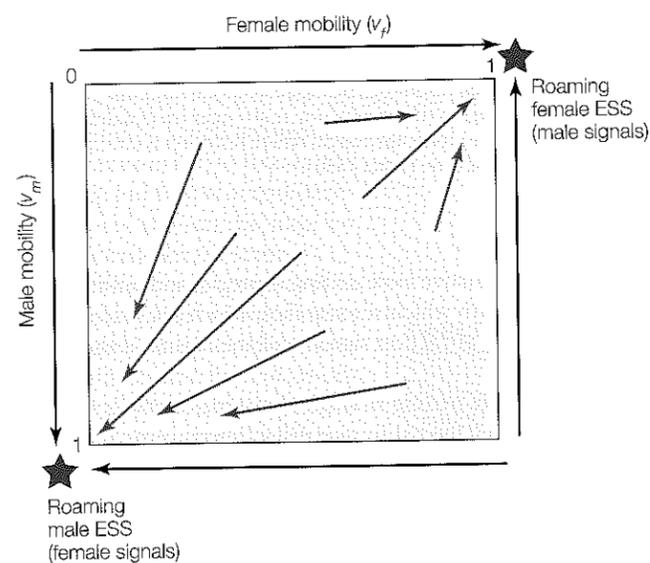


TABLE 12.2 Male mating strategies and their association with searching sex, signaling sex, and courtship display intensity

Mating strategy	Description	Searching sex	Signaling sex	Courtship
FEMALE DEFENSE	Males defend one or more females directly	M	F	Minimal display
Long-term association	Monogamous bond with one female or permanent harem with several females	M	F	Minimal display
Dominance hierarchy	Animals live in mixed-sex groups, dominant males have priority of access to females	M	F	Short-term consortship bond
Scramble competition	Females generally solitary or loosely clumped, males roam widely in search of females	M	F	Brief association for mating, can be coercive
RESOURCE DEFENSE	Males defend resources females need, such as food or nest sites	F	M	Moderate display
SELF-ADVERTISEMENT	Males position themselves in locations visited by many females	F	M	Highly elaborate courtship display

Sources: After [164, 244, 676].

**FIGURE 12.3** The mobility game In this continuous-strategy, asymmetric scramble game, each sex can vary its mobility while receptive from 0 (the animal sits and waits until a member of the opposite sex finds it) to 1 (animal moves during every time interval until it finds a mate). The male's velocity options are given by v_m and the female's by v_f . The solution is a double ESS denoted by the red stars for either maximally mobile females and stationary males (the roaming female ESS), or for maximally mobile males and stationary females (the roaming male ESS). The domain of attraction is stronger for the roaming male ESS because of the operational sex ratio favoring males. The sex that stays becomes the signaling sex. Species with roaming males include most mammals, reptiles, and insects. Species with roaming females include birds, frogs, and orthopterans. (After [244].)

females the signaling sex, as expected. But when males defend resources such as a food patch, nest site, or territory, they are selected to stay put and advertise the resource while females roam in search of good resources. Similarly, when males opt for the self-advertisement strategy, they establish display territories near locations with high female traffic. This system often results in aggregations of competitively displaying males called **leks**. When females are the searching sex, they are free to encounter, assess, and choose among a number of potential mates, and males may again evolve conspicuous and costly displays to attract them.

Signaling males often employ the visual and acoustic modalities, and mate attraction and courtship displays may be highly elaborate, especially in the case of lekking systems. By contrast, when males are the searching sex, females often employ the less costly olfactory modality for their attraction signals, and male courtship tends to be minimal or characterized by forceful control over females [676, 805].

Sexual Selection

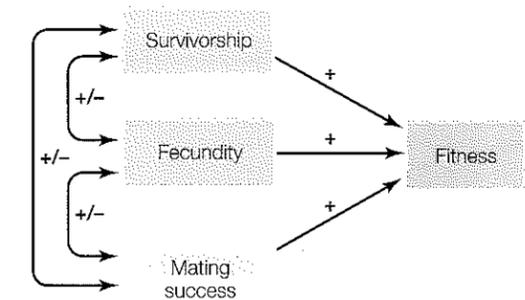
Sexual selection is the evolutionary process that arises from competition among members of one sex (usually male) for access to the limiting sex (usually female) [134]. It typically leads to **sexual dimorphism**, the different appearance of the sexes, via the evolution of specific traits in the competing sex that improve individual mating success. Because females are most often the limiting sex and males the competing sex, we shall use female and male in the next sections as shorthand terms for the limiting and competing sexes, respectively. As previously mentioned, there are important exceptions in which females are the competing sex and males the limiting one, and even cases where both sexes compete for mates, which we take up later in the chapter.

