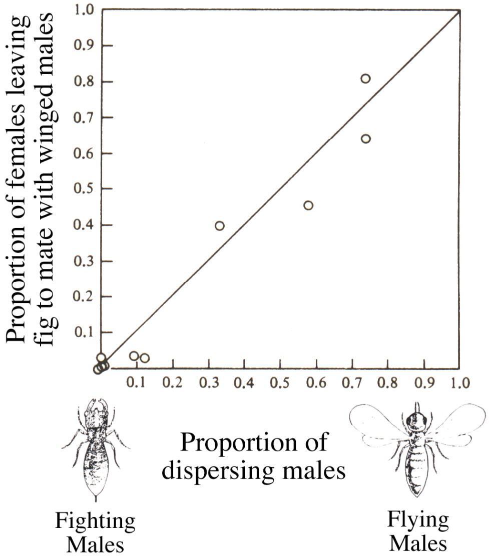


Dispersal morphs in fig wasp

Species of fig wasps have evolved two different morphs: a winged male that is capable of dispersing, and a wingless male that has powerful crushing jaws that are used to kill rival males (Hamilton 1981). The wingless males have evolved an extreme form of lethal fighting that is normally quite rare in the animal kingdom. At first glance, the evolution of **lethal fighting** would seem to violate the various theories of male contests discussed in Chapter 7. However, Enquist (1990) modeled such games and found that when the value of the current resource exceeds the value of future resource, lethal fighting will evolve. In the case of wingless males, the only resource they can get is the females that are emerging from the fig from which they just emerged. If they do not fertilize a female from that fig, they obtain no fitness. They cannot disperse to a new fig like winged males. Thus, they fight to the death.

Female fig wasp oviposit their eggs into figs. Upon emergence, females can either copulate with a male that is already at the fig, or disperse and copulate with a male somewhere else. If the female stays to mate at the fig, chances are good that this male will be one of the wingless ‘crusher’ males. If she opts for mating after emerging from the fig, chances are she will mate with a winged male. Variation in whether females stay and mate at the natal fig or disperse to distant figs determines the relative success of the two male morphs. The evolutionary equilibrium frequency of males is determined by the frequency of female dispersal. At the equilibrium, each morph has exactly the same fitness as the other male type, but the frequency of male morphs in a given species of fig wasps is set by the relative frequency of females that mate before versus after dispersing from her natal fig.

Figure 9.11. Species of fig wasps in two species of *Ficus* figs in Brazil. The relative proportion of two alternative male morphologies in each species is determined by the relative proportion of females that emerge from the fig and then mate with a local male (e.g., a fighting male), or females that emerge and mate after dispersing with a flying male. (redrawn from Hamilton 1981).



Genetic and Hormonal Control of Precocious Maturation in Males

The males of many fish species come in two alternative morphs that appear to be determined by a difference in the timing of maturation. For example, in the Pacific Northwest, *Oncorhynchus tshawytscha*, Chinook salmon males mature at two drastically different ages and thus end up with radically different body sizes and associated mating strategies (Fig 9.12a)(Gross 1985). Chinook salmon typically migrate from the streams of their birth within their first year of life, and head out to the ocean to feed and put on body weight. The reason salmon migrate to the ocean is that open salt water supports larger prey, which in turn is far more conducive for growing to large size than prey in the streams and lakes of their birth. A large male Chinook salmon can weigh in excess of 30 kg or more. Getting to this size requires at least 3 years at sea. Rather than spend this long period at sea some males forego the advantages of large size and mature at two years of age. The smaller males return to breed in the streams of their youth with an alternative strategy compared to the large adult male strategy.

‘Precociously’ maturing males are called **jacks** and they adopt a sneaker male strategy. The larger males that mature at >3 years of age adopt a fighting male strategy. As might be expected, success at fighting is positively related to body size. Only the largest fighting males are likely to get close to the female to deposit sperm. Proximity to the female is everything for a male salmon, because the fish fertilize the eggs of the female with externally released sperm into the water of a fast moving freshwater stream. While not fighters, jacks can get just as close to the female by being sneaky. Only the smallest jacks are likely to get close to the female to deposit sperm (Fig. 9.12b).

Gross argues that all males have the capability to become either male type. Depending on the body size of the males during early life, a "decisions" is made regarding development into one form or the other (Gross 1991). Males that grow rapidly mature earlier, and become the smaller jacks, and adopt the sneaky strategy. Males that grow slowly in the stream mature later, and adopt the fighting strategy. Such **condition-dependent strategies** are contrasted with **genetically-based control** over morphotype development.

Under a system of genetically based developmental control, males with different alleles at key genetic loci would express those genes during early development and turn into a specific morphotype. A recent study on hatchery reared salmon have found support for at least some genetic control over the development of small jacks versus the larger later-maturing fighting males. Rather than identify the actual genes that control precocious maturation, Health and colleagues (Heath et al. 1994) screened the two male types for a more generic difference in the kind of DNA located at a pair of loci that have a highly variable number of tandem repeats (VNTR). DNA probes for these two loci were used to score the alleles that each type possessed. They found that the allele frequency distributions were significantly different between jacks and fish that were likely to develop into large fighting males. This suggests some sort of genetic basis for the two morphs.

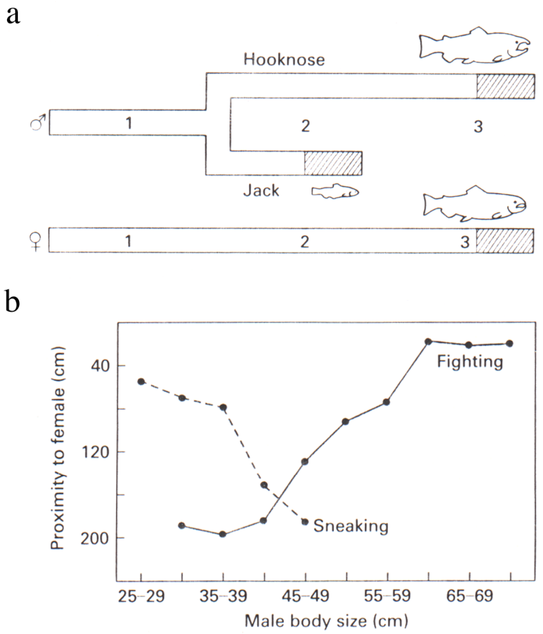


Figure 9.12. a) Alternative life history pathways in the Chinook salmon, *Oncorhynchus tshawytscha* are directly dependent on the age and size at maturity. Males that mature precociously at two years are also small. In contrast, males that remain at sea for at least an extra year are much larger. b) The ability of the two males to get close to the female and release sperm is related to body size. Successful sneakers are small. Successful fighters are large from (Gross 1985).

Separate work on the endocrine basis of the two alternative male types has shown that the hormone testosterone plays a role in promoting fast growth in fish destined to become the precociously maturing jacks.

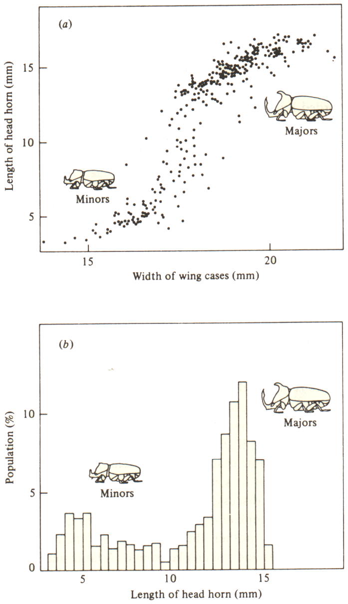
However, the jacks only grow fast over a short period of time as they reach a small mature body size. The fighting males, which delay maturity, take the steady-but-sure approach to a larger size. Growing a bit more slowly, but over a much longer period, fighting males reach a much larger body size. Males that are destined to become jacks had significantly elevated testosterone levels triggering their strategy of precocious maturation. Early in the growth phase of the jacks, they also had significantly higher plasma levels of thyroxine (T_3) a potent hormone produced by the thyroid gland of all vertebrates. Thyroxine is responsible for regulating metabolic rate, and processes important for energy turnover and growth (and as noted in Chapter 2, involved in the gene cascade governing amphibian metamorphosis). The authors did not find a difference in levels of growth hormone (GH), which was expected between fast-growing jacks and slower-growing fighting males. Health and colleagues (1997) did find that within the class of fish maturing as jacks, those with the fastest growth had the highest GH levels suggesting some kind of link between rapid growth and GH levels. While there was no difference between morphs in GH, their findings of higher plasma T_3 and higher testosterone, points towards the endocrine control of morphs.

