1 Sexual Conflict in Nature

During the mating season, male robber flies roam through the vegetation in search of females. When approached by a male, a female takes to the wing, and the male pursues. If overtaken and grappled by a male, females of most species struggle violently, often successfully, to free themselves. In a few species, however, females may use another strategy to achieve the same result; if grasped by a male, they play dead! Once a female stops moving, a male apparently no longer recognizes her as a potential partner, loses interest, and releases the female, who falls to the ground and flies off.

Over the course of the egg-laying period, a male penduline tit (a song bird) makes repeated forays to his partner's nest in an apparent attempt to assess how many eggs she has laid thus far. Female partners, however, seem to make sure that this inspection job is not an easy one for males. Females bury their eggs in the bottom of the nest, perhaps to hide them, and become aggressive toward their mates. Observations in aviaries have shown that these inquisitive males are sometimes injured or even killed by their secretive mates.

As in most spiders where courting males are at risk of being cannibalized by females, a male of the funnel-web spider *Agelenopsis aperta* approaches a female slowly and very carefully. Once close, he sprays an apparent "toxin" at the female, which makes her (and occasionally him) collapse and enter an "unconscious" state. The male then hauls the cataleptic female about the web, repositions her, and finally inseminates her while she is still "knocked out."

At the time of mating, a male Malabar ricefish will dart toward a nearby female with near-lightning speed. Dashing toward the female from below, he strikes her in the genital region with a complex clublike organ. If the organ, a modified anal fin, contacts the female body, it releases a spermatophore (a sperm capsule) with a dartlike spike. This spike is pushed into the female flesh, and the spermatophore becomes firmly attached because of a whorl of recurved barbs at its tip. Females are adapted to these repeated assaults; they can be found with multiple attached spermatophores, and the skin around their genital pore is markedly thickened and hardened.

If one looks closely enough, observations such as these abound in the biological literature. But what do we make of these? It is difficult to reconcile observations of open conflict between the sexes with the common view of mating as a joint venture of two individuals that, by virtue of being the same species, share a common genome. Often, those cases where male-female interactions involve overt coercion, manipulation, deceit, or harm have been stowed away

and otherwise obscured. If explanations are offered, they often rest on special circumstances.

The main message of this book is that, despite interacting males and females sharing the same genome, conflict between them is ubiquitous. In other words, some genes expressed in females will be in conflict with others expressed in males. Moreover, some genes expressed in both sexes may be favored to do divergent things when expressed in females and in males. Selection on these genes is therefore sexually antagonistic. We will argue that the robber flies, penduline tits, funnel-web spiders, and ricefish may all have something very important to tell us. That is, how males and females came to be the way they are.

1.1 Evolving Views of Sex and Reproduction

Biologists and laypeople have long regarded mating as a largely harmonious event in which males and females cooperate in producing offspring. In fact, if we assume the entire result of mating is the production of shared offspring, it is not immediately obvious why we should think otherwise. Embedded in this view may be an assumption of monogamy, where the reproductive success of each individual of the pair is equal to, and contingent upon, the other individual. In these cases, if one can elevate the reproductive success of a partner, both will reap equal benefits. If we accept all of this, it is easy to imagine that what is good for one partner is good for the other and, in fact, also good for the species. These three perceptions—harmony in sexual interactions, monogamy, and a concordance between what is good for the individual and the species—have a long history but are often incorrect.

Evolutionary views of the interactions between the sexes have been fundamentally influenced by the work of Charles Darwin. Darwin often portrays reproduction in general and sex in particular as being something essentially reserved for the monogamous and married couple. In his famous 1871 book *The Descent of Man and Selection in Relation to Sex*, he summarizes an experiment involving a small crustacean as follows: "The female, when thus divorced, soon joined the others. After a time the male was put again into the same vessel; and he then, after swimming about for a time, dashed into the crowd, and without any fighting at once took away his wife." Darwin did recognize the existence of polygamy, as evidenced in a letter to his friend Charles Lyell, where he describes female barnacles as having "two little pockets, in each of which she kept a little husband." Yet, he was clearly reluctant to entertain the idea that the "practice of polygamy" was widespread, and even saw this as the major problem for his theory of sexual selection. "Our difficulty in regard to sexual selection lies in understanding how it is that the males which conquer other males, or those which prove the most attractive to the females, leave a