Competition for mates can take two basic forms that affect the types of traits that evolve. **Intrasexual selection** involves overt competition among males to control or monopolize mating access to females. Male mating success here depends on an individual's relative weaponry, body size, muscular strength, aggressiveness, speed, endurance, and experience. As we saw in Chapter 11, many of these traits are hard to estimate directly during a contest, and this has favored the evolution of various displays that are correlated with the traits and used to mediate contests without overt escalation. **Intersexual selection** arises when females can choose which available males will serve as mates. Benefits of being choosy include access to a preferred male's territory, higher levels of paternal care, effective provisioning by the mate, minimal exposure to disease and parasites, and the production of male offspring that will themselves be favored as mates. Again, the relative benefits of mating with a particular male are often hard to evaluate directly during courtship, and intersexual selection typically leads to elaborate male structures, displays, vocalizations, and odors that provide females with information about the individuals as potential mates. In most species, both intrasexual and intersexual selection play roles in generating nonrandom mating success among males; the relative influence of the two processes will vary among species and contexts.

Although Darwin believed that sexual selection generally operated in concert with natural selection to improve the adaptedness of individuals to their environment, he recognized that the traits that evolve via sexual selection can have a negative effect on the survival of their bearers and thus work in opposition to natural selection. Therefore a more inclusive view is to consider these processes as strategies for optimizing the different components of fitness. Sexual selection leads to adaptations that maximize mating success or mate quality, while natural selection leads to adaptations that maximize fecundity and survivorship (Figure 12.4). Recognition of this trade-off is key to understanding the observed patterns of signaling associated with animal mating.

Intersexual selection models

Intrasexual selection, which affects the same traits and signals in competing senders and receivers, essentially follows the evolutionary processes outlined for contest signals in Chapter 11 and will not receive further theoretical treatment here. Intersexual selection jointly affects the sexually selected display traits in males and the preferences for particular values of those display traits in females [11]. Evolutionary models of intersexual selection thus must take into account complex coevolutionary interactions between the sexes. A diversity of models for intersexual selection has been proposed, ranging from verbal appeals to intuition to more formal game-theoretic and genetic treatments. Models differ in assumptions, and as discussed in Chapter 9, in the methods invoked to predict evolutionary trajectories. One model might focus on **direct selection** of female preferences for certain male traits that improve female reproductive success or survival,

**FIGURE 12.4** The components of fitness Fitness can be divided into three components: survivorship, fecundity, and mating success. Sexual selection describes variance in mating success (yellow), which includes successful fertilization and acquisition of high-quality mates, while natural selection generally describes variance in survivorship and fecundity. Curved double-headed arrows show the potential for positive or negative correlations among these components. (After [21].)

whereas another model might examine **indirect selection** for female preferences caused by a genetic correlation with another trait under selection. Some models find that likely initial conditions lead to an equilibrium solution of male trait value and level of female preference, while others result in nonequilibrium or cyclical solutions.

As we also discussed in Chapter 9, genetic models of evolutionary trajectories can track the consequences of different patterns of sex determination, recombination rates, mutation rates, and the strength and direction of selection on a trait. Quantitative genetic models have the additional advantages of specifying the response to selection for a polygenic phenotypic trait, and can better incorporate pleiotropic and correlated relationships among coevolving traits. Furthermore, they are based on parameters that we can usually measure in the field and laboratory. A very useful synthesis of intersexual selection models can be achieved with a **multivariate quantitative genetics framework**, which allows the models to be compared using a common language and viewed as subsets of a complete accounting of evolutionary change [201, 376, 395, 459]. All models in this framework consider the simultaneous coevolution of three traits: a **male display trait** or mating tactic (t), a **female preference** for the male display trait (p), and a **viability** or residual fitness trait (v) present although not necessarily of equal value in both sexes. Residual viability includes the fitness components of fecundity and survivability left over after excluding the fitness effects of mate number and quality.

Recall from Chapter 9 that the change in the mean value of a single quantitative trait after a generation of selection is approximately equal to the product of its heritability and the selection differential on it. In the case of multiple traits evolving in tandem, things are a bit more complicated. First, we need to incorporate any genetic linkages between the traits. As discussed in Chapter 9, this is usually accomplished by

(A) Initial conditions

	Sexual selection gradient			Natural selection gradient			Additive genetic variance			Additive genetic covariance		
	t	p	v	t	p	v	t	p	v	tp	vt	pv
Fisher process	+	0		^	0		+	+		+	0	0
Good genes	^	0	^	^	^	^	(+)	+	+	(+)	(+)	+
Direct benefits	^	+		^	^			+				
Sensory bias	^	0		^	+			+				
Sexual conflict	+	+			^			+				

(B) Equilibrium conditions

Fisher process	+	0		+	0		+	+		+	0	0
Good genes	+	0	+	-	-	-	(+)	+	+	+	+	+
Direct benefits	+	+		-	-			+				
Sensory bias	+	0		-	^			+				
Sexual conflict	+	+		-	-		(+)					