Many genetic loci may be required in the development of alternative male morphs. This hypothesis is surprising given the large number of phenotypic characters that seem to be displayed by alternative males. Alternative types differ in morphology, physiology, and behavior. While one locus might trigger the transformation between alternative morphs, the locus or loci that control morph development will undoubtedly require coordination and integration between many genetic loci, which are spread across the genome of a single species. In light of the many hormone pathways (e.g., gondal, growth, thyroid) that are involved in precocious vs. delayed maturation, it is not surprising that Heath et al (1994) found evidence that the morphs of males have different alleles at loci. These loci may not even be the key loci that control maturation and development. Each male type might be expected to be under continuous and strong selection for behaviors and physiology that prove most successful in one strategy versus the other. Alleles that benefit one strategy may harm another strategy. Thus, the key morph locus, which governs morph determination, and modifier loci of male strategy, should be under very strong correlational selection (Sinervo and Clobert 2003).

Environment and Genes Interact to Determine Horns in Beetles

The links among male morphs, genes, and hormones in salmon point to an endogenous control over development. Despite these genetic underpinnings of the control of male development in salmon, studies on hermaphroditic reef fish highlight the role of proximate environmental cues that trigger developmental events that lead to sex change. For example, by removing a large dominant male, a female transforms to take its place in the dominance hierarchy. Many other animals show a similar interplay between the genes for development of alternative behavior and morphology and the environment experienced by individuals during early life. The feeding environment during early life can also limit the body size of adult insects. Environmental differences in body size of many insects are associated with the expression of elaborate male ornaments and their associated behavioral strategies.

Figure 9.13 a) Male horned beetles, *Podischnus agenor*, develop into two distinct morphs with short and long horns. An s-shaped or sigmoidal relationship is found between width of the wing cases, which measures body size, and the length of the head horn. Males on the bottom the ‘s-curve’ grow to small size, and also put less into the development of the horn. Males on the top of the ‘s-curve’ grow to large body size and invest heavily in horn development. b) Two distinct modes in horn size of species of horned beetles often result from differences in development (Maynard Smith 1982) after (Eberhard 1980).



Male horned beetles were first use by Darwin (1871) as an example of the power of sexual selection during male-male contests. These contests led to the development of elaborate ornaments. Emlen (1994) has found that horned beetles use their large horn in fights with other males at mating sites. As expected, males with small horns are poor fighters, and tend to disperse to mating sites that are empty of competitors.

Emlen (1994; 1996; 1997) has shown that the early food regimes in the dung pile, which is experienced by developing larval beetles, *Onthophagus acuminatus*, leads to a difference in body size that triggers the development of discrete differences in horn length as adults. Adult males with long horns fight with rivals over dung piles. We are used to thinking of dung piles as having a rich pungent smell, but we typically do not think of the piles as a rich resource. Dung beetle females and males use the dung to fashion a ball into which they deposit their eggs. The larvae grow and feed in the dung ball and metamorphose into adults. Emlen (1994) manipulated the amount of dung, and thus the amount of energy offspring had for growth. He then compared the size of the horns in male offspring as a function of the father's horn length (e.g., a genetic effect), or alternatively as a function of the manipulated environmental variable (e.g., dung heap size). Horn length of male progeny was mainly a function of the manipulated variable, dung heap size, which had a cascading effect on the offspring's body size. Horn size did not depend on their father's horn size. Thus, horn length and the associated alternative behaviors associated with horn length are due to environmental factors.

Evidence of a salient proximate environmental cue for alternative development of male horn length does not mean that there is no genetic control over the plasticity that produces horn size. Emlen performed an artificial selection experiment to demonstrate that the threshold body size for the switch between large and small horns (e.g., the inflection point of a sigmoidal curve, Fig. 9.13) could be modified. After seven generations of selection, Emlen was able to increase horn length over that observed in control lines. Conversely, lines selected for small horns had significantly smaller horns than control lines. However, each of the high and low selected lines still produced the other type of male. Selection did not lead to a purely large or purely small horn size. Emlen observed a striking shift in the threshold point for body size switch. Selection for small horns increased the size threshold so that even males of large size produced small horns. Selection for large horns decreased the size threshold so that males with small sized horns now produced large horns. Artificial selection for horn size and alternative male morphs resulted in a response in the developmental genes that alter body size as a function of environmental conditions.

The evolution of a 'body-size threshold' for the development of male horn length allows the population to adapt to regions in which the availability of dung varies and consequently average body size varies. In areas, with rich but widely separated dung heaps, the threshold body size for elaborate horns would be expected to evolve to large size because many males can acquire the threshold, while only a few will gain access to the heap by fighting. Even a moderately large male might be expected to do better by dispersing and not fighting. In contrast, in areas with small and common dung heaps, the threshold body size for elaborate horns might evolve to small body size. Many moderately sized males might be able to fight and hold onto a dung pile.

Advertisements: Leks, and Hotspots

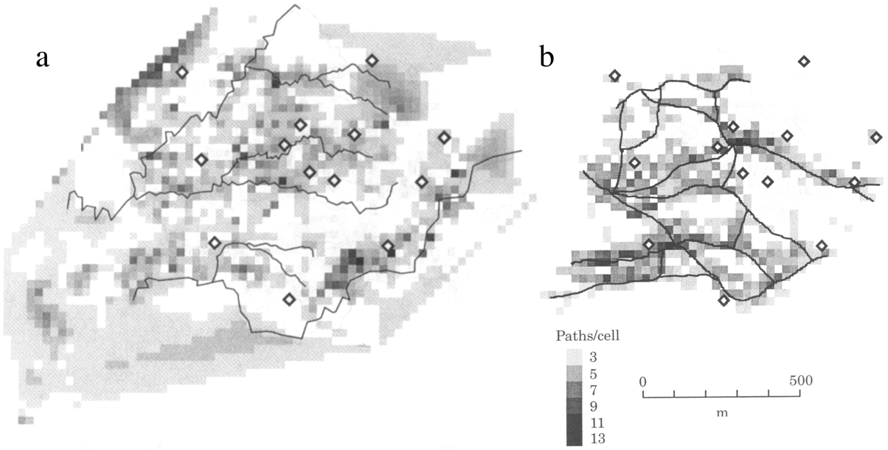
Not all male behavior is primarily aggressive or results in fighting or highly territorial behavior. There is a spectacular form of male-male competition that is widespread in the animal kingdom called lekking. At leks, males often congregate in the same place year after year, primarily to display in an attempt to attract females. Leks undoubtedly have attracted the attention of behaviorists because an enormous number of interesting behavioral observations, namely those that lead to copulation, can be made in a very small area. At a **lek** the primary activity is display and copulation. Strictly speaking, when males are lekking they are not defending a resource that might be used by females (Höglund and Alatalo 1995). This example, serves to highlight the role of females in driving male-male competition. Until now we have considered male strategies independent of female strategies, but females play a major role in shaping the patterns of male behaviors and morphology. This subject is of such importance that we devote much of Chapter 10 to the female choice and sexual selection.

There are a number of hypotheses for the origin of Leks, but the most famous of these is the '**hotspot hypothesis**'. The first premise of the hotspot hypothesis is that males cannot effectively defend a resource that females need. We will consider resource-based mating systems and territorial alternative to lekking in upcoming chapters. Given a male cannot monopolize a good site, he would be expected to congregate with other males in areas where they are likely to encounter females at a high frequency. Thus, the lek is a male's solution to finding many mates, all in one spot. Hotspots might be expected to occur in areas where the home ranges of several females overlap. Females might be found feeding at a slightly higher than average density in some locations, but not others. Alternatively, leks might be situated where females are likely to be moving and this is referred to as the '**female traffic hypothesis**'. Females may move between food patches, for example. Males may locate their leks in these areas of female traffic.

Wescott (1997) used radio telemetry techniques to track the habitat used by female ochre-bellied flycatchers, *Mionectes oleagineus*. These small birds are frugivores. They feed on a variety of small fruits. Females and males both forage extensively and the mean female home range size is 28.4 ha. Each female is likely to have 4.7 leks on her home range. A total of 13 leks were present on Wescott's study site and he used the pattern of female movement and habitat use to test several alternative hypotheses regarding the formation of leks in this species. The first problem faced by Wescott was how to determine if male leks formed close to where females spent most of their day feeding. The way to test this is with a randomization test. In a randomization test, you can imagine that we place the distribution of female habitat use on a dart board. If you were to throw darts at the board, and you were an exceptionally bad shot (as I am) the 13 darts would be randomly distributed in any one toss. You could then ask what is the density of females at each position of the darts. This process is actually carried out by a computer and you can program the computer to be a randomly shooting dart thrower. The alternative hypothesis is that male birds are actually excellent dart throwers; they place their leks in places they are likely to encounter females.

The process is repeated thousands of times to determine how likely chance alone would produce the observed match between male leks and the distribution of females (see Side Box 9.1). The leks did not tend to be associated with the overall pattern of habitat use by females, suggesting that leks were not located near habitats where females occur at high densities. The significance of this randomization was overwhelmingly non-significant at $P = 0.96$ (see Side Box 9.1). 96 times out of 100 randomization trials would find a randomly drawn location of leks actually closer to the distribution of females than the actual locations of the 13 leks plotted in Figure 9.14a).

