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Sexual Selection

MICHAEL D. JENNIONS AND HANNA KOKKO

In this chapter we explore the routes that link differences between the sexes to sexual selection. Why is sexual selection often stronger in one sex? Why is the choosier sex usually less sexually competitive? What is the relationship between sexual selection and parental care? We outline key theoretical models that apply to most taxa and account for the origin and evolution of sexual differences in parental care, mating effort, sexual conflict, and choosiness. This theoretical backdrop sets the scene for empirical studies that usually focus on quantifying current levels of sexual selection (Shuster & Wade 2003), identifying genetic constraints on the evolution of sexual traits (Blows 2007) and measuring the sex-specific costs and benefits of mate choice, mating rates, and alternative male mating tactics. These topics are covered in detail in chapters 21–25.

SEXUAL SELECTION: ALL PERVASIVE AND ALL POWERFUL

The theory of evolution by sexual selection has prospered from its humble origins in 1871 as a secondary refinement by Darwin to his earlier account of evolution by natural selection (Darwin 1871). Darwin's original goal was to account for elaborate male traits that could not be explained by natural selection for survival. How could the peacock's tail, the giant antlers of the extinct Irish elk, or the gaudy throat colors of male lizards have evolved through natural selection? Traits that are energetically wasteful, overly elaborate, and harmful to their bearer are difficult to reconcile with the view that natural selection continuously weeds out inferior, uneconomical variants (Cronin 1991). Darwin noted that selection will favor traits that increase male mating success and allow a male to sire more offspring, even if this is at the expense of a reduced lifespan. Today, however, sexual selection is more widely invoked to explain a broader range of pervasive and striking patterns in nature.

Sex-specific selection must be a powerful force to account for sex-limited expression of traits. Males and females often differ profoundly in size, shape, color, behavior, and life histories even though, regardless of their sex, members of the same species share the vast majority of their genome (Bonduriansky 2007). These phenotypic differences can be so extreme that taxonomists have occasionally assigned males and females of the same species to different taxa, as was the case with eclectus parrots *Eclectus roratus* (Forshaw & Cooper 1989). *Sexual divergence* is the process that leads to sexual dimorphism in traits associated with competing for fertilizations, choosing mates, and investing in offspring. Explanations for sexual divergence have expanded greatly since Darwin's initial account. We now know far more about factors determining mating success such as fighting behavior and mate choice (chapter 24), as well as postejaculation

processes such as sperm competition (chapter 22), cryptic female choice, and differential allocation.

Sexual selection theory can explain not only why males (and sometimes females) bear traits that decrease their own lifespan through an increased risk of predation, parasitism, or susceptibility to disease, but also why they have evolved traits that damage the opposite sex. As sexual selection theory developed, it shifted biologists' perspectives on reproduction. Mating is no longer seen as harmonious union. Instead, it is viewed as an arena for sexual conflict in which females are under selection to evolve traits to counter males' attempts to elevate their own reproductive success (chapter 23). In the last decade, empirical studies have confirmed that sexual conflict can elevate the rate of evolution of certain genes, biochemicals, and morphological traits (e.g., Arnqvist & Rowe 2002b; Dorus et al. 2004; Andrès et al. 2006; Ramm et al. 2008). More generally, sexual selection theory explains why secondary sexual traits, such as genitalic embellishments, courtship song, and breeding coloration, show greater variation both within species and among closely related species than do other traits (Arnqvist 1998).

Recent theoretical developments have prompted reexamination of the coevolution of parental investment, sexual selection, and sex roles. The current direction and intensity of sexual selection are usually attributed to greater female than male parental care, which removes females from the mating pool (i.e., the set of individuals available to mate) and thereby forces males to compete more intensely for mates (Trivers 1972). However, it is too simple to draw the arrow of causality from parental investment to sexual selection because it can also go in the reverse direction: sexual selection is itself an important causal factor driving the initial evolution of greater postfertilization care by females (Queller 1997). Stronger sexual selection on males can therefore account for the taxonomically widespread pattern that females provide more parental care (Kokko & Jennions 2008). The details of the coevolutionary process vary greatly among species, however, and understanding unique features of the breeding biology of some taxa can also explain why they do not obey this rule, such as *sex-role-reversed* species in which females compete for males and are sometimes more ornamental in appearance (e.g., Forsgren et al. 2004; Jones et al. 2005).

The power of sexual selection to shape phenotypes is impressive when one considers that a gene for a sex-specific trait is only available to direct selection when it is expressed in the appropriate sex. For example, half the genes for a favored male trait are currently hidden from selection because they are in the body of a female. Even worse, when these genes are expressed in females they are actively selected against if they produce an inferior phenotype (Bonduriansky 2007). The reason why sexual selection remains such a powerful force is that, unlike much of natural selection, sexual selection is based on a *zero-sum game* in which one individual's win is another's loss. Sexual selection occurs only when there is competition for mates. Thus if, say, female reproduction limits population growth, then for every offspring sired by one male, another male loses out on an opportunity to reproduce (Shuster & Wade 2003; chapter 25). It is therefore impossible for every male to enjoy elevated reproductive success by competing more efficiently for females. It follows that there is no single goal or common end point to sexual selection. In contrast, natural selection sometimes selects for a single target. For example, the most aerodynamically efficient wing shape can evolve and spread to all members of a population. Sexual selection is therefore typically an open-ended process, and selection is usually directional rather than stabilizing.

SEXUAL SELECTION: PUTTING DEFINITIONS INTO PRACTICE

Darwin (1871, p. 256) stated, "That kind of selection, which I have called *sexual selection*...depends on the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction." Darwin's definition was intentionally restricted to so-called *secondary sexual traits* that are advantageous when competing (either directly or indirectly) for mating or fertilization opportunities (Arnold 1983). *Primary sexual traits* affect fertilization success or the ability to mate irrespective of the presence of rivals. These traits are economically designed (i.e., no investment is made in offensive, defensive, or attractive components) and are solely attributable to natural selection even though they are used in a sexual context.

Darwin's definition obviously included traits that are advantageous when individual compete directly for mates, such as weapon-like tusks, horns, and spines used in fights. More controversially, he

proposed that female choice selects for male traits that satisfy female aesthetic preferences for mates (Cronin 1991). In short, Darwin's definition was that sexual selection favored traits that increase mating success when individuals compete for mates. Modern definitions of sexual selection are more expansive. They accommodate the fact that mating does not guarantee parentage when females mate multiply. A more widely acceptable modern definition is therefore as follows: *sexual selection favors investment in traits that improve the likelihood of fertilization given limited access to opposite sex gametes due to competition with members of the same sex.* Traits favored by sperm competition, such as increased ejaculate size or longer sperm, are also sexually selected.

All selected traits increase the net fitness of the bearer (chapters 3 and 4). The most sensible reason to distinguish between sexual and natural selection is if these two processes generate distinctive types of traits. Succeeding in sexual competition requires investment of resources that could otherwise be used to increase naturally selected components of fitness (e.g., survival, foraging efficiency). The first problem for researchers studying sexual selection is to distinguish between primary and secondary sexual traits: is a trait more elaborate or costly than expected if its sole function is to ensure sexual union? In practice, traits such as male genitalia are a composite of features shaped by natural and sexual selection (Eberhard 1985). It is therefore a complex task to decide what features would remain if we isolated the effect of natural selection and eliminated sexual competition. Fortunately, recent experimental evolution studies offer some insights. Under experimentally imposed monogamy, natural selection favors lineages in which sexually selected traits are reduced, because this allows for greater investment into naturally selected traits that enhance the lifetime reproductive output of a pair (Holland & Rice 1999). Perfect monogamy in the absence of mate choice should eventually lead to the loss of all secondary sexual traits.

There is always a temptation to extend the scope of sexual selection. For example, it was recently suggested that there is strong sexual selection for traits ensuring female dominance in group-living species with limited breeding opportunities, such as meerkats, because only top-ranked females breed successfully (Clutton-Brock et al. 2006; Clutton-Brock 2007). However, in cases in which breeding opportunities limit female reproduction while all females have ready access to male gametes, we think the relevant female traits should be ascribed to selection due to social competition. Socially selected traits represent an anomalous investment from the perspective of natural selection acting on individuals in isolation (West-Eberhard 1983; box 14.1, this volume). The terms *social selection* and *sexual selection* are not interchangeable, however, because social competition is more inclusive and, in addition to mates/gametes, includes competition for nonsexual resources such as food items or grooming partners. Social competition for nonsexual or sexual resources selects for traits such as aggressiveness and weaponry. Because it is a zero-sum game, competing for a limited number of dominant positions in a group can select for similar traits to those favored by sexual selection.

The real problem for biologists is deciding whether a sexual trait deviates from its naturally selected optimum and has, by extension, evolved under additional sexual selection. The schoolboy error is simply to state that traits that currently increase mating or fertilization success under competition are sexually selected. This usage is far too broad. It makes the products of sexual and natural selection virtually indistinguishable because it encompasses any trait that improves reproductive success in the chain of events that begins with a nonreproducing individual and ends with the production of independent offspring. For example, foraging efficiently increases body condition, which in turn often increases male attractiveness (Tomkins et al. 2004). If all traits that increase foraging efficiency are attributed to sexual selection, we lose the meaningful distinction between economical and wasteful traits that originally drove Darwin to formulate the theory of sexual selection.

LET'S TALK ABOUT SEX

Mating Types and the Evolution of Two Sexes

Sexual selection requires sexual reproduction. Sex involves germ line cells undergoing meiosis to create sex cells (*gametes*) that contain half the parental genome. Two gametes then fuse to form a zygote that develops into another individual. Sexual reproduction is not synonymous with the existence of males and females. In some species (e.g., certain algae and fungi), all gametes look the same (*isogamy*) but are

divided into self-incompatible negative and positive mating types. In a few species there are more than two mating types and whether gametes can fuse depends on their genetic compatibility, which is determined by the absence of shared alleles at each of one or more loci. Sometimes this creates only a few mating types, as in the protozoan *Tetrahymena thermophila*, in which there are seven, but in others, such as the fungi *Schizophyllum commune*, there are thousands of *mating types* (Whitfield 2004).