FIGURE 12.5 Conditions associated with alternative intersexual selection processes The three traits under potential selection are a male display trait t , a female preference p , and residual viability in either sex v . The tables show the predicted relationships between each trait and the two components of fitness (sexual and natural selection gradients; left-hand columns) and the genetic architecture (additive genetic variance and covariance; right-hand columns) for each intersexual selection process. (A) shows the initial conditions required to initiate that process, and (B) shows the conditions expected at the equilibrium. In both tables, selection gradients can be positive (+), negative (-), stabilizing for intermediate values of the trait (^), or flat (0). Variance and covariance components can be zero (0) or greater than zero (+). Values in parentheses may or may not be important. Because these models all focus on the evolution of female preferences, all require additive genetic variance of p to get started (eighth column from left in (A)); similarly, all equilibria in (B) require that the sexual and natural selection gradients on the male trait (first and fourth columns) have opposite signs. (After [201].)

combining the additive genetic covariances between the traits and the additive variances of each trait into a single G-matrix. The selection differentials on the three traits can be summarized in a vector that is usually combined with the overall phenotypic variation in the traits to produce a selection differential. Thus for multiple coevolving traits, the changes in mean values of the traits across a generation is approximately equal to the product of the G-matrix and the selection gradient. It will be additionally useful to subdivide the selection gradient into two components—a sexual selection component favoring increased number or quality of mates, and a natural selection component favoring fecundity and survival.

Five different models of sexual selection have been proposed to explain observed patterns of sexual dimorphism and display behaviors: the Fisherian runaway, good genes, direct benefits, sensory bias, and sexual conflict models. All invoke the same quantitative genetic process for intergenerational change, but they emphasize different components of that process. Note that the different subsets of the process invoked by these models are not exclusive—most can occur

simultaneously with others. Figure 12.5A summarizes the conditions that are most important for initiating each model process, and Figure 12.5B summarizes the likely conditions at equilibrium. For a more formal analysis of this quantitative genetic approach to sexual selection, see Web Topic 12.1.

Web Topic 12.1 Quantitative genetic models of sexual selection

An overview of the multivariate quantitative genetic approach to the evolution of female preferences and sexual conflict models.

FISHERIAN RUNAWAY MODEL The Fisherian runaway model largely focuses on the G-matrix component of the quantitative genetics equation. R. A. Fisher was the first to propose a genetic process for the evolution of female preferences that could explain Darwin's observation of exaggerated, costly traits employed by males to attract females [183, 569]. The model begins with the accumulation of females in a population who share a mating preference for males with a particular cue or display trait. In this early stage, the preference need have no natural selection benefits and imposes no costs on the females expressing it. The accumulation could simply be a result of mutation and drift. However the preference is acquired, females that use it in selecting mates will produce offspring that carry both the preference genes from their mother and the display trait genes from their father. Once the population hosts a minimal number of females expressing the same preference, a positive covariance between the preference and trait genes builds up. If the covariance is large enough, a positive feedback loop is set in motion, and the resulting "runaway" process can produce a rapid elaboration of the male display trait along with shifts in average female choosiness to match these more exaggerated male trait values. Males with an extreme trait benefit because more females prefer them, and females benefit because their sons are preferred as mates. While there is *direct sexual selection* on the male trait, there is only *indirect selection* on the female preference via the

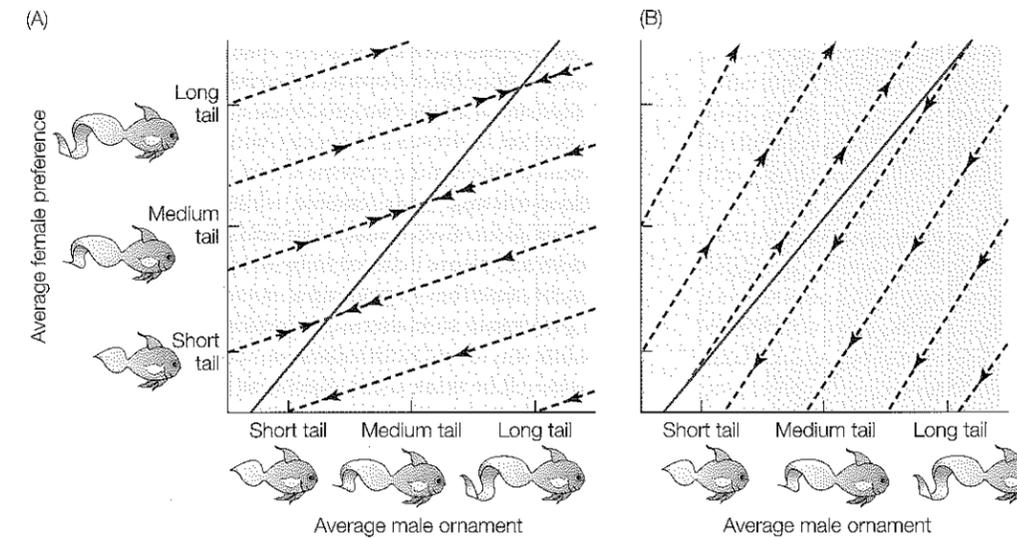


FIGURE 12.6 The Fisherian runaway model Both graphs depict the evolutionary equilibrium values for the average value of the male trait preferred by females (tail size, y -axis) as a function of the male trait (tail size, x -axis). If there is no cost of female choice, the outcome can occur anywhere along the red line of equilibria. The blue dashed lines with arrows show evolutionary trajectories. (A) If the covariance between female preference and male trait is small relative to the additive genetic variance, the population will slowly approach the equilibrium line and remain relatively stable. (B) If the covariance is large, the population will "run away" from an unstable equilibrium line, either increasing or decreasing. (After [394, 459].)

positive genetic covariance between the male trait and female mating bias for the trait (see Figure 12.5).