Figure 9.14. a) The distribution of stationary females on the study site does not seem to coincide with the location of leks used by males (diamonds). b) However, male leks appear to be tightly clustered around the pathways of movement that are used by females (from Wescott, 1998).

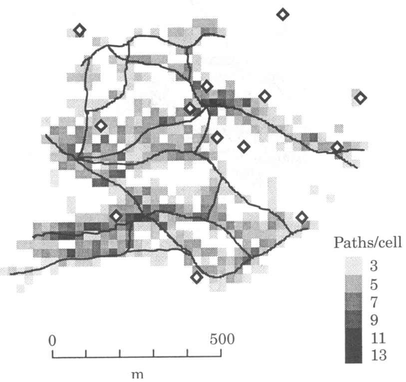


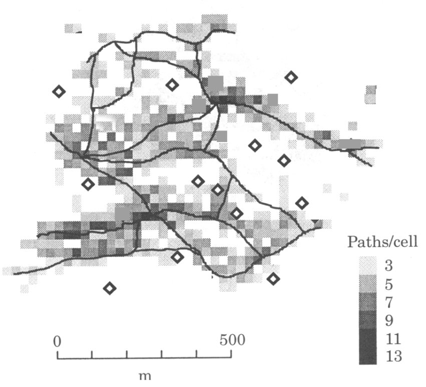
Next, Wescott restricted his attention to only those locations used by females as flyways. Two kinds of movements were made by females. In the first type of movement, females moved in a stop-start fashion often reversing and covering the same patch of ground, which is highly suggestive of foraging. In the second type of movement females flew in a straight-line direction with constant speed. Wescott only focused on the second directional mode of movement and plotted this type of movement on a map. The association between observed lek locations and patterns of female movement was astounding. Indeed, a randomly shooting computer (see Side Box 9.1) only bested the actual choices of lek locations by males less than 1 trial out of 100, a very slim margin indeed. Male leks of ochre-bellied flycatchers are non-randomly ($P < 0.01$) located near female flyways. The computer doesn't do a good job because it was programmed to assume that males spread themselves out randomly, which is not true. In contrast, male ochre-bellied flycatchers are non-random in their choice of lek sites, shooting their love dart into areas likely to intercept moving females.

Side Box 9.1. Randomization test for lek associations in space

The randomization test is often used in behavioral analysis of spatial distributions. It is often difficult to develop a standard statistical test to determine the significance of an animal's spatial distribution. However, with the advent of fast computation, spatial randomization tests have become the standard tools of the behavioral ecologist. The basic feature of any randomization is that the distribution of animals under the **null hypothesis** is made explicit. The null hypothesis in analyses of spatial distribution is that the two variables of interest are not associated with one another. Thus, the location of a male ochre-bellied flycatcher nest is no more likely to be near an area of high female traffic than an area of low traffic. The researcher gets the computer to crank up a piece of software called a random number generator that is an electronic pair of dice that spits out strings of random numbers. The random numbers get converted into x and y positions on a map of randomly distributed leks.

Comparison between observed distribution of 13 leks (left) and a single random 'drawing" of 13 leks generated by the computer and its random number generator (right). The computer software then makes a **test of association**, or how closely the observed leks lie to the distribution of female pathways, and how likely a randomly thrown set of leks would lie to paths. A simple average of the density of female pathways on thirteen leks could be used to test the strength of association between female density and lek location. The computer would then toss onto the landscape thirteen randomly thrown leks and compute a similar test of association. The computer calculates the association lots of times, say 5000. In the case of ochre-bellied male leks, only 43 out of 5000 randomly mapped leks had an average female density for the movement data that was higher than the observed association between leks, which gives a probability that the male leks were due to chance alone = 43/5000 = 0.0086. Thus, the observed distribution of leks is highly unlikely to have occurred by chance alone. It is quite likely that males position themselves in areas of high female movement.





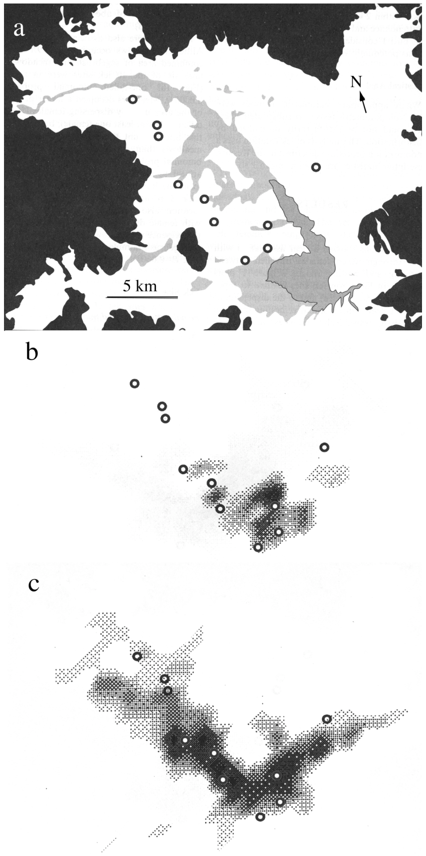


Figure 9.15. a) The location of sage grouse, *Centrocercus urophasianus*, leks with regard to the distribution of habitat: sagebrush (white), meadows (light grey), water (outlined grey), and forest (black). b) Radiotelemetry data of females during the pre-nesting phase indicates that females tend to congregate in a tight area around a few central leks. c) A much better association between the distribution of females and leks is found when the females begin a dispersal phase prior to nesting. It is during this phase that females move by the leks and mate with males. Spatial distribution of females and leks provides support for the female traffic hypothesis of lek location (redrawn from Gibson, 1996).

A similar radiotelemetry study by Gibson (1996) on another lekking species of bird, the sage grouse (*Centrocercus urophasianus*), has provided similar insights into the role of female movement in favoring the location of male leks. The sage grouse females congregate in a small area prior to dispersal. After dispersing from this area they build their nests. The association of female home ranges during the pre-nesting phase and the location of leks was very poor (Fig. 9.15.b). However, as the females disperse to their nesting sites, their pathways of movement (Fig. 9.15.c) were highly likely to pass right by a lek.

Early tests of the hotspot hypothesis have produced mixed results (see Wescott, 1997). However, few of these studies have explicitly distinguished between hotspots at high female densities and hotspots of high female traffic. Recent advances and the availability of telemetry equipment allow researchers to measure female distribution with high precision. Additional detailed observations on other lekking species such as the fallow deer, *Cervus dama*, indicate that dominant males take control of the entrances to leks where females are likely to emerge (Apollonio et al. 1990). Studies by both Wescott (1996) and Gibson (1996) carefully considered the pattern of female movements. Many of the previous tests of the hotspot hypothesis considered only the location of female territories, and not female movements. Certainly, the foraging patterns of ochre-bellied flycatchers are conducive to perceptive males settling at female flyways. Females might be exploiting different patches of fruiting trees in the forest that are found at great distance. In the case of sage grouse, males position themselves, much like the Casino billboards on highways in Nevada, aiming to attract the volumes of female traffic with their gaudy displays.

Alternative Male Types and Fitness

Alternative Male Behaviors in Ruff Leks

The distribution of leks highlights an important male strategy that governs fitness. Control of space is an important aspect of success even if the control of space is not for resources. The control of female location is a central theme of alternative male tactics. Some males by virtue of their large size, control a lot of space and thus a lot of females. However, success in turf battles has its downside. In many of the examples that follow, it is clear that alternative male strategies have evolved to exploit the territorial successes of a dominant male type.

The males on many leks are territorial, but they might only defend 'postage-stamp' territories. For example, male ruffs, *Philomacus pugnax*, are a lekking shorebird that defends an area that is 1.5 m^2. The space that a male controls is only enough to 'do a little dance, make a little love, get down tonight!' However, they defend this postage-stamp piece of turf with vigor. Males vary in their ability to defend even this small space. Male ruffs come in three plumage morphs, dark colored morphs that defend a territory, a light colored morph that does not defend a territory but is a satellite (Lank et al. 1995), and a third morph that is called a nape-necked male because they lack the ruff altogether (van Rhijn 1991). Ruffs use the puffy feathers on their neck, in the 'ruff-display', which is used to attract females, and intimidate rivals. Females lack the ruff so it is thought that nape-necked males might be female mimics. It is unclear how nape-necked males persist in the population, because the overall frequency of nape-necked males is low, it is difficult to estimate their fitness. New evidence indicates that nape-necked males are near-perfect female mimics (Jukema and Piersma 2006).