The most common situation in sexual species is two mating types representing two sexes: males and females. This characterization of mating types is used when individuals specialize in producing either large or small gametes (*anisogamy*). Anisogamy is widely attributed to disruptive selection when one type of gamete evolves to take advantage of the resources provided by another (box 20.1). By definition, males are members of the sex that produces smaller gametes: a seahorse whose mate inserts large gametes into its brood pouch, in which they are subsequently fertilized and protected until offspring emerge, is still a male despite its effective pregnancy. This definition works because gamete size typically has a strongly bimodal distribution in anisogamous species. This is true even when individuals are hermaphroditic and produce different types of gametes. Hermaphroditic plants, for example, still produce ova and pollen rather than a continuous size range of gametes.

Anisogamy does not always predict enormous differences in gamete size because there is sometimes secondary selection for larger sperm (chapter 22). For example, male *Drosophila bifurca* produce giant sperm that are less than an order of magnitude smaller than eggs (Bjork & Pitnick 2006). This is a tiny difference compared to that in mammals in which sperm are 4–5 orders of magnitude smaller. If *D. bifurca* sperm ever evolve to be larger than eggs, the sex currently producing sperm will be labeled females! This would probably not be remarked upon by an observer unaware of the species' history, who would follow the convention of assigning sex based on gamete size. This simple thought experiment is a reminder that, gamete size aside, there are no immutable behavioral and morphological characteristics associated with maleness and femaleness. It can sometimes appear so because relative gamete size seems to drive the evolution of other traits such as stronger sexual competitiveness or greater parental care that we closely associate with one sex. The existence of sex-role-reversed species is a stark reminder that gamete size is a fallible predictor of how sexual selection operates on

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**BOX 20.1** Anisogamy and the Parasitic Nature of the Origins of Sperm

Anisogamy (distinct gamete size classes that define males and females) can evolve in at least two different ways (Bulmer & Parker 2002). The first option is that the ancestral population consists of gametes that can freely fuse with each other. Disruptive selection initially creates two distinct size classes of gametes (Parker et al. 1972) before gametes evolve traits that discriminate against fusing with gametes of the same size (Parker 1978). Alternatively, an ancestral population with isogamous gametes might already have two mating types that fuse only with each other (e.g., because of chemotactic responses; Hoekstra 1982). In this case, the question is whether the two preexisting mating types evolve to differ in size. Assuming external fertilization, both cases lead to the evolution of small sperm and large eggs under relatively simple assumptions. The analysis is similar in both cases, and here we describe the latter route, which appears to hold in some taxa (e.g., evolutionary transitions of gamete size in green algae; Kirk 2006). The following is a simplified account of the model of Bulmer and Parker (2002).

Three important assumptions are required for anisogamy to evolve. First, given a fixed budget for gamete production there is a trade-off between size and number of gametes. This is usually modeled as $nm = M$, where n is the number of gametes produced, m is gamete size, and M indicates the total budget. Given a fixed budget, a clear benefit of producing many gametes is a larger potential number of offspring. Second, large gametes form well-provisioned zygotes that survive better: the size of the gamete represents parental

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investment. Third, the function that relates zygote survival to its size is nonlinear: linear relationships are, in fact, impossible because survival would eventually exceed 100%. Given suitable nonlinearity, if one parent reduces gamete size by, say, half (thus it produces what we can start to call proto-sperm), zygote survival will drop but—importantly—by less than half (figure I). Assuming that gametes form a large, well-mixed population in which other proto-sperm compete for proto-eggs, this parent has simultaneously doubled its expected offspring production (with fixed M, n will double when m is halved). Doubling of the expected number of zygotes more than compensates for their somewhat diminished survival: the parent specializing in small gametes that rely on the other gamete to provide the bulk of the necessary resources for zygotes experiences a net profit. Sperm competition is an important feature of this quantitative argument. Without it, a male would only have to produce enough proto-sperm to ensure that all the locally available proto-eggs are found with a reasonably high probability. Numerical excess beyond this would then hardly improve reproductive success. However, when many proto-males compete, a twofold increase in the quantity of sperm will double a focal male's expected fertilization success.

We have used a large change in gamete size (reduction by 50%) for illustrative purposes. Assuming suitable nonlinearity in zygote survival functions (Bulmer & Parker 2002), the argument generalizes to smaller and more realistic changes: one expects disruptive selection in which one sex becomes a "parasite" in the sense that it relies on the "host" sex to provide virtually all the resources for the zygote, and specializes in locating as many hosts as possible. The host cannot follow the same route of diminished provisioning because, if it is the only resource-provider, further diminishing zygote
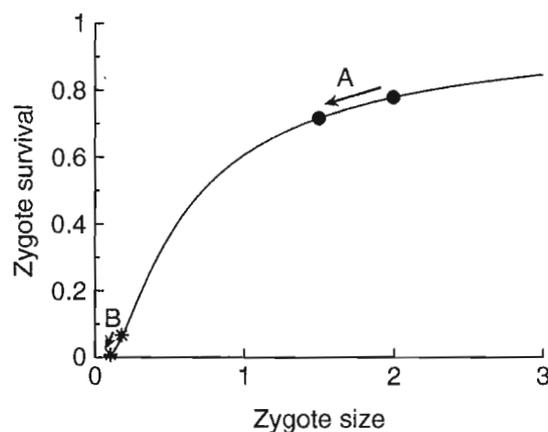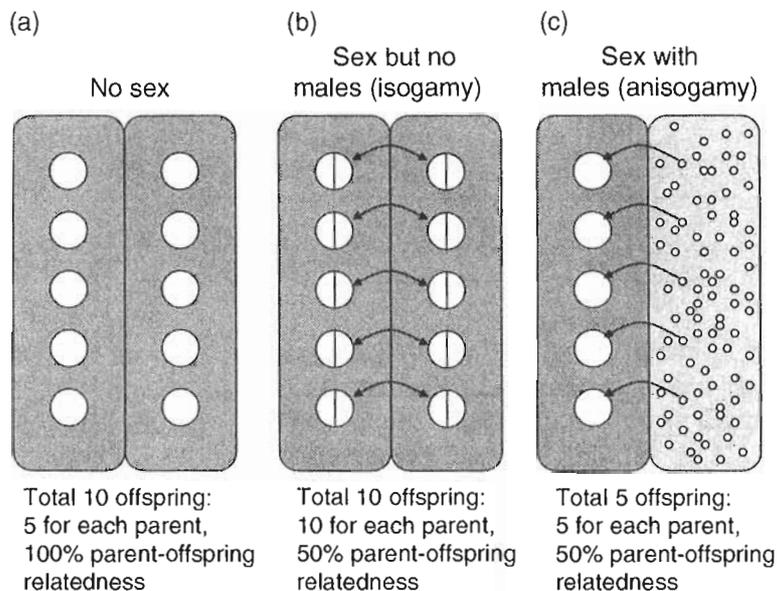

Figure I Initial steps in the evolution of anisogamy. Larger zygotes survive better, but the relationship between size and survival is nonlinear. The ancestral population is isogamous, with both parents spending their gamete budget ($M = 1$) on one gamete per time unit, thus the zygote size is 2. If one parent switches to making two gametes per time unit (arrow A), the zygote's size is $0.5 + 1 = 1.5$. Zygote survival drops from 78% to 72% in this example, but the parent's relative reproductive success has increased from 1×0.78 to $2 \times 0.72 = 1.44$. This does not assume that *all* gametes fuse with eggs, only that the expected number of eggs located doubles. It is not possible for both parents to keep diminishing gamete size in this way. If both invested very little, then further decreases eventually lead to much stronger drop in survival (arrow B). A more complete treatment of the evolution of anisogamy that takes gametic survival before fertilization into account is provided by Bulmer and Parker (2002).

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BOX **20.1** *(cont.)*

resources would harm it disproportionately: it is not possible for a host to become the parasite's parasite (figure I). If one parent does not contribute resources, the other must compensate. Sexual conflict is therefore an ancient and fundamental feature of reproduction involving two sexes (chapter 23). It will be absent only in restricted cases such as absolute monogamy, random mating, and an even adult sex ratio so that male and female reproductive interests perfectly coincide. In such cases, we might even predict a return to isogamy. Isogamy can, however, also be maintained if gamete survival requires that they remain relatively large (Bulmer & Parker 2002). The anisogamy argument can be generalized to cover internal fertilization. If females mate only with a single male, then males should evolve to provision zygotes instead of producing excess sperm. However, even if the proportion of matings involving sperm competition is very small, excess sperm production persists (Parker 1982).

Populations would grow best if all parents directed resources to zygotes, rather than trying to outcompete others of the same sex in a zero-sum game. From a population perspective (or from a female's view), resources used by males to compete are squandered. The famous *twofold cost of sex* is a consequence of the zero-sum nature of male reproduction, not a result of sex per se (see figure II). This cost halves the rate at which a sexually reproducing female's genes are transmitted to future generations, compared to that of an

(a) No sex	(b) Sex but no males (isogamy)	(c) Sex with males (anisogamy)

Total 10 offspring: 5 for each parent, 100% parent-offspring relatedness	Total 10 offspring: 10 for each parent, 50% parent-offspring relatedness	Total 5 offspring: 5 for each parent, 50% parent-offspring relatedness

Figure II Why a twofold cost of sex arises only when males evolve. Two individuals are depicted in each population, with the shaded area indicating the resources they use. In each case the resources are sufficient to produce 5 offspring. In (a), two asexual females produce 10 offspring in total. In (b), genetic exchange occurs because of sex, but isogamy allows resources to be pooled such that total offspring production remains at 10. In (c), half the population evolve to become males and the resources they access are used to elevate success in sperm competition; these resources are not used to enhance offspring production, so the population-wide growth rate, as well as the female's fitness, is halved.