greater number of offspring to inherit their superiority than their beaten and less attractive rivals. Unless this result does follow, the characters which give to certain males an advantage over others, could not be perfected and augmented through sexual selection. When the sexes exist in exactly equal numbers, the worst-endowed males will (except where polygamy prevails), ultimately find females, and leave as many offspring, as well fitted for their general habits of life, as the best-endowed males." Today, thanks in part to the advent of DNA fingerprinting, we know that true genetic monogamy is in fact extremely rare (Birkhead 1997). In the absence of monogamy, as we will see, partnerships are temporary and the lifetime reproductive success of partners is no longer equal.

It is equally clear from Darwin's writings and in line with the general moral that he considered interactions between the sexes to be inherently good; an "aid to ordinary [natural] selection." By this we mean that events leading to mating, such as female choice of certain males or competition among males for access to females, work hand in hand with natural selection to improve the adaptedness of the lineage: "Just as man can improve the breeds of his game-cocks by the selection of those birds which are victorious in the cockpit, so it appears that the strongest and most vigorous males, or those provided with the best weapons, have prevailed under nature, and have led to the improvement of the natural breed or species." Darwin's own theories were likely influenced by the writings of his grandfather Erasmus Darwin. In his book *Zoonomia* (1794), he argued that the "purpose" of reproductive competition is to improve the species. "The final cause of this contest amongst the males seems to be that the strongest and most active animal should propagate the species, which should thence become improved."

This heritage is echoed in two prevalent ideas in modern evolutionary biology, which both ascribe similar utility to reproductive interactions. One concerns the hypothesis that male secondary sexual traits used in reproductive competition are "honest indicators" of male genetic quality, which enable females to select the males with the "best" genes as fathers for their offspring (Zahavi 1975). The other poses that male sexual traits function to "preserve the species," i.e., by allowing species recognition and hybridization avoidance (Mayr 1940, Lack 1968), and the linked belief among ethologists in the 1950s and 1960s that male courtship functions to allow the female to choose a male of the correct species and strengthen conspecific pair bonds.

Theoretical analyses of the consequences of male-female coevolutionary interactions confirm, in some cases, Darwin's assertion that sexual selection works in lockstep with natural selection to increase population fitness (e.g., Siller 2001, Agrawal 2001, Lorch et al. 2003). But, in other cases, the opposite is true; the outcome of coevolution between the sexes is to decrease the fitness of populations (Lande 1981, Gavrilets et al. 2001, Kokko and Brooks 2003). Yet this latter result has not been widely acknowledged. Perhaps it is simply

that evolutionary change is just thought of as an inherently good thing! This underlying belief has sometimes been obvious to us when describing our own work on water striders to the public and some colleagues. In these species males grasp females without prior courtship and females struggle vigorously to get rid of males. Male mating attempts can be accounted for by selection to fertilize more eggs, and female resistance of these repeated male mating attempts can be accounted for because they are both superfluous and costly (e.g., Rowe et al. 1994, Arnqvist 1997a). Our studies suggest that both sexes have accumulated antagonistic adaptations, in a form of coevolutionary "arms race," that further their interests but at the same time are costly. The idea that mating interactions might cause the evolution of decreased fitness in a population has been particularly difficult for people to entertain, public and scholars alike, and has sometimes even been considered antiadaptationist.