Figure 9.16 (left panel) Genetic variation in the two common morphs of ruffs, *Philomacus pugnax*, the darker colored independent male and lighter colored satellite male (photos by Lank). The variation in patterns are thought to function in individual recognition (Lank pers. comm). The recently characterized third morph, a perfect female mimic (right panel) a) solitary nape-necked male, b) a nape-necked male mimicking females in a ruff lek (mimic is 3rd from left), c) a nape necked male copulating a female (from Jukema and Piersma 2006).

However, the frequency of the other two mating types, residents and satellites, is quite high. It is interesting to consider which behaviors allow these different morphs to persist. Resident ruffs can easily drive off satellite males, yet often the residents will allow the satellites a certain measure of peace. The residents gain success by displaying for females and then once the female makes a choice, the female copulates with her ‘pick’ male. Satellites gain quick and furtive copulations when two independent ruffs are engaged in a territorial squabble. Birds do not have an intromittent organ, or penis. Fertilization is achieved with a brief ‘cloacal kiss’, where the female bends over and the male flies up against her rear end to bring their two cloacae together (Figure 9.16c).

Independent males may benefit from the satellite males because females prefer to visit larger leks compared to smaller leks (Höglund et al. 1993). Additional satellites increase the attractiveness of a lek to passing females. Thus, while satellites ‘parasitize’ copulation opportunities from the residents, the residents must allow satellites onto the lek to enhance female visitation. While large leks appear to benefit both satellite and resident ruffs, large leks do not appear to attract females in all species. Effects of lek size on the frequency of female visitation were not found in the ochre-bellied flycatcher (Wescott and Smith 1994), Hawaiian *Drosophila* (Croney 1994). Effects of lek size were found in the Uganda kob, a lekking antelope (Balmford 1990) and the black grouse (Alatalo et al. 1992). The effect of additional males at a lek is akin to the size effects in advertising. It’s just a larger billboard -- the more males, the more females are attracted to a lek. However, males and females are both attracted to leks. Too many males is too much of a good thing, because males are after all competing amongst each other for copulations. For example, the advantages of satellite males attending a lek follow a law of diminishing returns (Fig. 91.7). If a satellite male is in a lek that has more than 5 males it should leave and find a smaller lek. Satellites exhibit this behavior (Alatalo and Hoglund 1995).

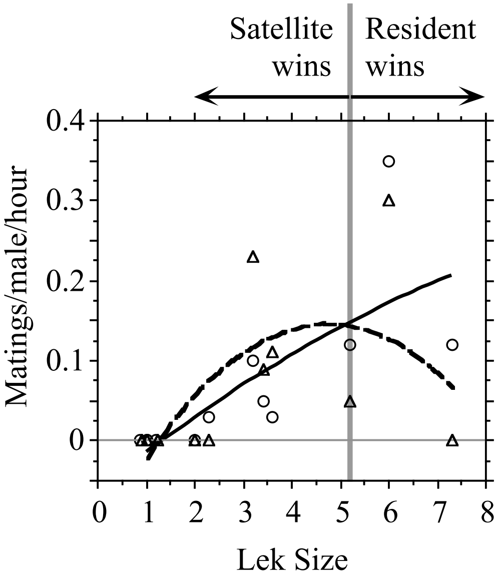


Figure 9.17. The effect of lek size (number of males) on the number of copulations in the ruff, *Philomacus pugnax*. The relationship between lek size and independent copulation success is positive (solid line). The relationship for satellites (dashed) is exhibits significant curvature relative to the independent line (from Höglund et al. 1993), however, data reanalyzed by Sinervo (2001).

Parental versus Satellite Behavior in Bluegill Sunfish

Bluegill sunfish, like salmon, possess alternative male types. Male Bluegill sunfish come in three different size morphs (Gross 1984). A large **territorial parental male** actively courts females in his territory, and then defends a nest into which the female deposits eggs. A medium sized **satellite male** mimics females and gains fertilization success by interrupting a territorial male while he courts a female. Often this interruption results in the **satellite** male squirting his sperm onto the eggs, and mixing it with the sperm of the territorial male. Finally, **sneaker males** are very small and they can dive in between a territorial male while he courts a female. When the female begins to lay the eggs, the sneaker quickly squirts an ejaculate of sperm in a ‘strafing run’.

An important component of the three behavioral strategies is that the male types mature at different ages. The territorial males typically mature at six to seven years, whereas the other two male types mature in two to three years. The frequency of morphs appears to be a function of the density and condition of males at maturity (1997). If there are abundant resources, males can mature into a parental male in their second year. If the resources in a pond are poor, the males take far longer to become a parental male. Many males will mature at a small size as either sneakers or satellites. These results highlight the environmentsl role in the development of the 3 alternative strategies. Expression of parental behavior in the bluegill sunfish is controlled by 11-ketotestosterone (Figure 9.18) -- the same hormones involved in sex transformation of reef fish (Figure 9.7). Like horned beetles and reef fish, morphs of bluegills appear to be determined by the environmental conditions of their youth, rather than by genes, yet fitness of the types in all systems is frequency dependent.

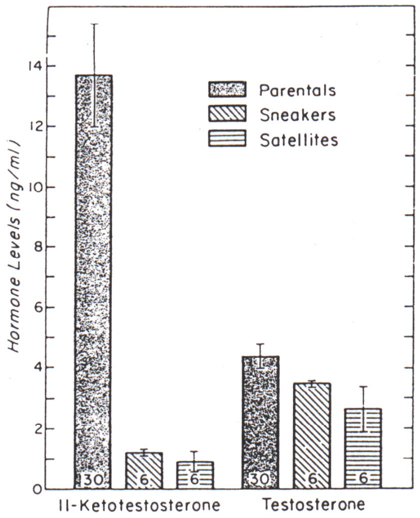


Figure 9.18. Aggressive 'parental' males of bluegill sunfish, *Lepomis macrochirus*, have higher plasma concentrations of 11-ketotestosterone than either the diminutive sneakers, or the female-mimicking satellite males (from (Kindler et al. 1989).

Mart Gross (1991) has calculated the probability that a male of a given morphotype will be successful in fertilizing a female based on the amount of time he spends in the vicinity of female. Estimates of successful paternity from behavioral observations have since been confirmed with genetic markers that discriminate between parental males or sneakers as the putative sires (Philipp and Gross 1994). Based on these calculations, males of all three mating types have approximately equal fitness. An ESS-style of analysis (c.f., Side Box 8.1) complements these calculations. The territorial male can exist in a pure form. However, the territorial male is always invadable by a rare mutant sneaker or satellite. Neither the sneakers nor the satellites can exist in a pure form. Eggs do not survive unless the eggs are cared for by a territorial male.

No morph satisfies the conditions of an ESS. Because no strategy can be an ESS, Mart Gross has referred to the system as an **Evolutionary Stable State** in that the mating system of three morphs in blue gill sunfish is a stable over evolutionary time. The territorial males must live with the burden of being parasitized by sneakers and satellites. The poor territorial male cannot reject eggs that have been fertilized by a sneaker or satellite from his nest. He has to take care of them all.

Marine Isopods and Genetically-based Strategies

Males of the marine isopod species *Paracercis sculpta* also come in three dramatically different size morphs (Shuster and Wade 1992). Large α males, which have elaborate horns coming out their telson, defend 'harems' of females in a spongocoel, which is a hollow chamber found in sponges. Medium-sized β males, which are the same size and morphology as a female, lurk among the females in the harems. The third type of male, γ, is much smaller than females. The α males evict any other males out of the sponge, if they detect them. The α male use the long posterior facing 'horns' to wrestle males. The β males, on the other hand, impersonate females, and wander around an α male's harem. The γ males have been described by Shuster as little sperm bombs (personal communication). The γ males lurk in crevices of the spongocel waiting for the opportunity to strafe a pair in copula.

Shuster has also shown that there is a fairly simple genetic basis to the three types of male morphs with the traits being controlled the *AMS* locus with 3 alternative alleles (α, β γ, see Chapter 2). The **genetic control** of the isopod mating system (Shuster and Sassaman 1996) is different from that seen in bluegill sunfish, which are thought to be environmentally determined. Shuster and Wade (1991) addressed the stability of the three kinds of males. In the long run, will one morph tend to dominate because it has higher fitness?

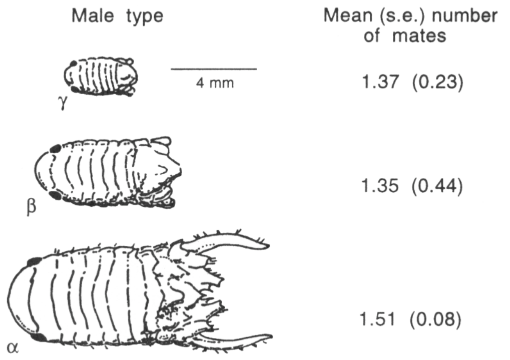


Figure 9.19. Three alternative male morphs in marine isopods have a genetic basis. Fitness and number of mates is not significantly different among the morphs, suggesting that all three may persist over long time scales. (from Anderson, 1982, drawing from Shuster (1989).