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asexual female who produces only daughters. It is the main reason that the maintenance of sex is among the most challenging questions in evolutionary biology (West et al. 1999).

The evolution of two sexes is a fascinating example of a *tragedy of the commons* in which individuals strive to secure resources for themselves (at the expense of competitors) with eventually negative consequences for the entire population. The metaphor originated with Hardin (1968) and refers to the medieval practice of allowing cattle or sheep to graze a common pasture that, without policing, leads to overgrazing (chapter 18). The tragic modern analogue is the overexploitation of marine fish stocks. Evolutionary tragedies of the commons are common (Rankin et al. 2007), and investment into winning at zero-sum games is, in general, prone to such tragedies. In the same way that a prudent fisherman who invests only in a small vessel will lose out in competition with big trawlers, a male who avoids producing excessive amounts of sperm ("excessive" because most will never fertilize an egg) will be outcompeted by males who invest more. Resources that could have provisioned offspring are "wasted" on competition that lowers the population-wide reproductive output (figure II). Of course, this does not prevent anisogamy from evolving because selection acts on individuals more strongly than it does on populations.

The evolution of males is an unusual "tragedy," though, because it contains an internal feedback that halts the spread of exploitation. In real host-parasite systems, parasites can greatly outnumber hosts, but once sperm fuse only with eggs, and vice versa (Parker 1978), Fisherian sex ratio theory (box 20.2) predicts that the rarer sex will have greater reproductive prospects so that parents will tend to invest equally in sons and daughters. Even so, anisogamy still means that up to half the individuals in a population are exploiting the rest, so there is a 50% reduction in the efficiency with which resources are converted into offspring. It should be noted that the cost of sex is twofold only if males do not interact with females or their offspring, aside from providing sperm to fertilize eggs, and all the resources males use are spent on mating effort (figure II). In the original anisogamy model the males' total budget is spent on gametes, but in reality the use of this budget itself can evolve in response to sperm competition risk (chapter 22) and trade-off with other traits, creating more prudent sperm usage in some cases (Wedell et al. 2002). Sperm limitation can cause the cost of sex to be greater than twofold (if some eggs go unfertilized). Likewise, it is reduced if there is paternal care, and increased if males actively harm females (chapter 23) or, more generally, reduce female access to food.

A reduction in the twofold cost of sex due to care is unlikely to provide a general explanation for sexual reproduction, because male parental care is a more recently derived trait than sexual reproduction, and because substantial male contributions to rearing offspring are relatively rare. It should also be noted that even though individual-level selection makes it easy to evolve from state (b) to (c) in figure II, this still does not constitute an explanation for sexual reproduction. This is because individual-level competition between asexual and sexual forms typically takes place directly between states (a) and (c), which sometimes coexist within a single species (e.g., Jokela et al. 2003).

each sex. So why are there so many species in which gamete size does predict sex roles?

Anisogamy Rather than Sex Leads to Sexual Divergence

It is conceivable that sexual selection occurs in isogamous species: for example, in *Chlamydomonas* algae positive and negative mating types are both flagellated and thus motile, presumably an outcome of selection to improve mate encounter rates. There are, however, very few phenotypic differences among mating types in most isogamous species, which is why genetic techniques are required to identify mating strains. In contrast, in anisogamous species the sexes diverge not only in the size of their gametes but in innumerable other aspects of their lives ranging from their size and shape (Fairbairn et al. 2007), to color and ornamentation (Andersson 1994), to immunocompetence and average lifespan

(Moore & Wilson 2002). This sexual divergence appears to have its origins in how sexual selection acts on each sex, so it follows that anisogamy generates additional forces of sexual selection that extend well beyond those acting on gamete size.

There are countless differences between the sexes. To explain them in a concise manner, we need to identify the most fundamental forms of sexual divergence that are likely to drive secondary differences. Theoreticians highlight three key differences. First, males are more likely to compete for a mate than are females. The most extreme weaponry in animals, such as antlers, tusks, and enlarged claws are expressed more fully, and more often, by males than females. Second, females are usually choosier than males about their mates; hence the greater occurrence of male than female sexual ornaments. Third, there is often a positive correlation between prefertilization and postfertilization parental investment. Prefertilization investment occurs at the gamete level: Trivers (1972) noted that eggs (and sperm) represent parental investment because they contain resources that improve the success of the current offspring at a cost to the parent's future reproductive success. Postfertilization parental investment occurs whenever there is costly parental care (chapter 26). In birds, mammals, reptiles, insects, and most arthropods, females provide care more often than males (Clutton-Brock 1991; Tallamy 2001; Reynolds et al. 2002). If there is biparental care, females still tend to make a greater effort than males (Schwagmeyer et al. 1999). The most notable exception to this rule occurs in fish in which male-only care is common (Reynolds et al. 2002).

FROM ANISOGAMY TO SEXUAL SELECTION

Anisogamy reflects a primordial sexual conflict whereby small male parasitic gametes exploited the rich resources provided by larger female host gametes (box 20.1). Competition among males, female choice, and sexual coercion represent the subsequent extension of this conflict to interactions among individuals rather than gametes. In this section we explain how anisogamy promotes sexual differences in the strength of sexual selection. We focus our attention on the differences between the sexes, as the evolutionary processes that lead to sexual divergence create the fundamental differences that subsequently determine how sexual

selection operates within each sex. Measuring the effects on fitness of trait variation within each sex is the goal of most empirical studies that tackle issues such as how sexual competition creates niches that promote alternative mating tactics in the more competitive sex (chapter 25), or the consequences of sexual conflict over mating rates for trait evolution within each sex (chapter 23), or the benefits of mate choice for each sex (chapter 24).

Gamete Availability and Competition for Fertilizations

If the only initial difference between males and females is the type of gametes they produced, we would *a priori* predict an even *adult sex ratio* (ASR) in diploid species. This prediction arises because of the *Fisher condition* (box 20.2), which states that each offspring in a diploid species has one genetic mother and one genetic father so that the total number of offspring produced by each sex is identical. A consequence of the Fisher condition is that selection does not favor reproductive strategies that equalize the population-wide number of male and female gametes; rather it favors equal investment in individuals of either sex at conception because, on average, offspring of the rarer sex will produce more descendants (box 20.2). For the ASR to be even, male and female mortality rates must be identical. This follows from the starting premise that the only sexual difference is in the size of the gametes they produce if there is no difference in the total investment in gamete production. This last assumption will probably be violated once sexual differences other than gamete size evolve, but it remains useful to highlight the absence of any *a priori* reason for one sex to be consistently rarer in the ASR. Together these factors create the causal route from anisogamy to an excess of sperm searching for eggs: males can produce more sperm than females can produce eggs, and the number of females is not expected to greatly exceed the number of males. Many sperm will fail to locate eggs, whereas most eggs will be fertilized.

Selection can arise only if there is variance in fitness among individuals (chapters 3 and 4), and a male bias in gamete numbers sets the stage for sexual selection as variance in reproductive success is potentially far higher for males than females because fertilization success is a zero-sum game (chapter 25). The term *opportunity for sexual selection* (Shuster & Wade 2003) is often used to describe measures of variance in reproductive success, but it should be

BOX **20.2** Sex Allocation Theory and the Fisher Condition

Why create sons if most of them will produce unsuccessful gametes, whereas almost every daughter will successfully breed and have all her eggs fertilized? By analogy, to maximize their profits, chicken farmers retain no more cockerels than are needed to fertilize their hens. To date, however, animal breeders have been unable to produce strains that steadily conceive more daughters than sons (i.e., a female-biased *primary sex ratio*) despite the enormous economic incentives. Is the inability to bias offspring production toward females due to a lack of variation for selection to act upon (perhaps there is no proximate mechanism to bias sex ratio), or is there a deeper counteracting force at work?

Although a female-biased population has a higher growth rate, natural selection acts on individuals, not groups (box 20.1: the twofold cost of sex), and favors equal investment into both sexes. Consider the simple argument of R. A. Fisher, who asked what happens if the primary sex ratio deviates from 1:1 in a large, outbred population of a diploid species (Fisher 1930). Take, for example, an efficiently reproducing population in which every female produces three times as many daughters as sons. If, on average, a daughter produces n offspring ("on average" accounts for the fact that some daughters die before breeding and any variation in fecundity), how many offspring will the average son sire? No matter how many males die as juveniles or how strongly skewed mating success is, there are, on average, $3n$ offspring sired by each son. This is the only number to balance the account books when each offspring has exactly 1 genetic father and 1 genetic mother. Offspring of the rare sex, in this case, sons, are more valuable, and selection favors parents who bias production toward this sex, even though this typically reduces the population-wide growth rate.

The *Fisher condition* states that in diploid, sexually reproducing organisms, total offspring production through males cannot logically exceed that through females (or vice versa). It implies that the per capita production is higher for the rarer sex. Whenever male zygotes are rare, they grow into adults that, on average, produce more offspring than do female zygotes. Selection will therefore favor any mutation that increases the production of sons. If female zygotes are rare, the exact counterargument applies. Given certain widely applicable assumptions (e.g., that brothers do not compete for mates), negative frequency-dependent selection will result in an evolutionarily stable state in which the population invests equally into offspring of each sex. The Fisher condition holds, regardless of juvenile or adult mortality patterns, the extent of mating skew among males, or reproductive skew among females and whether either or both sex mate multiply or provide parental care. This near universal applicability in diploid species makes it an incredibly strong and fundamental force that equalizes sex allocation into males and females.