The Fisherian process with its runaway stage has also been called the "sexy sons" model because females only benefit by producing male offspring that have high mating success. As the runaway process continues, the extremely elaborated male trait is likely to become a hindrance due to developmental constraints, production costs, or predation risk. Display elaboration halts when the naturally-selected viability cost balances the sexually-selected mating advantage. Thus for a purely Fisherian trait, attractive males with extreme traits should suffer correspondingly higher mortality. Fisherian traits are sometimes referred to as "arbitrary" in form because their selection during the runaway process is related only to female attraction, not to male fitness [260, 363]. This unfortunate terminology overlooks the fact that even if preferences begin due to random processes, they often end up becoming informative indicators of male condition [373]. In addition, the Fisherian process is likely to accompany *any* of the other intersexual selection processes since all of them begin with expression of female preferences for particular male display traits. This has led to unnecessary disputes over whether a given example is due to Fisherian runaway or some other model: in most cases, both are likely to be contributing factors [373, 374, 376].

Quantitative genetic analysis of a pure Fisherian model predicts lines of equilibria with increasing values of both female preference and male trait expression (Figure 12.6), but only if there is no cost to females for being choosy [362, 394]. If females eventually experience a cost of mate choice, such as more time spent searching for high-quality males or increased effort rejecting low-quality males, the line collapses to a single point where the female's cost and benefit of choosing are balanced [568, 570]. The Fisherian process by itself is notoriously unstable and easily knocked into a nonequilibrium state, producing rapid changes and frequent differences in male and female trait values among populations. It has been argued that where a Fisherian process plays a major role, it could lead to rapid and high levels of speciation, such as are found in lekking birds-of-paradise (see Figure 9.3) [394, 526].

GOOD GENES MODEL Good genes models assume that females can produce fitter offspring by preferring mates with evidence of heritable viability and health; the relevant evidence is usually an exaggerated male signal trait that reveals meaningful aspects of male residual viability. Because of the temptation for males to cheat, it is also usually assumed that the display is a handicap and only males in good condition can afford the most costly versions of the signal. The process given this combination of assumptions is often called the **indicator model** (Figure 12.7).

Good genes models start with the presence of some male display trait correlated with the male's heritable viability. This can happen when display intensity is condition dependent or indicates some other aspect of male viability such as age, body size, or immunocompetence. Assortative mating between females with the preference and males with the trait leads to indirect selection on the female preference via the positive genetic covariance between female mating bias and male viability (see Figure 12.5A). There is no direct sexual

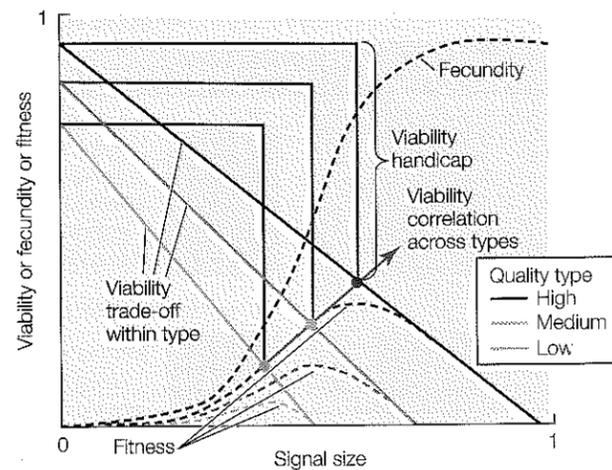


FIGURE 12.7 The good genes indicator model Relative male viability, fecundity, and net fitness (y -axis) as a function of their signal size (x -axis) for males of three different quality types: high (blue), medium (green) and low (orange). Mating success (fecundity) increases with increasing signal size (black dashed line). Higher-quality males experience a lower marginal cost (less steep slope of solid colored viability lines) when producing signals of different intensities, and also have higher viability in general (higher y -intercept). Dashed colored lines show the net fitness (= viability \times fecundity), and colored dots show the optimal signal size and viability (survival rate) for each type of male. Evaluated across individuals at the equilibrium (red arrow), higher-quality males have higher net fitness, higher mating success, and higher survival. The vertical drop in fitness (viability handicap) is the same for all three male types in this case, but could differ for different fecundity curve shapes. In theory, reliable signaling could occur even if high-quality males experience higher marginal costs (steeper slope of viability line), as long as their viability line y -intercept was very high and the fecundity curve increased more gradually. (After [215, 216, 514].)