The null hypothesis in this case is that all three morphs have equal fitness. If the morphs have the same fitness then no morph has an advantage in the long term, and all will persist. **The alternative hypothesis** is that one morph has higher fitness, and the morph with high fitness would tend to increase in frequency until it became the only male type present in the population. Shuster and Wade found that they could not reject the null hypothesis. They did not detect any statistically significant differences in the mean number of progeny each male type was likely to produce. Sexual selection is defined as variation in mating success. Does equal fitness among morphs imply that there is no sexual selection on isopods? Shuster and Wade did not find variation in mating success among morphs. However, they did find substantial mating success among males within each mating type. Some α males mated more successfully than others. There may be strong selection among alphas to be a good α (e.g., strong fighter), or for β males to be superb female mimics, or for γ to have exceptionally large sperm storage organs. This is very likely to be the case; each morph should be under very strong correlational selection for other loci that carry **strategic alleles** that enhance one strategy over another strategy. However, another source of the variation in mating success is directly related to the variation in composition of social neighborhoods and frequency dependent selection. I have reanalyzed their data in Side Box 9.4. The isopod mating system is another example of a three morph mating system like the ruffs and blue gill sunfish. What maintains three types?

The rock-paper-scissors game

The rock-paper-scissors game has a simple dynamic in which rare rock ties common rock, loses to common paper, and beats common scissors (Table 9.2). Rare paper beats rock, ties with paper, and loses to scissors. Rare scissors loses to rock, beats paper, and loses to scissors. In his treatise on evolutionary game theory Maynard Smith (1982) speculated that organisms might exhibit RPS dynamics, but he could think of no examples. We (Sinervo and Lively) reported on first biological example in 1996. An RPS satisfies fitness relations as follows, where subscripts denote $W_{rare,common}$:

$$W_{R,S} > W_{R,R} > W_{R,P};$$

$$W_{P,R} > W_{P,P} > W_{P,S};$$

$$W_{S,P} > W_{S,S} > W_{S,R} \qquad (9.1)$$

An unusual game is being played out in the Coast range of California. Three male morphs of side-blotched lizards, *Uta stansburiana*, have evolved a variant on the ‘rock-paper-scissors’ game (Sinervo and Lively 1996). Throat color is genetic and heritably passed from father to son (Sinervo et al. 2001). Gene mapping studies (Sinervo et al. 2006a) indicate that the color is due to a simple Mendelian locus with three alternative alleles (*o*, *b*, *y*), which generate six genotypes (*oo*, *bo*, *yo*, *bb*, *by*, *yy*). Because of genetic dominance relations among the alleles the six genotypes reduce to three phenotypes: **O**= *oo*, *bo*, *yo*; B= *bb*; and Y= *by*, *yy* (i.e., *o* is dominant to *b* and *y*, and *y* is dominant to *b*)

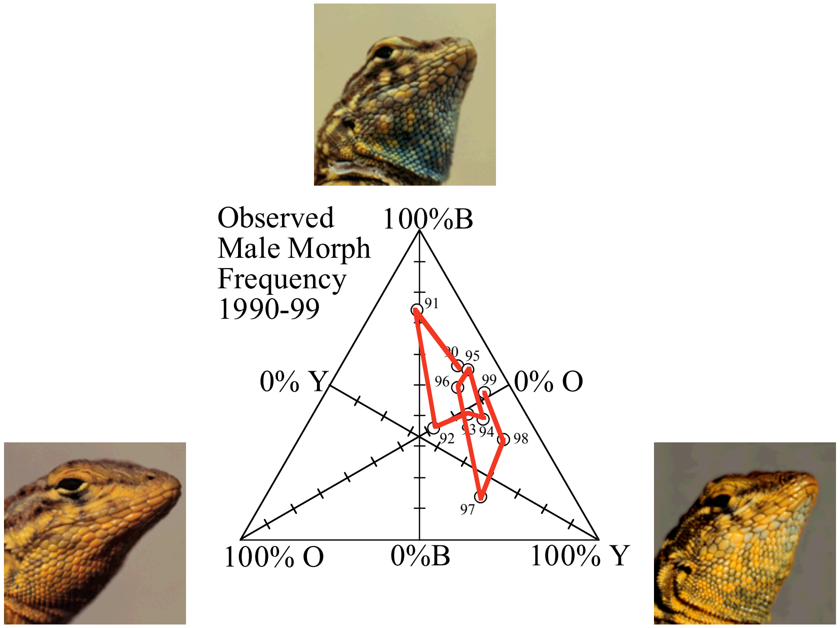
The metaphorical ‘rock’ is embodied by males with bright orange on their throats and sides (**O**). Orange-throated males are ultradominant lizards that attack other males when they make incursions onto the orange male’s territory. If an orange is challenged by another orange, there is likely to be a stalemate because orange-throated lizards are equally matched in aggression. The metaphorical ‘scissors’ is embodied by males with blue coloration on their throats (**B**). Blue-throated males have lower stamina than oranges. Orange males, by virtue of their great RHP, can invade a blue-throated male’s territory and copulate with the females on his turf. The orange-throated males sire more progeny than the blue-throated males. Rock beats scissors.

Over the course of a few years the composition of the population of side-blotched lizards changes as the successful orange-throated males gradually increase in frequency and slowly drive blue-throated males down in frequency (Fig. 9.20). The success of orange-throated males does not remain unchecked for long. The metaphorical ‘paper’ is embodied by yellow-throated males (**Y**) who lurk in the cracks and crevices of orange male territories. Whereas blue and orange males fight for territory, yellow-throated males never fight. When cornered the yellow males elicit a ‘female rejection display’, which female lizards use to indicate that they are not yet ready for copulation. Orange males

Table 9.2. Rock-paper-scissors payoffs		**Common Morph**		
		Rock	**Paper**	**Scissors**
Rare Morph	**Rock**	0	-1	1
	Paper	1	0	-1
	Scissors	-1	1	0

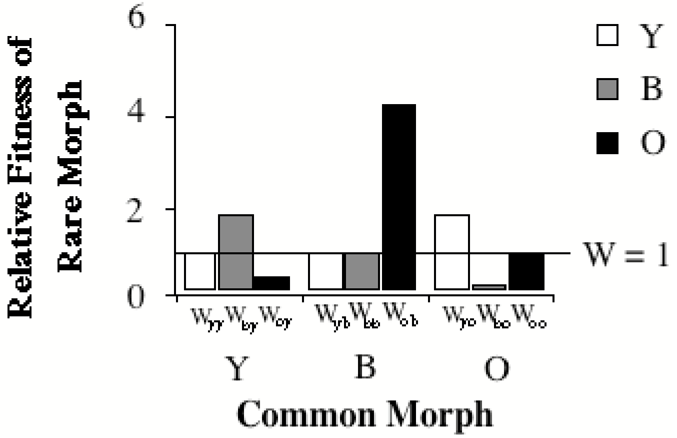
appear to fall for the charade of female-mimicking yellow-throated males and leave them alone. Orange males also leave their females unguarded. They roam their territory, and adjacent territories of blue males searching for females to court and copulate. Sneaker yellow-throated males inseminate females on orange male territories and sire more progeny than orange males (Fig. 9.20). Over the course of a couple of years, the frequency of orange-throated males begins to decline, and the frequency of yellow-throated males begins to rise. Paper beats Rock.

Figure 9.20. Changes in the frequencies of three color morphs of side-blotched lizards, *Uta stansburiana*, during the years 1990-1999. Rather than plot frequency on an x-y plot that only has 2-axes, a 3-axis triangle is useful for following frequencies of three types. On such a plot, the frequency of the blue male increases from the base of the triangle to the apex, the frequency of yellow increases from the left side to the lower right vertex, while the frequency of orange increases from the right side to the lower left vertex. The cycle in frequency from 1990-1995 changed from common blue (91) to common orange (92) to more common yellow (93-94) and back again to blue being more common (95). The cycle repeats from 1996-1999. Each male type wins at some point in the cycle, and each male loses (from Alonzo and Sinervo 2001).



When yellow-throated males become common in the population and oranges are rare, blue-throated males gain a mating advantage that is not possible when orange-throated males are common. Blue-throated males are diligent at mate-guarding their females, particularly from sneaky yellow-throated males. The blue males are aided in this regard by evolutionary cooperation (see Chapter 4) in which blue males seek out and find a genetically similar partner. When two blue males are surrounded by sneaky yellow and the blues do not have to contend with aggresssive orange, they can effectively mate-guard several females. Blue males get more progeny than yellow males. Over the course of a couple of years, yellow males decline in frequency and the blue males begin to increase in frequency. Scissors beats paper.