There are certain inequalities that lead to deviation from the production of equal numbers of each sex (Hardy 2002). The most important is that Fisher's argument is better framed in terms of equal parental investment of resources into each sex, rather than the production of equal numbers of each sex. This takes into account any difference in the cost of production of each sex. Given a 1:1 primary sex ratio, it is initially more profitable to produce the cheaper sex, until the lower cost of production is counterbalanced by the decline in the average number of offspring produced by this sex due to its greater abundance (hence lower average rate of offspring production). Equilibrium is reached when the primary sex ratio is the inverse of the cost ratio (i.e., when the investment per sex is identical). We do not know if animal breeders have ever attempted to manipulate the life history cost of producing males. If, for example, all offspring are used for breeding but each cow is killed after she has weaned her first son, the cost of producing sons is elevated. Fisherian sex ratio theory then predicts a shift to a female-biased primary sex ratio. This manipulation allows no cow to produce more than one valuable son, whereas those that produce daughters have a higher lifetime number of offspring (including one valuable son).

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BOX **20.2** *(cont.)*

Female-biased primary sex ratios also arise if brothers compete for mates (local mate competition; Hamilton 1967). A parent has less incentive to produce sons when the degree of competition among brothers is high. This is because parental fitness does not depend on which son mates, only on the total number of matings their sons achieve. Competition among sons is wasted effort from a parental perspective, and parents benefit if they reduce this competition by decreasing the number of sons and investing more into producing daughters. In fig wasps, females lay eggs inside figs and their offspring then mate in the fig before their inseminated daughters disperse. The average number of females laying eggs inside a fig varies among species, which affects the average likelihood that brothers will compete for mating opportunities. Local mate competition theory has been spectacularly successful in predicting the primary sex ratio in fig wasps (Herre 1985). Another factor influencing the primary sex ratio is whether parent-offspring interactions affecting the parents' fitness differ between sons and daughters. For example, in cooperative breeders, parents should bias offspring production toward the sex that is more likely to assist them in rearing offspring (Komdeur & Pen 2002). This has been shown to occur in Seychelles warblers in which a series of stylish experiments have demonstrated that the sex ratio is highly skewed toward female helpers when the territory quality and number of existing helpers makes this beneficial for the parents (Komdeur 1998). More generally, whenever there is a nonlinear relationship between total investment in each sex and the marginal returns, this can lead to modest deviations from the more simple Fisherian prediction of equal investment into both sexes (Frank 1990; Sheldon & West 2004).

These refinements to sex allocation theory are not applicable to the general argument that in the early stages of anisogamy, in which the sexes differ only in the size of the gametes they produce, there will be frequency-dependent selection favoring equal production of both sexes. So it is reasonable to conclude that there will be many more male than female gametes seeking partners. That noted, we should not forget the important caveat that a primary sex ratio of unity does not automatically lead to an even adult sex ratio if the life histories of the two sexes differ so that one sex has a higher mortality rate. Once evolution by sexual selection occurs, mortality rates might well diverge between the sexes. If such differences are limited, however, male gametes will still be more readily available than female gametes.

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noted that variance is a prerequisite for sexual selection to occur. It is not a guarantee. Higher variance in male than female reproductive success is also consistent with a scenario in which male fertilization success is entirely random and no selection occurs (Sutherland 1985). For sexual selection to operate, elevated fertilization success in the face of competition must be correlated with the expression of a trait that varies among individuals (i.e., variation in mating success has a nonrandom component). Whether the trait then evolves will depend on how it is genetically correlated with other traits (Blows 2007).

If we assume that anisogamy initially evolved in an external fertilizer, the most likely immediate response to intense sexual selection on males is for increased rates of sperm production or sperm that are more efficient at finding eggs. Selection could further lead to males modifying the timing of sperm release to improve the likelihood of fertilization. These types of adaptive shifts in the timing of gamete release occur in many extant sessile marine invertebrates (chapter 21). A longer-term evolutionary response would be for males to actively locate females and ejaculate when they release eggs. This form of simultaneous spawning could eventually culminate in the evolution of copulation and internal fertilization. These selective processes could also act upon females (e.g., selection for improved ability to locate mates), but selection will be weaker if there is an excess of sperm relative to eggs.

Mate Availability and the Operational Sex Ratio

The evolution of internal fertilization raises new issues. The most obvious is how it will affect the

intensity of sexual selection. The relative number of male and female gametes no longer fully captures the strength of sexual competition. Sexual selection is not tenfold stronger in a species that has 10^6 rather than 10^5 sperm per ejaculate. Once mating and internal fertilization evolve, sexual selection is usually measured as the intensity of competition for mates (and, secondarily, in terms of ongoing sperm competition if females mate multiply). Under these new conditions, does anisogamy still lead to greater competition for mates among males than among females? The data say yes, but explaining why is more difficult than it first appears. For example, sexual selection can create scenarios in which there are more adult females than males, as occurs in many mammals in which sexual selection favors increased male body size that elevates male mortality above that of females (Moore & Wilson 2002). So why do males still compete more intensely than females if gamete counts are an incorrect measure of sexual competition and there are more adult females than adult males? The short answer is that at any given time, only some adults are available as mates.

Trivers (1972) operationally defined *parental investment* (PI) as care that increases the success of the current offspring at a cost to the parent's ability to invest in future offspring. PI includes parental care as well as the cost of producing gametes as they provide the initial resources zygotes use to develop, but it excludes energy invested into competing for mates. Trivers noted that the sex with the higher PI will usually take longer to complete a breeding event and reenter the mating pool. This has been codified in terms of the duration individuals of each sex spend in *time-out* after a breeding event before they become *time-in* and return to the mating pool seeking a mate (Clutton-Brock & Parker 1992). Differences in time-out can create a marked sexual asymmetry in the availability of mates. Unless there is a counterbalancing bias in the ASR, the sex with the greater relative PI will be the limiting sex and the other, limited sex will compete for mates. This is why understanding patterns in the direction of sexual selection (which sex competes more intensely for mates) is inseparable from an understanding of why one sex, usually the female, provides relatively more parental care.

A PI asymmetry is reflected in the *operational sex ratio* (OSR), which is the instantaneous ratio of sexually active males to sexually receptive females (Emlen & Oring 1977). All else being equal between the sexes, the sex with the shorter time-out (less PI)

will be more common in the mating pool and its members will compete for the rarer sex. For reasons outlined shortly, this is often the male (see below). However, it should be noted that the asymmetry in male and female time-out may decrease once there is sexual conflict over fertilization when females mate multiply (Simmons & Parker 1996). This is because polyandry is associated with the evolution of female traits that make fertilization more difficult (Birkhead et al. 1993) and sperm competition. Both factors selects for a greater number of sperm per ejaculate (chapter 22), which should increase male time-out. However, the net effect of multiple mating on male time-out is not straightforward because multiple mating also selects against male parental care, reducing this component of male PI (see below).

The OSR Is a Shortcut, So Measure the Actual Benefit of a Higher Mating Rate

A male-biased OSR together with the Fisher condition (each offspring has only two genetic parents) means that males in the mating pool have a lower mating rate than females. Even so, the assumption of a linear relationship between the OSR and sexual selection on the more common sex is rarely justified, and empirical studies have even reported negative relationships (Fitze & Le Galliard 2008). An implicit assumption is that greater competition for mates increases the strength of selection for traits that confer a mating advantage. Clearly, sexual selection relies on nonrandom variance in male mating success, not on a low average mating rate, and a male-biased OSR guarantees only the latter (Downhower et al. 1987). It is possible that changes in the OSR also increase the effect of stochastic sources of variance in mating success. The most obvious factor to take into account is the absolute density of each sex. Traits that have a causal effect on mating success and are therefore favored by sexual selection at lower densities might have no effect when the number of male-male interactions exceeds a threshold value (Kokko & Rankin 2006). For example, the ability of males to influence their own mating success by repelling rivals can break down when the OSR is highly male biased so that it becomes too costly to defend successfully a resource or a mate due to the sheer number of challengers (Mills & Reynolds 2003). A more general point is that the OSR concept was introduced as an index of

the relative ease with which mates can be monopolized (Emlen & Oring 1977). However, the extent to which selection actually favors an individual who achieves a higher mating rate as a result of such short-term monopolization was not explored, and whether the OSR accurately predicts the mating skew was assumed rather than explicitly derived.

The *Bateman gradient* (BG) is a direct measure of the benefit of an elevated mating rate and therefore a more explicit predictor of the current direction of sexual selection than the OSR (see chapter 21). It is now defined as the slope of the regression of offspring production on mating rate (Arnold 1994b), and its origins lie in experiments conducted on *Drosophila melanogaster* in the 1940s by Angus Bateman (Bateman 1948). He counted how many offspring were produced by males and females that mated varying numbers of times when a small group of males and females were housed together. His best known experiments showed that offspring production by males increased linearly with mating success whereas that of females barely increased after a single mating, and that variation in mating success and offspring production was far higher for males than females (Arnold 1994b). The interpretation is straightforward. Due to the faster rate of ejaculate versus egg production, male time-out after mating is short compared to that of females. It follows that male fitness will increase more rapidly than female fitness with an elevation in mating rate. In such cases, males have a steeper BG than females and there is stronger sexual selection on males for traits that increase mating success.

In general, theory predicts a steeper BG and stronger sexual selection on the limited sex. Recent evidence that having several mates per breeding event can elevate female fitness (Jennions & Petrie 2000) means that there are species in which females also have a positive BG. Indeed, although rarely mentioned in textbooks, this was actually the case in some of Bateman's own experiments (Tang-Martinez & Ryder 2005). Even so, offspring production by females is usually more strongly dependent on the rate of egg production than the availability of mates, whereas offspring production by males is typically constrained by the availability of mates rather than a male's capacity to rear offspring. The general value of the BG in predicting the direction of sexual selection is illustrated by the switch to a steeper BG in females in sex-role-reversed species in which males provide the bulk of parental care (Jones et al. 2005). Focusing solely on sexual differences in PI or time-

out to predict sexual competition is, however, a mistake (Kokko & Monaghan 2001). The ASR must also be taken into account because it, too, affects the availability of mates (e.g., Forsgren et al. 2004; Sogabe & Yanigisawa 2007).