selection for the preference. Female preference for the indicator trait will result in females producing more viable sons and daughters. This indirect benefit of producing high-quality offspring will likely lead to females becoming increasingly more selective and consequently experiencing some costs of choosing good mates. The male display trait itself does not need to be genetically determined (e.g., it could be age-based), but if it is, a genetic covariance between the trait and female preference will be established that can augment the good-genes process with a Fisherian one [294]. The male trait and female preference can also undergo cycles of elaboration and diminution in a good genes framework. Thus a number of selective forces come into play during the good genes process and they combine to impose direct and indirect selection on all three traits [201, 315, 316, 567].

Because the good genes process contains the conditions for the Fisherian process, it is misleading to conceive of these two processes as alternative hypotheses. Instead, most theoreticians suggest that the Fisherian process is inevitable, and the issue is the degree to which good-genes effects are also present [166, 373, 459]. Both processes can

be combined into a single conceptual model of indirect benefits, sometimes referred to as the **Fisher-Zahavi model** of sexual selection. Numerous factors may determine the relative importance of the two processes; for instance, the Fisherian process is stronger in species with highly polygynous or promiscuous mating systems where a few males can succeed in attracting many females, while good-genes effects are stronger in monogamous systems. Indirect selection effects in general are believed to be weak compared to direct effects, because they depend upon a longer causal pathway from preference to male trait to total fitness (viability). A weak link anywhere in this pathway means that the entire pathway will be weak [364]. Key weak links are the potentially low additive genetic variance of total fitness and of the male trait itself, brought about by persistent female choice for certain male traits that quickly drives the preferred alleles to fixation and erodes genetic variance. This problem is called the **lek paradox**, a reference to the conundrum of how lek-mating females can continue to derive a good-genes benefit from their strongly skewed mate choice, generation after generation, for highly ornamented males that provide no resources [363]. In fact, a variety of factors are known to maintain genetic variation, including high mutation rates, heterozygote advantage, selection in variable environments, frequency-dependent selection, sexually antagonistic selection, flexible female preferences, and preference for condition-dependent traits [45, 104, 124, 241, 294, 571, 596, 638, 728]. These surely account for the finding that the additive genetic variation of total fitness in real populations is never zero but usually accounts for 1–10% of overall phenotypic variation [93]. Thus indirect selection on female preference remains a viable option [31].

DIRECT BENEFITS MODEL Direct benefits models represent the least controversial case of intersexual selection [363, 376]. Females that have a genetic predisposition to choose mates that provide them with material resources obtain the immediate benefit of an increase in their fecundity, survivorship, or offspring survival rate. No genetic correlations are required. The key component is the presence of some male cue or signal associated with the males' ability to provide direct benefits, which results in positive direct sexual selection for the preference trait (see Figure 12.5A). The direct benefits process does not require heritability of the male trait for its initiation—benefits to females can be determined entirely by environmentally generated differences among males, as long as some reliable cue or signal of male ability to provide the benefit exists. However, it is likely to become heritable as a consequence of the female selection pressure. This pressure will then lead to the evolution and elaboration of a male trait that indicates these benefits via the process outlined in Figure 10.2. Most models assume that a condition-dependent handicapping mechanism will produce a signal that honestly reveals male ability to provide direct benefits [263, 279, 580]. At equilibrium, both males and females will experience some naturally-selected fitness costs of this selection (see Figure

12.5B). The costs for females may include lost foraging time, predation risk, or delays in reproduction while searching for acceptable males, and males pay a cost of producing and displaying the trait. Net fitness should be positive for both sexes [580, 659].

SENSORY BIAS MODEL No formal **sensory bias model** for female preferences exists. We have at best a verbal model proposing that female mating preferences evolve as a byproduct of natural selection on sensory systems used in nonmating contexts such as foraging or predator detection [37, 38, 363, 644–646]. As we described in Chapter 10, males that develop a display that mimics this feature may gain a mating advantage because females more readily detect them. In the quantitative genetics framework, the female preference is initially a preexisting naturally-selected sensory bias. If males then develop a display that mimics some aspect of this feature, and there is additive genetic variance for this display, a sexually-selected mating benefit will accrue to males possessing better matches to the feature. Female mating preferences thus emerge as a correlated response to natural selection on other behaviors. In other words, there is indirect selection for female mating preferences arising from pleiotropic genes that affect both mating and other behaviors [201, 202].