Figure 9.21. The payoff for each throat-color morph of side-blotched when rare and when common. The payoff, or fitness, of each male ‘strategy’ when rare is expressed in terms of number of females that they control when they are found in a ‘neighborhood of males’ that are comprised of the common morph. The values for the payoff matrix were computed from territory and home range use by color morphs of male side-blotched lizards. Data are derived from nature, but payoffs reflect ‘ideal neighborhoods’ in which a rare male must compete against a single type of competitor. The home range used by each rare male type would be entirely surrounded by the home ranges of males with the common throat color (from Sinervo and Lively 1996, see Sinervo 2000 for paternity payoffs)



Sinervo and Lively derived the pay-off of each of the strategies when rare, and in competition with the other more common strategies (Fig. 9.21). A baseline for how each morph performs is the line where relative fitness of the common type W=1 (each male type gets a single female, on average). Notice that when a rare male competes against males that have the same throat color, nobody wins and nobody loses; each male gets W = 1. When blue is rare in a neighbor of all yellow males the blue male gets nearly twice as many females as yellow. Conversely, when orange is rare in a neighborhood of yellow males they get only a fraction of the females. However, when orange is rare competing against blue males they get more than 4 times as many females. Finally, when a rare yellow-throated male competes against an orange-throated male, the orange gets twice as many females. A rare blue competing against orange only gets a fraction of the females. As in the rock-paper-scissors game where rock beats scissors, paper beats rock and scissors beat paper, the ultradominant orange-throated strategy beats the blue-throated males, the sneaker strategy of yellow males beats orange, and the mate-guarding strategy of blue-throated males beats yellow. This estimate of fitness from territory overlap has been confirmed with estimates from DNA paternity analysis of siring success (Zamudio and Sinervo 2000).

Genetic versus Environmental Control of Male Morphs

The complexity displayed in alternative mating systems with three morphs in both isopods and lizards are only an expansion of the themes played out in other more simple two-morph systems described above In all cases where strategies are clearly genetically based, males persist in the long run because each male mating type has equal fitness. However, the long-term ‘equal fitness’ of male types also is due to an advantage to the male type that is rare in frequency (e.g., the lizards and isopods).

When fitness of a male depends on frequency of other mating types, we refer to sexual selection as being **frequency dependent**. The nature of frequency dependent selection (FDS) determines who will win and who will loose in the long run, or if all male mating types will be preserved. A key condition that would prevent a unique ESS (e.g., only one male type wins) would be an **advantage to each strategy when rare**. This is another way of stating that a rare mutant can always invade the population. Consider a male morph that is declining in frequency because one other type has an advantage. If the morph has an advantage when rare in frequency, then it will be protected from being eliminated. However, as this ‘rescued morph’ becomes common, another types gains an edge in fitness. In the RPS game no male type is an ESS because as each morph becomes common, each is invaded by one of the other rare types. The three morph mating system of lizards is an example of an evolutionarily stable state like the three morph mating system of bluegill sunfish (and isopods, ruffs, salmon, elephant seals, etc.).

The very existence of alternative male strategies in a species is strong evidence indicating that no male type has a long-term advantage. This chapter has focused on some of the more bizarre male morphologies and behaviors. It is important to realize that males in a species may adopt the different strategies even if they do not differ in size or morphology. A **mixed ESS** is likely in which a male adopts a different or mixed strategy depending on environmental circumstance. In a mixed ESS, a single male can adopt different strategies (e.g., beetles). These situations arise when environmental circumstances cause the development of alternative morphs (e.g., beetles) or short-term changes in alternative behaviors (e.g., wasps). It is possible that a mixed ESS is comprised types that are genetically determined (e.g., isopods, ruffs, and lizards) or that are environmentally determined (e.g., blue gill sunfish, reef fish: female, IP, TP). Rules governing transitions among types are governed by FDS.

When there is a strong environmental component to the alternative male strategies, male types need not have equal fitness in the long run. In such cases, some males may be making the **‘best-of-a-bad’ job**, trying to limit their losses by adopting an alternative tactic. For example, males with small horns never appear to do better than males with large horns, but by employing the strategy of dispersal rather than fighting, the males with small horns might be able to limit how poorly they do. If they were to try to fight, they might get nothing. If they were to use the standard strategy used by all males, they would not be successful in copulating with females. By changing their behavior and perhaps their morphology, they have the potential to be somewhat successful in mating and limit their losses. However, best-of-a-bad cannot be a genetically fixed strategy because this would be purged by selection. At some point in the future, progeny derived from a best-of-a-bad male must get high fitness so that the genes, which confer **best-of-a-bad plasticity**, are preserved.

Side Box 9.2. Null Hypotheses and Equal Male Fitness

The philosopher Karl Popper (1962) provided scientists with a guiding rule for scientific inquiry. It is impossible to prove that a hypothesis is true, however, we can become very certain that a hypothesis is false. Falsification is the only truth we can know. This is because any pattern, any process, might be explained by many different processes, rather than the hypothesis of interest. The world can often be stranger than our scientific imaginations. Popper's ideas can be couched as a statistical test. One can never be sure that alternative hypotheses are true. Nor can one really be sure that the null hypothesis true. The only thing we can be sure of is that if enough data is collected that refutes a hypothesis, we can probably safely reject that hypothesis.

With Popper's ideas in mind, arguing that male types have equal fitness is a little unusual with regards to how scientists view acceptance of the **null** versus **alternative hypotheses** (Austad 1984). The null hypothesis for a system of alternative male strategies is that the male types have equal fitness and thus the morphs will persist in a population. The alternative hypothesis is that the morphs do not have equal fitness and one morph will ultimately prevail. We know that there are different morphs so the goal is to collect enough data to accept the null hypothesis. This is contrary to the way we traditionally construct null versus alternative hypotheses. We usually want to collect enough data to *reject the null hypothesis* and accept alternative hypothesis.

The null hypothesis is often rejected in favor of the alternative hypothesis because we often construct the null hypothesis as a 'statistical straw man' of sorts. For example, the randomization test for a lack of association between female movements and lek positioning is an example of a null hypothesis. The alternative hypothesis is that males are somewhat strategic in the placement of leks so that they coincide with the pathways of female movement. We reject the null hypothesis of random placement, with a measurable amount of confidence, which in the case of leks is measured in terms of the frequency with which a process would occur by chance alone ($P < 0.0086$).

However, in the case of the equal fitness tests, we are trying to establish that the null hypothesis is likely to be true. The alternative hypothesis, a more complicated view of the world, is that the male types have a different mean fitness. We had better collect a large volume of data to convince ourselves that the null hypothesis is true. Shuster and Wade (1992), in their treatment of isopods collected a convincing amount of data ($N>300$) to show that the males had equal male fitness, thus, the case for equal male fitness gets stronger and stronger, but according to the Popperian view of science, we can never know for sure. If Shuster and Wade had collected far fewer data on individual males, they would have had little **statistical power** in asserting that the male types had equal male fitness. The **pattern** of equal male fitness is superficially quite appealing but it supplies no process of how male types persist.

Process-based arguments avoid such statistical ambiguity by identifying mechanisms that lead to the morphs being preserved when they become rare. In the case of male strategies, it is the social environment that leads to a change in fitness. The advantage of a rare morph is a powerful mechanism for preserving variation. The rock-paper-scissors game preserves variation. Likewise, in hermaphrodite reef-fish, the precise balance between the number of females in a harem, the number of IP males, and the frequency of TP males is maintained because of strong frequency dependent selection. Females should not transform into IP males at too great a frequency, because success of IP males require that there be lots of females in a TP male's harem.

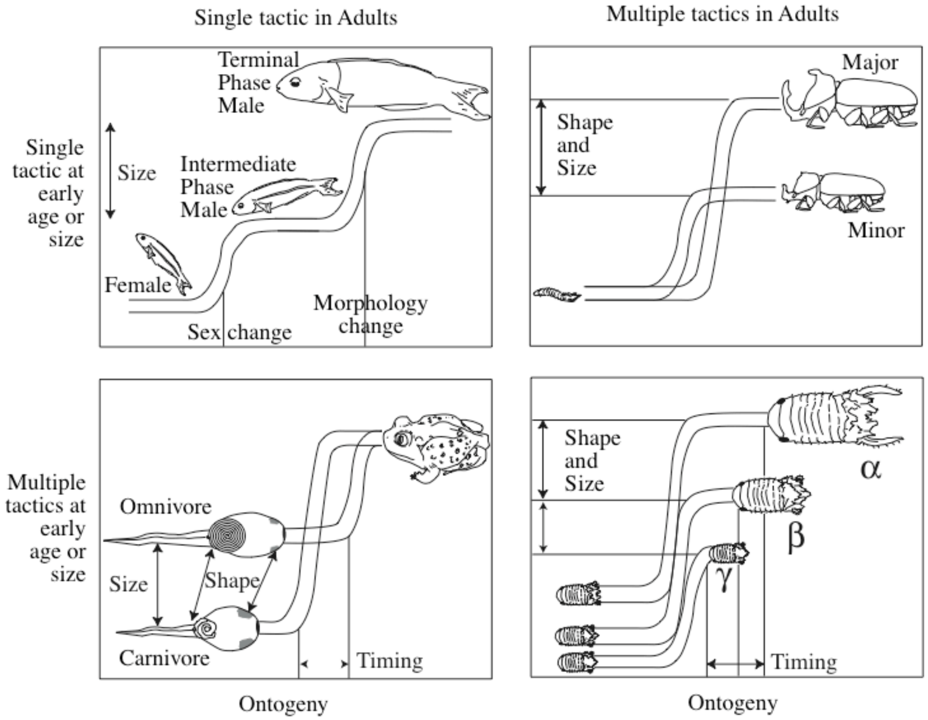
The relative fitness among morphs might be equal, but this does not describe the selective mechanisms that preserve the forms. Couching the fitness of the morphs in terms of the environmental conditions that lead to the frequency dependence of the male strategies encapsulates mechanisms in a succinct form. In many cases, the dominant male type, which is aggressive or territorial, is always invadable by males that parasitize reproductive opportunities (e.g. blue-gill sunfish).