Finally, it is worth remembering that the BG and the OSR consider different aspects of sexual competition. The BG measures how much an individual's fitness improves if it increases its mating rate. There is no consideration of how difficult this task might be. The difficulty of acquiring a mate for the average member of each sex is captured by the OSR, but this quantity, in turn, does not specify the associated fitness gain from each additional mating. In short, although they provide important clues, neither the OSR nor BG directly specify trade-offs between a current attempt to acquire a mate and other fitness-enhancing options. These trade-offs are readily apparent, however, when one investigates mate choice. It elevates offspring fitness or the number of offspring per mating, but trades off with maintaining a high mating rate. Similarly, parental care elevates offspring survival, but it again typically reduces the mating rate. We therefore now turn our attention to the evolution of mating preferences and parental care strategies.

What Is the Relationship between Sexual Competition and Mate Choice?

So far we have ignored the details of how sexual selection operates and what traits it favors (e.g., weapons or ornaments). One well-studied process is mate choice. Broadly speaking, mate choice occurs when traits create mating biases that reduce the set of potential mates (Kokko et al. 2003b). This does not necessarily involve direct rejection of a mate. For example, a preference for mating in a particular habitat can generate mate choice if only certain mates reach these locations (*indirect mate choice* sensu; Wiley & Poston 1996). There is a clear theoretical distinction between sexual selection and mate choice. The two processes are not synonymous. Mate choice generates sexual competition within the chosen sex, but it does not logically follow that competition for mates (sexual selection) must be associated with the other sex being choosy.

In many cases the evolution of mate choice means that the mating rate of the choosy sex is not maximized. If the BG is positive, fitness improves

with each successive mating, which selects against the reduction of the mating rate that follows from mate choice. Choosiness will therefore more often evolve in females because they usually have a very low BG so lower gains from mate choice are sufficient to compensate for a reduction in the mating rate. If the BG is negative, then females directly benefit if they reduce their mating rate by rejecting males (a form of mate choice). It is, however, incorrect simply to assume that the sex with the lower BG will be choosy. If, for example, the female BG is lower than that of males but both are positive, both sexes still pay a mating rate cost by being choosy. Unless there are benefits to choosiness that are not captured by the BG, neither sex should be choosy. Evidence for mutual mate choice in some species (Servedio & Lande 2006) and male mate choice in other species (Wedell et al. 2002), when combined with the fact that males almost always have a positive BG, suggests that BGs fail to capture some biologically relevant factors. As stated above, the information missing from the BG (as well as the OSR) is an explicit consideration of a key trade-off: choosiness typically changes both the number and the identity of actual mates.

Consider the simple case of two rodent species whose hybrid offspring have low viability. Should males, females, or both sexes avoid mating with heterospecifics? Simply quantifying BGs does not adequately capture the situation because offspring production depends on a mate's identity. This situation requires an explicit examination of the trade-off between mating rate and the average gain per mating under different choice rules. Rejecting heterospecifics will lower the mating rate, but elevate the average number of viable offspring produced per mating. Whether a choosy individual can achieve a net benefit in the face of this trade-off will be affected by the extent to which rejecting some individuals (heterospecifics) increases the mating rate with more profitable individuals (conspecifics), as well as the relative number/fitness of offspring from each mating type, the frequency with which each type of mate is encountered, and the relative effect of hybrid and conspecific mating on mortality rates and time-out.

It is easy to see why sexual differences in mate choice might evolve given costly hybridization. If PI is low for males (e.g., sperm is cheap to produce and males do not provide parental care) so that their time-out is brief, they gain little by rejecting heterospecific females, even if hybrid matings yield fewer offspring of lower fitness. This is because a hybrid mating hardly reduces their mating rate with conspecifics. In contrast, if female PI is high (e.g., eggs are costly to produce and there is female parental care) a prolonged time-out means that there is a stronger trade-off between the gains per mating and mating rate. Female mate choice should therefore evolve more easily. It is too simplistic to claim, however, that relative PI is the sole driver of sexual differences in choosiness. The trade-off between the gains from an indiscriminate current mating and the future rate of offspring production has to be specified. If, for example, there is a hybridization asymmetry and far fewer offspring are produced when a male of species B mates with a female of species C than when a female of species B mates with a male of species C, then it is possible that species B males evolve to be choosier than species B females, even if they have a lower PI because the relative benefits from an indiscriminate mating are far smaller for males.

Hybridization is, of course, an extreme case study, but it illustrates the main principles of mate choice evolution. Choosiness does not evolve simply because individuals of the opposite sex vary in the number and/or fitness of the offspring they produce. If mating incurs no cost in terms of future reproductive success and there is a current benefit to mating, then individuals should mate with every potential partner encountered. Mate choice evolves only if mating is costly: it might elevate predation or trade off with foraging, or, perhaps most important, indiscriminate mating might reduce the mating rate with individuals that confer greater benefits per mating. Male mate choice is a weaker force than female choice because the time-out for sperm replenishment is short and, therefore, it is less likely that a male who mates will lose out on an opportunity to fertilize the eggs of a better quality female. In contrast, when females mate they often have a longer time-out for egg production. This means that females are more likely than males to lower their mating rate while waiting for better quality mates. Anisogamy is therefore a driving force of sexual divergence in mate choice.

There is one situation in which males are effectively forced to choose. Consider a case in which males who court certain females with increased vigor (elevating the likelihood of mating) cannot court other females with the same vigor (lowering the likelihood of mating): courtship feeding forms an example. Initially, selection will favor males

that preferentially court the most fecund females, but there is a population-level feedback that halts the spread of such a preference. The process is analogous to that of feeding patch selection and the resultant ideal free distribution of individuals across patches that offer different rewards (chapter 11). Strong universal male preferences for fecund females are unlikely because if all males focus their mating efforts on the most fecund females, they place themselves in an increasingly competitive situation (Servedio & Lande 2006; Servedio 2007). A male with a preference for courting less fecund females (or, more generally, females who are less heavily competed over) will be favored by selection because a greater likelihood of actually mating compensates for the reduced fecundity per mating. Directional mating preferences therefore tend to be weaker in the sex that competes for mates.

The above assumes, however, that all males express the same preferences. A mating preference will evolve more readily when not mating with some individuals improves the chances of mating with other individuals. For example, in species in which males guard females prior to mating, males of low competitive ability might choose to ignore more fecund females and preferentially guard less fecund ones. They are then less likely to be displaced by more competitive males who, in turn, can afford to prefer more fecund females. If competitiveness and fecundity depend on body size, this could, under certain conditions, generate size-assortative mating (Fawcett & Johnstone 2003; Härdling & Kokko 2005).

PARENTAL CARE: LINKING ANISOGAMY AND SEXUAL SELECTION

Is Anisogamy Linked to Parental Care Because Females Invest More to Start?

Anisogamy represents a clear difference in PI between the sexes, but it is only one of several factors that determine the time-out for each sex. Trivers (1972) pointed out that the bulk of any difference in relative PI is often determined by which sex provides the most parental care. This sex will often become the limiting sex in the mating pool if an individual providing care cannot simultaneously acquire mates. (In some species, most notably nest-spawning fish, this trade-off does not occur.) The level of parental care each sex provides can readily

override asymmetries in total gametic investment per offspring. In eclectus parrots, for example, the greater female cost to future reproductive output of producing eggs rather than sperm is outweighed by the subsequent provisioning of fledglings by males (Heinsohn 2008). In principle, either sex could provide the bulk of care and become the limiting sex. In most species, however, females provide more care than males (chapter 26), so the OSR is male-biased, the male BG is steeper, and sexual selection on males is stronger.

So far, we have simply stated that producing larger gametes tends to be associated with greater parental care. We have not explained why this is so. This is consistent with the traditional approach of many theoreticians studying sexual selection, whereby PI differences are taken as given. The effect of these differences for sexual selection on each sex is then explored. This practice reflects the influence of Trivers (1972), who directly ascribed greater female parental care to the initial difference in PI that defines anisogamy. Some theoreticians (e.g., Dawkins & Carlisle 1976; Queller 1997) and empiricists (e.g., Gonzalez-Voyer et al. 2008) have, however, pointed out that a plausible causal pathway was never provided. In Tanzanian cichlids, for example, changes in sexual selection have preceded evolutionary transitions between female-only, male-only, and biparental care rather than the reverse (Gonzalez-Voyer et al. 2008). More generally, recent theory shows that females are not selected to provide more parental care simply because of higher PI at the gametic stage, nor are males selected to invest more into elevating their mating/fertilization success than caring for offspring simply because an ancestrally low PI creates a male-biased OSR (Kokko & Jennions 2008).

The main argument Trivers invoked to explain why anisogamy typically leads to greater female care is summarized in a quote: "since the female already invests more than the male, breeding failure for lack of an additional investment selects more strongly against her than against the male" (Trivers 1972: 144). Unfortunately, this argument does not identify the source of selection. Past investment cannot directly determine the best decision about the future. To continue to invest simply because you have already paid a high cost is to commit the *Concorde fallacy* (named after the backers of the supersonic plane who continued to invest in its development even after being told that it would not run at a profit; Dawkins & Carlisle 1976). Of course, past investment can influence subsequent decisions if it changes residual reproductive value and thereby alters the

future benefits of various courses of action (Coleman & Gross 1991). Even so, this line of reasoning has never been explicitly used to link anisogamy to greater female care. Recent attempts to do so suggest that, if anything, the greater initial investment by females into gametes makes female care less likely than male care (e.g., the effect of initial investment on body condition selects against further care; details in Kokko & Jennions 2008). The flaw in Trivers' argument is readily apparent if one considers the wider implications of the Fisher condition (box 20.2). If offspring die for lack of care, both parents lose the same number of offspring. Unless the ASR is biased (an issue we return to shortly), the proportion of an individual's lifetime breeding formed by these offspring is, on average, the same for both sexes because males and females reproduce equally often. It is incorrect to assume that males can more rapidly compensate for such a loss by remating sooner.