This sharing of the sensory system for two different functions is unstable and could be resolved in several ways. In one equilibrium solution, the female pays no cost for the male mimicry trait and her bias remains at a local, naturally-selected equilibrium point. Male display is maintained at a balance between natural selection that seeks to return the display to the original optimum and sexual selection that favors further exaggeration (see Figure 12.5B) [201]. A second possibility is that a genetic correlation develops between the male display trait and the female bias as a result of assortative mating. Once this covariance has been established, both the display trait and the bias for it now have the potential to be exaggerated via the Fisherian process, and there will be indirect positive sexual selection for the female preference. A third scenario is that the male display trait increases in size or intensity to the point where it becomes very costly; for example, it attracts predators or is energetically expensive to produce. It could then become a condition-dependent indicator of male viability, and female preference for the display could be indirectly selected under the good genes process. Finally, the male display trait could exploit the preexisting bias in a way that is manipulative and costly to females, for instance by causing them to mate more frequently than is optimal. Females would then evolve to resist, and males would counter by further increasing their expression of the manipulative trait, as described

in the chase-away model below. Sensory bias is unlikely to be an equilibrium solution by itself, but in conjunction with other coevolutionary processes may be an important mechanism for generating new signal systems, initiating speciation in different environmental contexts, and explaining some of the species-specific diversity in mate attraction signals [72].

SEXUAL CONFLICT MODEL Female mate choice (intersexual selection) always occurs against a backdrop of male-male competition (intrasexual selection), and in some cases this competition may limit a female's ability to choose a preferred mate or reproduce at the optimal rate. In the 1980s and 1990s, observations of overt physical conflict over forced mating in water striders and cryptic conflict during internal fertilization in *Drosophila* flies generated new insights and a view of males and females engaged in a **sexual arms race** [21, 105, 112, 283, 533, 534, 605–607, 637]. Competition among males to circumvent female preferences leads to increasing male persistence parried by increasing resistance by females, as illustrated in Figure 12.8. The resulting **sexual conflict** (or **chase-away**) model depends on the existence of a female preference for male traits, previously evolved via one of the processes described above, to create the opportunity for sexual conflict [21, 211, 283, 299, 781]. Initial conditions for this model include positive sexual selection (direct benefits) on the female preference; positive sexual selection on the male trait; and stabilizing natural selection on the female preference (see Figure 12.5A). Once females evolve a preference for a male trait that provides direct or indirect benefits, males with the preferred trait are then under selection to further increase their mating advantage by directly manipulating female fitness, such as increasing the mating rate above that

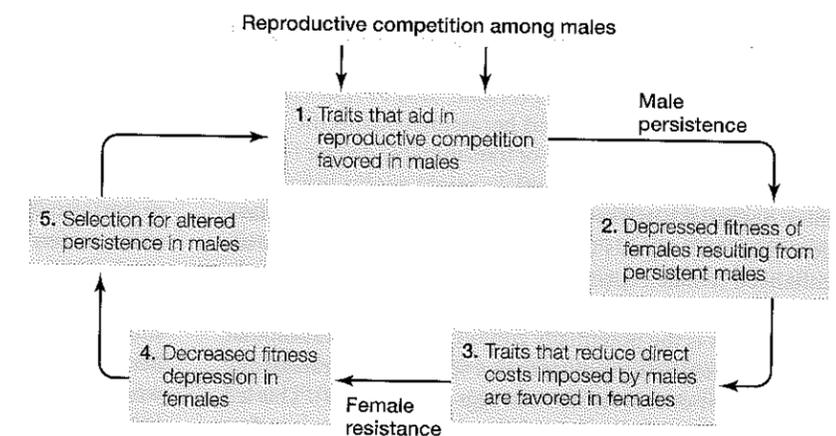


FIGURE 12.8 The sexual arms race Interlocus sexual conflict (involving genes at different loci in the two sexes) can result in perpetual cyclical or escalating coevolutionary reproductive traits in the two sexes. The process is driven by reproductive competition among males, which favors exploitative, manipulative, and persistent mating behaviors because males have a higher potential reproductive rate than females (1). For example, males evolve a chemical component in their semen that increases female fecundity or mating rate. These male adaptations can depress the fitness of females (2), causing them to evolve adaptations to resist such manipulation (3, 4). Males then evolve new persistence techniques (5) and perpetuate the cycle. (After [21].)

which is optimal for females. Sexual conflict is characterized by direct antagonistic selection between the sexes, where traits that enhance the fitness of one sex reduce the fitness of the other. The consequence is a negative natural selection gradient that balances the positive sexual selection gradient for both sexes (see Figure 12.5B). Even though females pay a direct cost by mating with manipulative males, they benefit by producing sons that are good manipulators. Other outcomes are also possible. Females may evolve insensitivity to the male trait, or evolve resistance against it, as a way to avoid such manipulation [639]. Nonequilibrium, cyclical solutions can occur [459, 741]. Finally, males are likely to incur significant costs to manipulate females, which can limit the extent of their manipulation.

Evidence for alternative sexual selection models

To rigorously discriminate among these processes, one would have to measure a number of the selection gradient and variance/covariance components listed in the columns of Figure 12.5. Several of the component values are common to all of the processes and therefore will not aid in discriminating among them. For instance, all require additive genetic variance for female preference as an initiating condition, and at equilibrium all predict positive sexual selection and negative natural selection for the male trait [82]. Even some of the remaining components make overlapping predictions for different processes, so demonstrating a key prediction for one process does not necessarily eliminate the others.