This view also permits us to construct experiments to falsify a hypothesis of negative frequency dependent selection (FDS) as the force that maintains male morphs. For example Bleay et al. (2007) recently manipulated the frequency of *Uta* morphs in the RPS game and proved that the RPS relations are driven by morph frequency, relative to the null hypothesis of no FDS (how boring would like be with FDS). Similar experiments on FDS of guppy morphs have also been conducted.

Side Box 9.3: Summary of the development of morphs

Caro and Bateson (1986) have provided a classification system for representing the diversity of alternative behavioral tactics that might be found in a population. Their system only shows two possible tactics (such as fig wasps, Fig. 9.11, Hamilton, 1981), though the scheme can be readily expanded to encompass three or more discrete types in a population (see below). This simple classification presents the possible alternative tactics as discrete alternatives, while many animals show a continuous range of variation in behavior (e.g., parasitic male wasps).

Figure 9.22. A classification scheme to describe the diversity of alternative male tactics that vary as a function of age. The y-axis reflects a change in any trait (gender, behavior, morphology) while the x-axis reflects age. The 'ontogenetic trajectory' or developmental change and individual can undergo is depicted by the possible dashed lines (from Caro and Bateson 1996).



Caro and Bateson's first category depicts a simple age-related change that occurs in an individual during its lifetime. All individuals go through the same developmental stages. For example, protandrous hermaphroditic reef fish are females during early life, IP males in mid-life, and TP males during older phases of life when they grow to a sufficiently large size that they can defend a nesting territory. In category I, all individuals have the capacity to be any morph. The environment governs the change in behavior and morphology.

In category 2, a single tactic is possible in juveniles. Two are possible in the adult. Horned beetles all pass through the same larval stage as they burrow through dung piles and gorge on food, but the nutritional state at metamorphosis dictates whether a male will develop into an adult major or adult minor. In principle, all individual males should be capable of one form or the other alternative form and environmental conditions of dung pile size trigger their alternative developmental pathways.

In category 3, two tactics are possible in juveniles while only a single tactic is possible in adults. Larval spade-foot toads can begin life by developing into either an omnivore or a carnivore (see Chapter 2, 7). The alternative behaviors and morphology of the tadpoles types are triggered by an environmental circumstance, the presence or absence of shrimp in their natal pond. Upon metamorphosing to the adult form, the differences between individuals that life out a carnivore or omnivore lifestyle as juveniles disappear (or differences disappear by maturity).

In category 4, two tactics are present in the juvenile and two tactics are present in the adult. The differences in trajectories might depend on genetic differences between morphs such as those found in isopods. Those salmon destined to become jacks diverge very early in life, and develop a different pattern of growth in the juvenile phase.

Caro and Bateson's scheme (1986) places emphasis on the ontogeny of tactics and on control mechanisms underlying development of alternative strategies. However, any of the four categories could easily be governed by genes (e.g., lizards and isopod males) or environment (e.g., spade foot toads or bluegill sunfish), or the interaction between genes and environment (e.g., horned beetles). Generally the mechanisms arise from genes of major effect, such as endocrine genes (Chapter 16).

Why is the RPS common?

Many male mating systems appear to be caught in this kind of evolutionary dilemma. The rock-paper-scissors game of lizards appear to have male types chasing each other in a cyclical frequency game, causing us to wonder how and why such systems evolve. The lizard system is an example of an evolutionarily stable state. Beginning with a population of males that are monomorphic or composed entirely of a single strategy, mutations will invariably arise that lead to the alternative types. To explain the diversity of male morphs, we need only look at how large differences (e.g., between males and females or between territorial and sneaker males) can be controlled by simple changes in steroids hormones. The simple developmental control of alternative male strategies (e.g., hormones) implies that a simple mutation can lead to a drastically different kind of behavior owing to widespread effects that variation in hormones have on the development and expression of adult male and female behaviors (e.g., reef fish, alternative morphs of lizards, see Chapter 2, and 8). Nature is splendid in its diversity, but nature abhors complexity. If there is an easy way to do something cool, it will evolve. Three morphs have evolved all over the animal kingdom.

The trimorphism referred to as the rock-paper-scissors game (RPS) (Maynard Smith 1982) is named for intransitive fitness interactions in which rock beats scissors, paper beats rock, and scissors beats paper (Table 9.2). In each pair wise interaction, players are involved in **negative FDS** of their own type that enhances fitness of another type. However, RPS cycles in biological systems may necessarily involve **positive FDS** within forms (Sinervo et al. 2006b). In the lizard RPS, blue males (**B** = *bb*) are self-attractive. Blue males can also eliminate yellow. Thus, when blue begins to build, it can fuel very strong positive FDS. The only thing that stops it in its tracks is orange, which specializes in invading territorial partnerships of blue. When mixtures of negative and positive FDS interact, a system can become destabilized and oscillate. Forces of positive FDS cause RPS cycles to spiral outward from the attractor (to 100% B). Forces of negative FDS cause the RPS to spiral inwards from the absorbing boundaries and towards the attractor.

The mating system of male side-blotched lizards is an RPS because:

$$W_{Y,O} > \mathbf{W_{O,O}} > W_{B,O};$$

$$W_{O,B} > \mathbf{W_{B,B}} > W_{Y,B};$$

$$W_{B,Y} > \mathbf{W_{Y,Y}} > W_{O,Y} \qquad (9.2)$$

This mating system only deviates from a true RPS in that $W_{O,Y} > W_{Y,\,Y}$. However, payoffs based on overlap show $W_{Y,\,Y} > W_{O,Y}$, Sinervo 2001).

In other mating systems, pure apostatic selection of 3 forms is common. **Apostatic selection** is a form of selection in which rare has an advantage and all common types have a disadvantage. Trimorphisms of female damselflies of Europe and North America are maintained by pure apostasis among 3 female morphs based on equations for fitness of the damselfly *Ischnura elegans* (Svensson et al. 2005). Sinervo and Calsbeek (2006) re-expressed these equations as a payoff matrix (Figure 9.23). **Apostatic FDS** is thought to arise from search image formation in males for common female morphs (Fincke 2004). Given intense sexual conflict arising from male harassment, rare cryptic female morphs gain higher fecundity, thus involving sexual conflict, which is discussed in Chapter 11 and 14. We define evolutionarily stable state (ESState) conditions for an apostatic RPS, based on the damselfly mating system:

$$W_{IO,A} > W_{I,A} > \mathbf{W_{A,A}},$$

$$W_{A,I} > W_{IO,I} > \mathbf{W_{I,I}},$$

$$W_{I,IO} > W_{A,IO} > \mathbf{W_{IO,IO}}. \qquad (9.3)$$

The marine isopod *Paracerceis sculpta* (Shuster & Wade 1991a,b). also exhibits and RPS. Apostatic male mating strategies (β female mimic or cryptic γ) can invade the despotic α male strategies that guard female harems. Reanalysis of Shuster & Wade (1991a) data in the form of a payoff matrix (Fig. 9.23) shows it is a mix of the true and apostatic RPS:

$$W_{\beta,\alpha} > W_{\gamma,\,\alpha} > \mathbf{W_{\alpha,\,\alpha}}\ ;$$

$$W_{\gamma,\,\beta} > \mathbf{W_{\beta,\,\beta}} > W_{\alpha\,,\beta}\ ;$$

$$W_{\alpha\,,\gamma} > W_{\beta,\gamma} > \mathbf{W_{\gamma,\,\gamma}}\ . \qquad (9.4).$$