## Does It Matter that Males Have a Higher Potential Rate of Reproduction?

Given that sexual selection is largely driven by the availability of mates, which is influenced by how long each sex spends caring for young, we need a better explanation for the general trend for female-biased parental care if we are to understand why sexual selection acts on males. Trivers (1972) had a second line of argument that invoked the trade-off between caring and mating and implied that this is of greater concern to males than females.

The *potential reproductive rate* (PRR) is the average of the maximum rate at which each individual can produce offspring, assuming unlimited mate availability (Clutton-Brock & Parker 1992; Parker & Simmons 1996). Anisogamy implies a higher PRR for males than females (assuming that producing small gametes allows males to divide the same total investment into smaller packages and invest less per mating than females). There is a widely held view that males should provide less care than females because a high PRR equates to greater mating opportunities, and thus males suffer a higher cost in terms of lost mating opportunities when they care for their current offspring instead of seeking out new mates. This sentiment is captured in the following sex-specific quote: "male-male competition will tend to operate against male parental investment in that any male investment in one female's offspring should decrease the male's chances of inseminating other females" (Trivers 1972: 144). Once we

recall the Fisher condition, however, a logical flaw is apparent. The rate at which offspring are sired by males cannot differ from the rate at which they are produced by females. The PRR is a theoretical term that assumes conditions (unlimited mate availability) that are never fulfilled in nature. Selection acts on actual fertilization events. Any argument that uses the sexual difference in PRR as the sole reason to argue that males gain a greater fitness payoff by deserting offspring is simply wrong (Queller 1997; Kokko & Jennions 2003).

From an OSR perspective, male desertion of dependent offspring is a conundrum. Less male care leads to a male-biased OSR, which increases competition for mates. It is easy to see why males must then invest in competitive, sexually selected traits to succeed. It is less obvious why a male-biased OSR does not simultaneously select for a male to delay his return to the mating pool and stay to care for his current offspring. When the expected fitness gains from one activity (competition with the payoff of mating) decrease and those from another activity (caring and elevating offspring fitness) stay constant, one would expect investment to shift toward the latter activity. This is precisely what happens when an increasingly male-biased OSR makes success in the mating pool harder for males (figure 20.1). Surprisingly, general sexual selection theory rarely follows this line of argument, although it is sometimes invoked by empiricists to explain unusual breeding systems (e.g., Segoli et al. 2006).

Recent formal mathematical models have confirmed that the preceding argument is sound. When the only difference between the sexes is anisogamy, and there is a trade-off between caring and mating, the outcome is egalitarian parental care (the full model is presented in Kokko & Jennions 2008). Why? If the limiting sex provides more care, the OSR is biased toward the opposite sex, and there is now selection on members of the limited sex to care for longer instead of attempting to compete in a zero-sum game when the total benefits are smaller (fewer mates available per unit time). The model shows that whichever sex currently provides less PI is selected to provide more, until the system reaches an evolutionary stable state when the OSR is even. In short, when we derive care patterns from first principles, the Fisher condition predicts that mating systems evolve toward egalitarian parental care and an even OSR. The logic of the argument is analogous to that used by Fisher (1930) to predict an even primary sex ratio due to frequency-dependent selection (box 20.2).
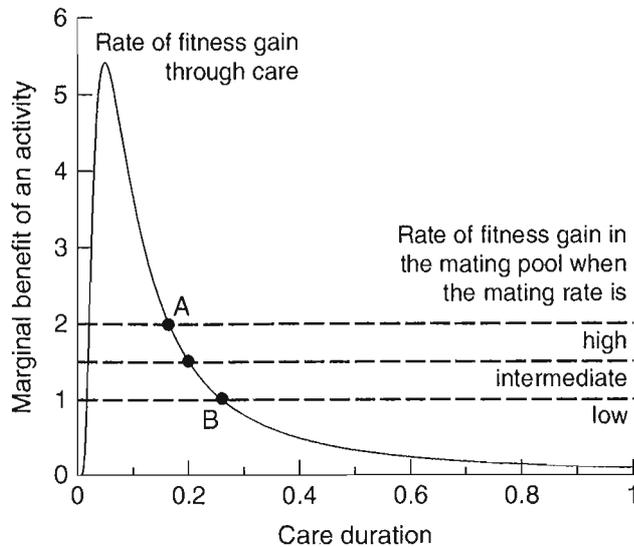
FIGURE **20.1** Frequency-dependent selection toward egalitarian care. Offspring survival depends on the care they receive: too little care hardly brings about a benefit, whereas extremely prolonged care likewise yields only a small additional (i.e., marginal) benefit. The marginal benefit therefore peaks when offspring have been given some care (here at a duration of 0.1 units), but additional care still greatly improves their survival chances (until the absolute increase in survival becomes minimal after 0.8 units of care). Parents should not desert their offspring at the peak but stay until the marginal benefit of further care falls below that which the parent can achieve after deserting its young (here determined by the time taken to remate after deserting). If two parents (a male and a female) give simultaneous care then, all else being equal, parent B, who will find it more difficult to acquire a mate (low mating rate) should desert later. Because a biased OSR lowers the mating rates for the sex that deserts earlier, there is frequency-dependent selection: whichever sex cares for a shorter time is selected to prolong its care, and vice versa. This is why additional factors must be invoked to explain sexual divergence in care. First, sexual selection can elevate the horizontal mating gain line for mated individuals. Second, low parentage within a brood can lower the marginal benefit curve for current care. Third, an ASR bias can shift the horizontal lines upward or downward.

So Why Do Females Care More Than Males? The Return of Sexual Selection

If an ancestral difference in PI due to anisogamy does not automatically become exaggerated but

tends to diminish once care evolves, why is egalitarian parental care rare? A satisfactory explanation for sex roles must invoke factors other than the ancestral gametic difference in PI. In nature there are at least three additional forces that affect the outcome of the simple anisogamy scenario (Kokko & Jennions 2008) and counter frequency-dependent selection for egalitarian care. Two modifications, highlighted by Queller (1997), are consistent with patterns in nature and lead to the prediction that females are predisposed to provide more care. The third modification—relaxing the assumption that the ASR is even—produces especially interesting predictions. It is relevant because there is good evidence that sexual selection and caring create sex-specific mortality rates (Liker & Székely 2005). The effect of the ASR on sexual selection has been surprisingly poorly investigated, although Trivers (2002, p. 61) has stated that his 1972 ideas relating sexual selection to mortality rates are actually more valuable than his introduction of the concept of PI.

Sexual Selection on Males Reduces Male Parental Care

Males are usually the more common sex in the OSR, and the preceding statements about fewer mating opportunities apply to the average male. There is, however, usually nonrandom variance in male mating success so that sexual selection exists. It might appear obvious that the subset of males with a mating advantage under sexual selection should be less inclined to participate in caring if it conflicts with acquiring mates. It is important, though, to ensure that we are not making a mistake by focusing on a few successful males and ignoring the effects of selection on the rest (chapter 25). The tendency to do just this is evident in scientific jargon itself: for example, the term *polygyny* literally means "males mate with multiple females," but high variance in mating success in most polygynous systems means that most males have extremely low or even zero mating success! If most males have little chance of mating quickly once they return to the mating pool, these less attractive or competitive males might do better by caring more for their current offspring, instead of competing in a mating pool with a male-biased OSR.

Deriving predictions about parental care requires caution for at least three reasons. First, when we consider all males, it is no longer clear whether stronger sexual selection on males will

favor greater sexual divergence in sex roles (i.e., males gain more by investing in sexually selected traits and females by spending more time caring for offspring). Second, it is a mistake to focus on variation in a single component of fitness within a sex without considering how it might correlate with other traits that increase fitness. If a male-biased OSR creates stronger sexual selection on males than females, this does not immediately mean that males should shy away from care: the relative benefit of caring might simultaneously become more important for those males whose prospects of succeeding in the mating pool are worse than those of females. Third, if care can be provided by either parent, when one sex provides more, the other can do less to achieve the same level of offspring survival. This is a postfertilization extension of the sexual conflict inherent in the difference in resources transferred to offspring because of anisogamy. If some males care more, then females can care less, which will feed back into the OSR. Offspring fitness depends on the parental decisions of both sexes, so we need to be precise and quantify what differences between the sexes predict female-biased care.

Having raised these complications, we note that there is some good news: models that take into account sexual selection can counter frequency-dependent selection toward egalitarian care and generate the most commonly observed sex roles. The argument is rather subtle, though. If mating success is nonrandom, then deserters (individuals who must have mated) do not have the same expected success as the average member of their sex. Every male who reenters the mating pool has already successfully induced a female to mate, despite having had to compete for mates because of a male-biased OSR. Unless obtaining a mate is a purely chance event, these males must possess sexually selected traits that confer an advantage during male-male competition or female choice. In other words, variance in mating success matters because it elevates the average expected mating success of those individuals who are most often in the position to decide whether to care for or desert young.