In principle, direct benefits are relatively easy to document. The resources that males can potentially provide to females include: a good supply of sperm to fertilize a female's clutch of eggs [275, 439, 494]; nuptial gifts and courtship feeding that enhance female fecundity [86, 95, 148, 226, 235, 503, 674]; male parental care that improves offspring survival [240, 576, 705, 783]; defense of good-quality territories that ensure a food supply or good nest site for the female and her offspring [99, 145, 146, 252, 594, 599, 601]; male defense against predators and harassing conspecific males [67, 122, 359]; and avoidance of transmittable disease [1, 624, 792]. What kinds of male displays might evolve to indicate these potential benefits to females? Numerous studies have described male signals that are significantly correlated with enhanced female reproductive success, which we describe in a later section of this chapter [477]. One concern with such studies is the potentially confounding observation that females mated to attractive males sometimes strategically increase their own investment in eggs [92, 368, 788]. This led to the **differential allocation hypothesis** which argues that females might be willing to pay a cost for such augmented investment, as long as they can reap the benefit of more or higher-quality offspring [673]. Thus a major reason why females might increase their investment when mated to an attractive male is to obtain indirect benefits. To accurately assess the magnitude of direct material benefits provided by males, careful experimental studies, such as cross-fostering of offspring with different parents where paternal care is

the issue, are required to sort out the role of maternal versus paternal effects, as well as environmental versus genetic sources of the reproductive benefits.

Over the past three decades, major research effort has been expended to find evidence of the good genes process. This requires measuring the fitness of males and females over at least two generations and looking for evidence of male trait heritability and the correlations between the male trait, female preference, and viability (especially the positive preference–viability covariance). A metadata review examined the association between male traits and their survival and found that most correlations were in fact positive, supporting the viability requirement of the good genes process [330]. Another metadata analysis of 22 studies examined the strength of the correlation between the male trait and the survival of the male's offspring, and found a small but significant positive average correlation that accounted for 1.5% of the variance in total offspring fitness [475]. Assuming maternal effects have been controlled for, this result can only occur if attractive males pass on their superior viability to their offspring. More recent studies have obtained similar results, and have also corroborated the heritability of the male trait and survival benefits for both male and female offspring [83, 149, 193, 327, 331, 728, 776]. Nevertheless, one recent review concludes that indirect effects may be a less compelling driving force for female mating preferences than direct effects and nonrandom mating caused by sensory exploitation, male–male competition, and female minimization of search and harassment costs [380].

The Fisherian process is typically documented with evidence that females mated to attractive males benefit by producing sons that are also attractive as mates [82, 168, 256, 339, 769]. However, only a few studies have argued for a pure Fisherian process by measuring the fitness components that might exclude good genes and direct benefits processes. One example is a study of the lek-breeding sandfly (*Lutzomyia longipalpis*), in which females approach small swarms of males located close to a prey host where the female flies obtain a blood meal before mating. Each female freely chooses a mate, presumably based on a pheromone signal. A laboratory study established small leks of males comprised of either preferred or nonpreferred individuals, and monitored the fitness consequences of females mating in these two contexts in terms of direct costs and benefits and the subsequent success of their sons and daughters (Figure 12.9). No direct benefit or good genes effects were found, but females mating with preferred male types did produce highly successful sons [339]. Similarly, a series of studies of *Drosophila simulans* has shown that the primary fitness benefit of mate choice to females occurs via the mating success of sons [288, 715–717].

Some procedures used by researchers to distinguish the roles of pure Fisherian from good genes effects in a given system have proven to be theoretically misguided [374]. For example, only the Fisherian process requires the existence of a positive trait–preference genetic covariance. To document this covariance, researchers conduct artificial selection