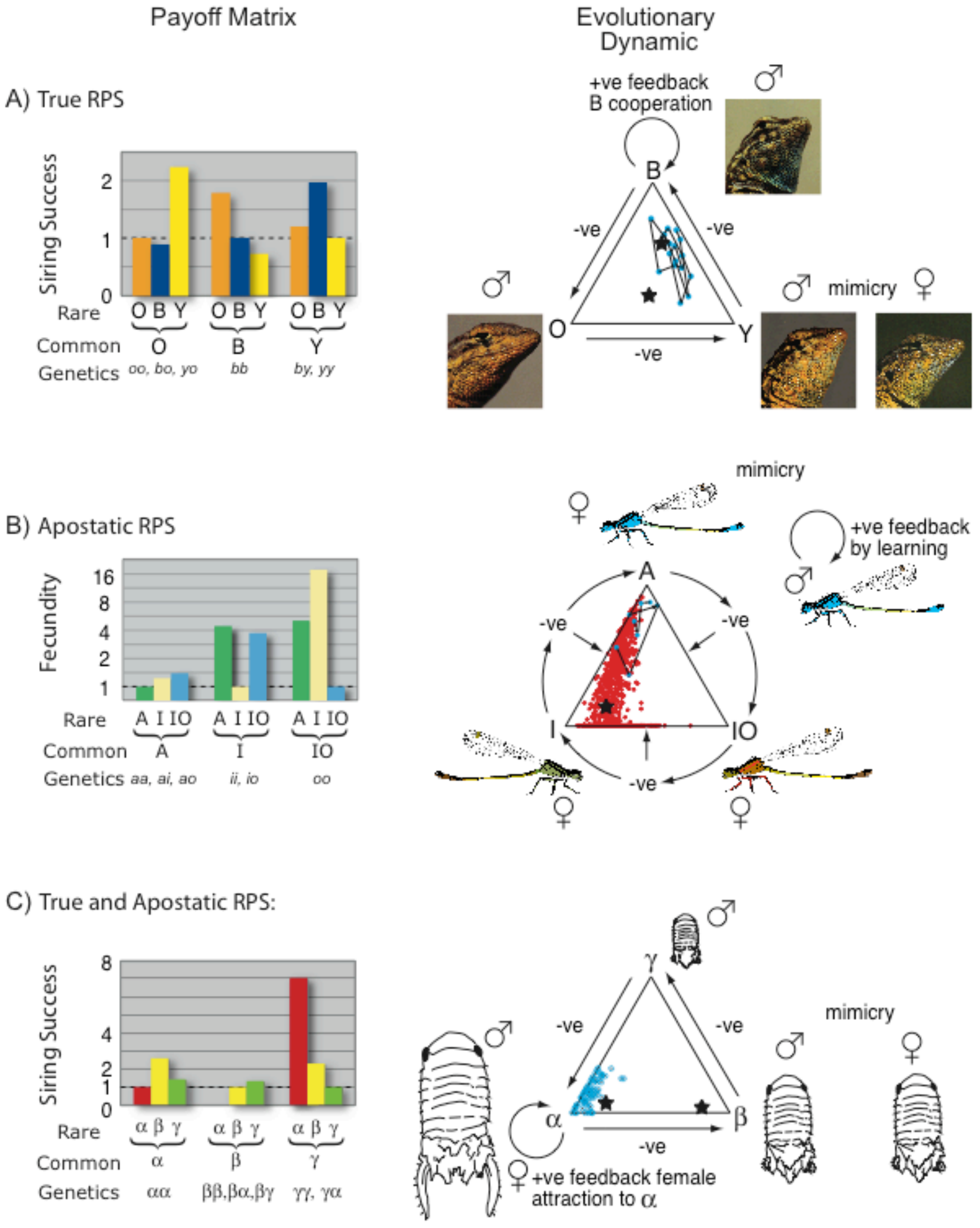
Side Box 9.2. FDS and rock-paper-scissors cycles

Figure 9.23 Diagnosing frequency-dependent selection (FDS) in mating systems with payoff matrices (*left panels*: $W_{rare,common}$), evolutionary dynamics (*center panels*: ternary plots with calculated or theorized attractors the evolutionary equilibrium, ★). All mating systems due to one locus control (*genotypes* below **P**henotypes).

(A) Data on siring success of side-blotched lizards, *Uta stansburiana* (Sinervo 2001), are nearly consistent with true rock-paper-scissors (RPS) fitness intransitivity in which one rare strategy has high fitness while the other rare strategy has low fitness relative to the common strategy (B) FDS (Svensson et al. 2005) on fecundity of the damselfly, *Ischnura elegans*, is consistent with a purely apostatic mating system, which is diagnosed by both rare strategies having higher fitness than each common strategy. The payoff matrix also exhibits RPS intransitivity (Equation 9.3, see text). In this case the morphs are in female strategies. (C) Reanalysis of data (Shuster & Wade 1991a) on siring success and female harems in the isopod, *Paracerceis sculpta*. Isopods exhibit a mixture of true RPS and apostatic RPS (Equation 9.4). The despotic αmorph (R = rock) controls harems, but is self-limiting (*right panel*) at high harem densities, when two cryptic (P = paper) morphs (β, γ) invade. Sinervo and Calsbeek (2006) review frequency dependent selection and discuss RPS dynamics, genetics, and methods to derive payoff matrices in the online supplementary materials.

Negative frequency dependent selection: Notice that each RPS has negative FDS that pushes frequency towards an attractor(s) labeled by ★, which is the evolutionary equilibrium. In lizards there are actually two ★ equilibria because the OBY gene generates a density cycle in females, which destabilizes the male RPS (Sinervo 2000). In isopods there are two ★ equilibria because of the sex transformer locus (Chapter 2), which destabilizes the isopod game.

Positive frequency dependent selection: One vertex in each mating system exhibits positive FDS that acts as an absorbing state. For example the positive FDS on cooperating blue males sends the cycle to blue, but negative FDS (e.g., rare O invades common B) pulls it back into the RPS orbit. In isopods, females are attracted to α males, thus more α males enhance α success (up to a point). Positive FDS is so powerful it sustains 2 kinds of cheaters (β, γ) that invade by negative FDS. Finally, the female morphs of damselflies are destabilized by the positive FDS of learning by males, which is self-reinforcing (Chapter 14 and 17).



Therefore ESS analyses (Figure 9.23, Eqns. 9.2-9.4) indicate that all 3 mating systems exhibit RPS fitness intransitivity. In an apostatic RPS, common strategies lose to rare strategies. In a true RPS (lizard) each rare strategy loses to one common strategy and each beats one rare strategy. In a pure apostatic RPS common types have lower fitness than the rare types, but the three rare types exhibit RPS intransitivity (damselflies). The isopods are a mixture of true and apostatic RPS.

To answer the question, "Why is the RPS so common?" we need to look at the features common to all 3 known RPS systems, the key is mimicry of some kind. The other feature is an despotic type of some kind (damselfly females have a male mimic). All three exhibit positive FDS that pulls the system from the evolutionary equilibrium (lizards blue male cooperation, damselflies – male learning and search image, isopods – female copying and preference for α males). All three exhibit negative FDS that brings the system back to equilibrium (rare advantage). The end result of these two forces is an orbital cycle in the frequency of three types that never decays. You can analogize the force of negative frequency dependent selection to the force of gravity that keeps the planets in orbit around the sun. The force of positive frequency dependent selection is like the centripetal force that keeps the planets in motion around the sun (the mathematics of the forces governing mating system cycles and orbital cycles of planets are actually quite similar!).

New examples of the RPS are constantly being discovered. Sara Pryke et al (2006) has described 3 genetic color types in Gouldian finches, *Choebia gouldia*, which is likely to be the newest RPS. The bacteria *E. coli* exhibits an RPS (Kerr et al. 2000). This RPS is in your stomach; even as you digest, it cycles. We (Sinervo et al. 2007) have just described a new RPS in European common lizards. The RPS is one of the most common mating systems on the planet. I will be spend my 2007 sabbatical studying elephant seals with α, β, γ males.

Study Questions for Alternative Strategies

1.How are sperm and egg the basic reproductive strategies?

2. Draw a graphical model that explains why reef fish should transform from male to female.

3. Describe an ultimate reason why sex has evolved?

4. Why is a 50:50 sex ratio stable?

5. What is meant by condition dependent versus genetically determined strategies? Use the isopod and blue gill examples to explain your answer.

6. What is the hotspot hypothesis for the origin of leks? What is the traffic hypothesis? Outline an example that proves or disproves one?

7. How do the lizards of the rock-paper-scissors game illustrate the three basic male mating strategies? Why does no strategy win in the long run in the rock-paper-scissors game? Describe each strategies strength and weakness.

8. What is an Evolutionary Stable State? Contrast an ESState with an ESS. Is the RPS and ESState?

9. In Caro and Bateson scheme, contrast genes versus plasticity as sources of variation. Give four examples in which you illustrate purely genetic, purely plastic and mixtures of plasticity and genetic control.

10. What two types of frequency dependent selection contribute to the RPS cycles in isopods, lizards, and damselflies? Describe the force that destabilizes the frequency from the equilibrium and the force that tends to return the frequency back to the equilibrium.