Males with low expected mating success have little influence on the relative amount of care provided by males (and thus females) when averaged across all mating events. For example, elephant seals live in societies with an extreme skew in mating success toward large males. A male cannot make any caring decisions when he is young and too small to sire offspring. By the time he does

obtain a mate, however, this very fact indicates that he is now more competitive than the majority of other males. In effect, nonrandom variance in mating success provides a male with information about his expected future success. This is why a male who mates is unlikely to stay with the first female with whom he pairs if there is strong sexual selection on males (Queller 1997; Kokko & Jennions 2008). It is hard to succeed, but if you do, it is a sign that you will succeed again. The effective OSR for males whose decisions about parental care are exposed to selection is actually less male-biased than it appears. In a sense, males invest in competing rather than caring despite the male-biased OSR, not because of it.

The above process does not require phenotypic plasticity. It is based on the simple fact that selection only acts upon parenting traits of males who mate (and thus tend to have high mating rates). Even so, sexual selection might also lead to males showing phenotypic plasticity in how much care they provide (see Trivers 1972). If less successful males have the good fortune to acquire a mate, they should be more inclined to provide parental care than the average mated male because their future mating prospects are low. Selection for plasticity will, however, be weak if variance in mating success is high, because it is then rare for unsuccessful males to mate. Conversely, if they mate fairly often, then sexual selection must be weaker so the gains from deserting sooner are relatively larger. Plasticity also requires that males obtain reasonably accurate information about their future prospects. Behavioral details of male-female interactions might allow a male to self-assess his attractiveness when female choice is important, but, more generally, information can be gained from relatively crude measures such as the time taken to mate successfully for the first time.

Sperm Competition: More Males Than Females per Breeding Event Lowers the Benefits of Male Care

So far, we have assumed that the absolute gains from caring for the current set of offspring are the same for both sexes (e.g., in figure 20.1 the marginal fitness gains from caring are identical for males and females). This is a valid assumption given evolution from an ancestral state in which the only factor distinguishing the sexes is anisogamy. Of course, once the time devoted to care diverges between the sexes,

this will select more strongly for efficient parental care by the sex that spends more time caring. This could result in sex-specific traits (e.g., female lactation in mammals; but see Kunz & Hosken 2009) that create phylogenetic inertia biasing care toward one sex in a given taxa. There are, however, numerous phylogenetic transitions in care provisioning, so shifts in relative levels of care can still occur (e.g., Reynolds et al. 2002). More important, the wider pattern despite such transitions is still a greater level of care being provided by females. This raises the possibility that the gains from current offspring care are systematically higher for female than male parents.

Why should one sex generally care more? One explanation lies with the evolution of polyandry and/or sexual selection promoting alternate male mating tactics such as sneak spawning that result in sperm competition. If there are more potential fathers than potential mothers involved in a given breeding event, then, regardless of whether fertilization is internal or external, average relatedness to young is lower for males than females. Most breeding events involve more males than females due to a male-biased OSR, sexual selection on males to evolve alternate ways of obtaining fertilization success, or multiple mating by females. Females are consequently more closely related than males to the offspring produced, and lower average relatedness must reduce the payoff from parental care (chapter 26).

This issue of how variation in paternity affects care decisions has been investigated most thoroughly in the context of male birds provisioning their young (Sheldon 2002). Simple models show that an individual does not improve his fitness by providing less care to the current brood if his paternity is, on average, always reduced by the same amount: future and current reproductive success are similarly discounted by relatedness to offspring, and the optimal solution to the life history trade-off between caring and his own survival is unchanged (Westneat & Sherman 1993). In general, there are no simple predictions about how consistent differences among males in their ability to gain paternity will be associated with how much care they provide (Sheldon 2002). It is easy to create models in which males who gain high paternity provide less care than those who gain low paternity (Houston & McNamara 2002). This is because how males respond to a lower payoff due to reduced paternity depends on what else they can do to elevate fitness aside from care for the current set of young.

When comparing average parental effort between the sexes, the Fisher condition must be taken into account. It leads to the unequivocal conclusion that, all else being equal between the sexes, the sex with lower relatedness to offspring will always care less (Queller 1997). To understand why, consider a socially monogamous bird with high levels of extra-pair paternity. So every male has low paternity with his social mate. The Fisher condition requires that males gain extra-pair young elsewhere: every offspring must have a father (Houston & McNamara 2002). Only some of the offspring a male cares for increase his fitness. So whenever there is a trade-off between investment in caring for young and increasing success at gaining extra-pair paternity with other females, we expect males to shift some resources toward the latter. In contrast, unless females dump eggs, their investment in caring returns benefits from all the young in a nest. It follows that males will care less than females if parentage per breeding event is, on average, lower because they pay the cost of care, they receive a smaller benefit, and there are fertilization opportunities available elsewhere. This example again highlights how important it is to count all the offspring of all males (see Fromhage et al. 2007).

Sexual Selection Produces Life History Differences That Bias Adult Sex Ratios

The Fisher condition precludes sexual differences in the average rate of reproduction unless the adult sex ratio differs from unity. If the ASR is biased, then "if one sex is consistently rarer [...] it will be less likely to be parental" (Queller 1997, p.1555). This is because the Fisher condition creates a higher mating rate for members of the rarer sex, who therefore suffer a greater mating opportunity cost when they care. It is worth remembering that the ASR and the OSR are not necessarily correlated. For example, in many mammals the OSR is strongly male-biased because males have a low relative PI, whereas in birds the OSR is usually only weakly male-biased because there is biparental care. The ASR patterns are very different. In mammals, there are usually many more adult females than males because of high male mortality due to male-male competition. In contrast, in birds females tend to have higher adult mortalities than males so the ASR is male-biased (Liker & Székely 2005; Donald 2007).

We highlight the role of the ASR because it has an independent effect on desertion (for details, see Kokko & Jennions 2008). The relative payoffs from caring and deserting more strongly favor desertion by individuals of the sex with fewer adults: members of this sex must reproduce more often, so the average rate of fitness return upon reentering the mating pool is higher (figure 20.1). The source of a bias in the ASR has important effects on sexual selection (figure 20.2). If the cost of breeding is the main source of adult mortality, then whichever sex provides more care will be rarer in the ASR. Members of the opposite sex then experience greater difficulty acquiring mates. But does selection then favor increased investment in sexually selected traits to succeed despite greater competition, or

natural selection for greater care for offspring? An unfavorable bias in the ASR limits the absolute gains that come from competing, so the latter route to enhancing fitness is more profitable. In this case, frequency dependence arising from the Fisher condition counteracts sexual selection and sex role divergence is restrained.

The reverse situation occurs when a bias in the ASR arises due to high mortality attributable to the expression of sexually selected traits. Such traits often increase mortality during juvenile development or when competing for mates. In Kudu antelope, for example, large male body size is favored by sexual selection. This has resulted in strong selection for high male growth rates and delayed sexual maturation, with high male mortality and a heavily
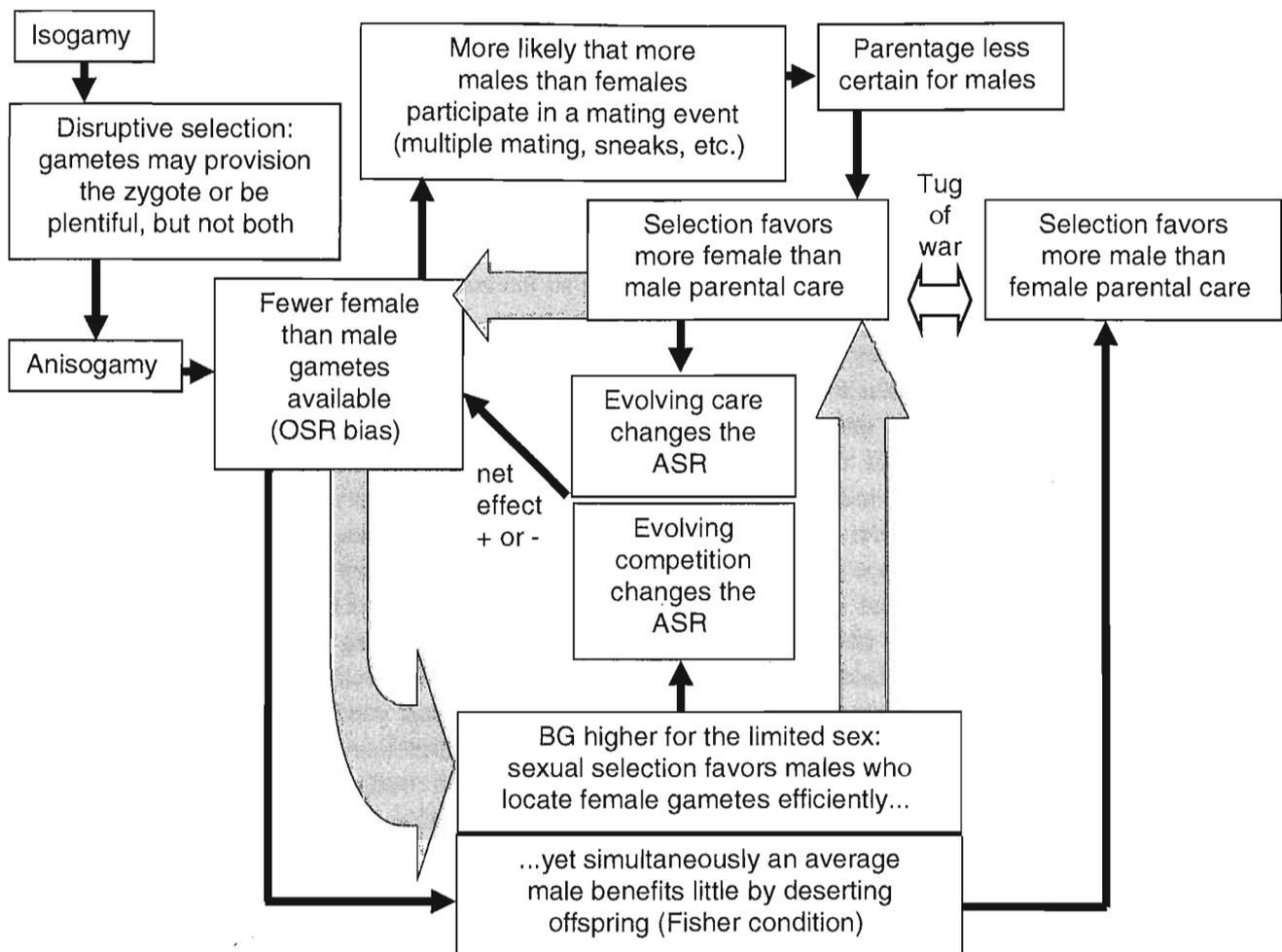
FIGURE 20.2 A graphical summary of the chapter. Broad arrows represent traditional accounts of sexual selection. They form a positive feedback loop. If they are the only forces at play, the sexes will always evolve to be maximally different. The other arrows represent forces that can be decisive in making predictions about where the positive feedback is halted. These include feedback from the ASR, the prevalence of multiple mating, and the tug-of-war between frequency-dependent selection for more care in the sex that cares less and selection for less care in favor of competitive traits. (BG = Bateman's gradient; ASR = Adult sex ratio; OSR = Operational sex ratio.)