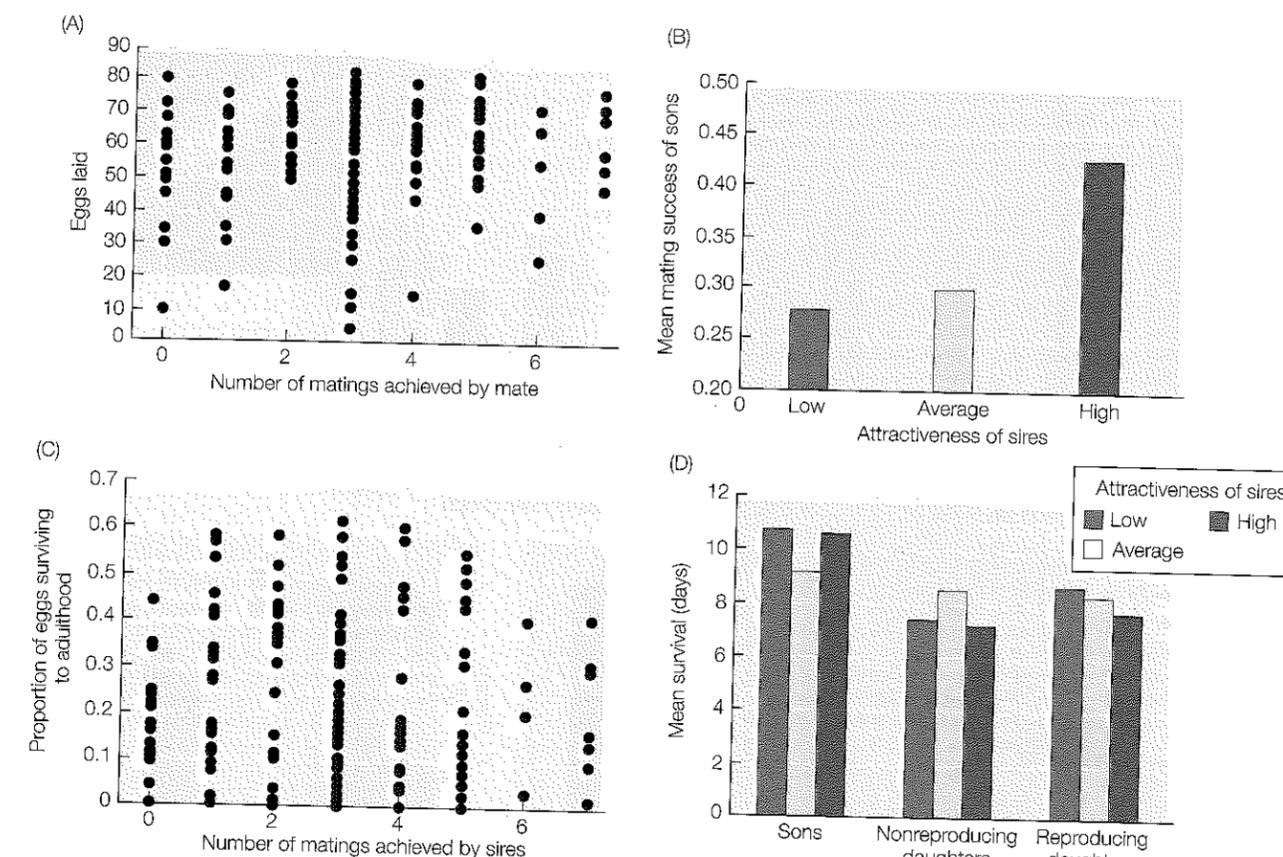


FIGURE 12.9 Evidence for sexy sons in the sandfly *Lutzomyia longipalpis* Males aggregate and display in swarms or leks, and females choose mates based on a male pheromone signal. Some males are consistently preferred by females over other males. In this laboratory study, males were pretested for attractiveness and sorted into small groups of low, average, and high attractiveness. Virgin females were released into one of the treatment groups and allowed to mate once with the male of their choice (known paternity), after which they were isolated and allowed to lay eggs. These offspring were then monitored for survival, fecundity (daughters), and mating success (sons). (A) The number of eggs laid by

a female was not correlated with the attractiveness of her mate to other females (measured as the number of matings he achieved in the pretest), indicating no direct benefits of mate choice to females. (B) The sons of attractive sires were themselves more attractive. (C) There was no correlation of the fecundity of daughters (measured as the proportion of their eggs surviving to adulthood) with the attractiveness of their sire (i.e., the grandfather of the eggs). (D) Adult survival of sons, nonreproducing daughters, and reproducing daughters was not affected by the attractiveness of the sire. (After [338, 339].)

experiments on the male trait, making it either larger or smaller, to determine if the mean trait value preferred by females changes in the same direction. Such an effect has been demonstrated in stalk-eyed flies and guppies [81, 293, 785]. But this correlation is also very likely to occur in the good genes process and should not be used to distinguish between them. In a similar vein, one cannot distinguish between Fisherian and good genes processes by comparing the relationships between trait magnitude and male survivorship. Although we expect the “size” of Fisherian male traits to show a negative relationship with survivorship and good-genes traits to show a positive one, good-genes traits can have a slightly negative slope with survival, as long as this cost is more than compensated by mating success and offspring performance benefits [372]. Finally, the good genes process is expected to lead to female preferences for

condition-dependent viability-indicating male display traits. But as we have already mentioned, all of the other processes also are likely to reach an equilibrium where trait elaboration is balanced by costs, and the outcome is often a condition-dependent trait.

In addition to these overlapping theoretical predictions, Fisherian, good-genes, and direct-benefit effects are not exclusive and can operate together, as suggested earlier. One such example is illustrated in Figure 12.10. The arctiid moth *Utetheisa ornatrix* has been the subject of a long-term investigation. In Figure 6.12, we described the male pheromone hydroxydanaidal, which is derived from a toxic pyrrolizidine alkaloid contained in the food plant of this species. During mating, males provide females with a spermatophore laden with the alkaloid. Females prefer males with a high concentration of hydroxydanaidal pheromone, which