female-biased ASR (Owen-Smith 1993). In mammals in general, sexual size dimorphism is widely attributed to strong sexual selection on males to defeat rivals during direct physical contests. Comparative studies show that as sexual dimorphism increases, males suffer greater rates of parasitism than females, which could be related to lower investment into immune defense to fuel growth. The net result is that male mammals have a shorter life span than females (Moore & Wilson 2002). When the deserting sex is the rare sex in the ASR, it must enjoy higher reproductive opportunities than the caring sex. This generates self-reinforcing selection to provide even less care and desert sooner.

To illustrate these two scenarios, compare the fate of a male in a population of finches with a male-biased ASR so that 30% of males fail to acquire a mate and that of a male antelope that faces ferocious sexual competition for mates due to a strongly male-biased OSR whereas the ASR is female-biased. Which male is more likely to evolve parental traits? Given the Fisher condition and a shortage of unpaired females, a male finch cannot be too optimistic about fertilizing offspring of many (or any) females even if he deserted his current young and increased his mating effort elsewhere. In contrast, the average male antelope in a female-biased population must, because of the Fisher condition, sire more offspring than are born to the average female. The average male therefore gains several reproductive opportunities by deserting. If there is strong sexual selection, then the future mating prospects for the average mated male are even better. This is why we do not expect male antelope to care, despite the heavily male-biased OSR that diminishes the odds that a male will succeed in the mating pool. The take-home message is that examining the OSR in isolation can mislead as to whether there is selection for the limited sex to care more. Consistent with the importance of the ASR for the evolution of sex roles, polygynous birds (i.e., birds with mammal-like breeding systems in which female compete) tend to have a more mammal-like ASR than bird species that form socially monogamous pairs (Liker & Székely 2005; Donald 2007).

Summary: The Path between Sexual Selection and Parental Care Is a Two-Way Street

The two main components of PI generate stronger sexual selection on males and make eggs less readily available than sperm: anisogamy and female-biased parental care. PI is, however, itself affected by sexual selection so that the evolutionary process involves a feedback loop (figure 20.2). Initially, anisogamy creates a numerical bias toward sperm and, even in the absence of parental care, makes the relative parental investment per breeding event greater for females. This means that females take longer to reenter the mating pool so that the OSR becomes male-biased. A male-biased OSR selects for increased male care (due to the Fisher condition), but if sexual selection creates a subset of males who are sufficiently successful at gaining matings in the face of competition, the net effect is actually reduced male parental care. If parental care is required, it is then more likely to be provided by females. This, in turn, exacerbates the difference in the speed with which females and males enter the mating pool because the relative PI of females is further increased. This makes the OSR even more male-biased, which generates still stronger sexual selection on males creating a positive feedback loop (figure 20.2). However, an increasingly male-biased OSR also means that males take longer to mate so they experience selection to become more parental instead of attempting to succeed in the increasingly difficult task of acquiring another mate. The evolving tug-of-war between these opposing forces means that the feedback loop can stop at very different evolutionary end points. These will partly depend on how strong sexual selection is as the OSR changes and on certainty of parentage (and it is worth noting that rates of polyandry or group spawning often shift with changes in the OSR). In addition, it will depend on the evolving mortality rates of the two sexes due to sex-specific investment in sexually selected traits and parental traits as well as sex-independent differences in the mortality associated with caring and competing that influence the ASR and the availability of mates (Kokko & Jennions 2008).

So Long, and Thanks for All the Fish

A key assumption in our account is that parental care trades off with mating rate. This is not always the case. Despite frequent loss of paternity by nest-building males to sneaky males in fish with external fertilization, male-only care is actually more common than female-only care (Reynolds

et al. 2002). Many male fish can rapidly switch back and forth between guarding eggs and courting females. There is even evidence that parental care is sexually selected because females prefer males who are guarding eggs, due to either mate choice copying (Goulet & Goulet 2006) or a direct preference for caring males (for insect examples, see Tallamy 2000). If true, caring males pay no mating opportunity costs and might even elevate their mating rate. This effectively blurs the distinction between time-in and time-out. We therefore conclude by thanking fish for reminding us that although general theoretical models are valuable, we should never lose sight of biological contingencies. When empiricists discover that the predictions of theoretical models are not upheld, rather than rejecting modeling out of hand, a more useful approach is to look more closely at the natural history of their study organism. Working out how animals violate current modeling assumptions is often a major route to empirical and theoretical progress.

FUTURE DIRECTIONS

Most empirical work on sexual selection, with the possible exception of comparative analyses and attempts to compare Bateman gradients, has one of two goals. One is to measure the current level of sexual selection on traits in the competitive sex and understand how they function. Another goal is to quantify selection for choosiness, which requires measurement of the cost of rejecting some mates, and the magnitude and sources of variation in the benefits of mating with different individuals. Here we have taken a different path and focused on why sexual selection differs between the sexes. We chose this route because the general patterns in nature are so striking (females care, males compete, females choose, males fight) that it is easy to treat them as inevitable. In reality there are still exciting research avenues to be traveled. The unwarranted transition between a higher potential reproductive rate and a claim of greater lost mating opportunity costs when caring illustrates the tendency to jump to conclusions instead of recognizing that sexual divergence still poses theoretical and empirical questions. For this reason we have focused on the basic logic of sexual divergence. The next six chapters provide the subsequent finer-scale details of topics such as how females choose males, how male traits reliably signal offspring fitness, or what selects for alternative mating tactics in males.

In our view, the population-level consequences of the Fisher condition are still underappreciated. This has recently been emphasized for specific questions about parental care (Houston et al. 2005), but the effect of this simple fact of life on the evolution of multiple mating, adaptive sperm allocation, and other traits subject to sexual selection remains poorly explored. Too much theory, and resultant empirical work, is based on the premise that the PRR or OSR predict mating behavior. Moreover, even when models allow levels of care and competition to evolve from first principles (rather than, say, simply stating that the OSR determines which sex will compete more strongly), the evolution of the associated traits is considered in isolation (e.g., Kokko & Monaghan 2001). In reality traits coevolve due to trade-offs that should be explicitly studied. Placing numerical values on the OSR, BG, or opportunity for sexual selection does not capture the nature of their trade-offs even though the diversity of sexually selected traits is largely attributable to the vast array of potential trade-offs. For example, producing more sperm can allow a male to outcompete rivals, but a large sperm expenditure can damage a female (chapter 23) or act in the completely opposite way and provision a female's young so that the distinction between mating and parental investment becomes ambiguous.

The insightful arguments of Queller (1997) about the evolution of parental care have recently been modeled by Kokko and Jennions (2008), but the effect of the Fisher condition on sexual selection (e.g., Bateman gradients and mate choice) is still unexplored. In particular, shifts in adult sex ratios might change the net effect of the tug-of-war between sexual selection, which makes successful males care less, and the Fisher condition, which makes males care more when they are the limited sex. Quantifying relationships between the adult sex ratio, mortality rates for different activities, the amount of time each sex spends caring and competing, and variance in male mating success is therefore likely to become a fruitful area for empirical study. In sum, we still do not fully understand the sequence of events that link anisogamy to parental investment, sex roles, and different forces of sexual selection. Given the jaundiced view that we already understand sexual selection, it is exciting to realize that basic questions remain unanswered.

SUGGESTIONS FOR FURTHER READING

A highly readable account of the historic development of sexual selection theory is *The Ant and the Peacock* by Cronin (1991). A comprehensive overview of recent sexual selection theory is that of Andersson (1994), and short reviews of many topics related to sex ratios are contained in Hardy (2002). Fairbairn et al. (2007) explore the evolution of sexual size dimorphism, which offers general insights into sexual divergence. The papers of Trivers (1972) and Emlen and Oring (1977) are still classic presentations of basic ideas about the origins of sexual differences in the intensity of sexual selection (and Trivers 2002 contains amusing and rewarding introductions to his landmark papers). Clutton-Brock and Vincent (1991) introduced the concept of potential reproductive rates, and the limitations of this approach were then highlighted by Queller (1997), who drew attention to the Fisher condition (Kokko and Jennions [2008] formally model and extend Queller's ideas). Shuster and Wade (2003) provide an exhaustive overview of the importance of variance in mating success for the evolution of mating systems and male mating tactics. Finally, the question of which sex will express stronger mate choice has been tackled in a series of papers, each of which emphasize different aspects of the process (Johnstone et al. 1996; Kokko & Monaghan 2001; Fawcett & Johnstone 2003; Servedio & Lande 2006, Servedio 2007).

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