The understanding among many biologists of male-female interactions has, nevertheless, changed over the last two decades. The view of reproduction as an exclusively cooperative endeavor has been challenged by the realization that the mates' interests in any interaction are often conflicting. Tracing the history of this shift is not easy. Although a few early contributions hinted at sexual conflict (e.g., Wickler 1968), the major players certainly include Robert Trivers, Richard Dawkins, and Geoff Parker. Robert Trivers (1972) was the first to provide a compelling evolutionary discussion of differences between the evolutionary interests of the sexes and the implications this might have for the evolution of parental care in particular. Richard Dawkins put the idea of sexual conflict before a wide audience—most notably in a book chapter entitled "Battle of the Sexes" in his widely read 1976 book *The Selfish Gene*, but also in a few other early contributions (e.g., Dawkins and Krebs 1978, 1979).

There is, however, no doubt that the most thorough discussion of the role of sexual conflict in the evolution of the sexes was a contribution by Geoff Parker, which was unfortunately published in a little-known book (Parker 1979). Although Parker (1979) made "no claim to originality for the suggestion that this asymmetry [in the relative interests of the sexes] can occur commonly in animals," certainly he contributed more than anyone else to the introduction and subsequent development of the field. This material was first drafted several years prior to its publication, and Parker's ideas likely influenced many other early thinkers in the field. Most ideas expressed by Parker (1979) were much ahead of their time. His landmark paper remains arguably underutilized, although it has recently begun to draw the attention it deserves (figure 1.1). Parker has continued to build the field with a steady flow of influential contributions regarding conflict in his model system, dungflies, and more generally with new theory (see the list of references). During the 1980s, the concept of sexual conflict was given some attention in the theoretical literature, but empir-

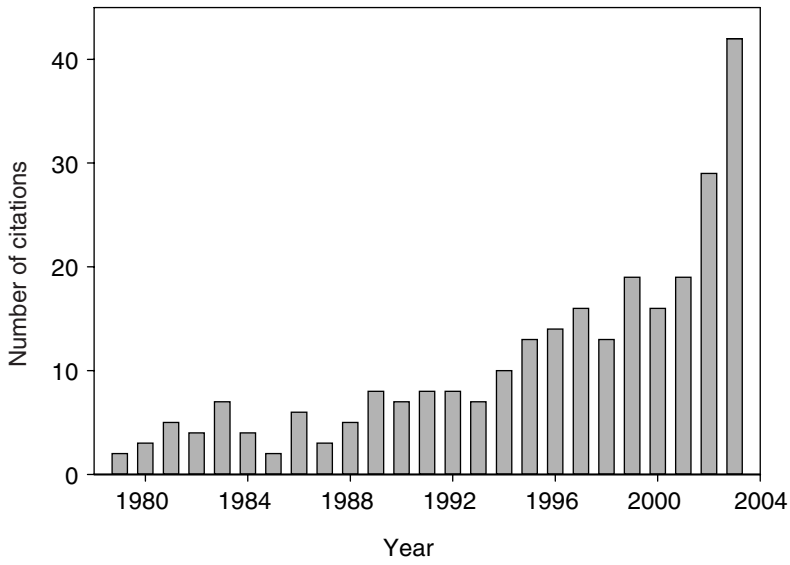

Figure 1.1. Interest in sexual conflict, and the resulting evolutionary processes, increased substantially during the mid-1990s. This point is illustrated by the number of citations/year of the classic paper by Parker (1979) that have appeared in the scientific literature since its publication. This landmark book chapter by Parker was much ahead of its time—few can hope that the citation rate of any of their contributions will continue increasing some 25 years after publication.

ical work on conflict and its consequences remained very rare. It was not until the 1990s that research on sexual conflict hit the mainstream of research in ecology and evolution, and interest has since increased dramatically. Why this sudden increase in attention?

We believe that several more or less coinciding factors have contributed to the almost explosive growth of the field. Students of animal behavior began focusing on females as active participants in coevolutionary interactions with males (e.g., Hrdy 1981, Kirkpatrick 1987a,b, Ahnesjö et al. 1993, Eberhard 1996, Gowaty 1997a, 2003, Zuk 2002). This fact may have resulted in part from philosophical shifts in thinking brought about by the feminist movement. The focus on the selective forces acting upon females in their interactions with males revealed that selection was often sexually antagonistic. Comprehensive data illustrating this point in dungflies were collected by Parker in the late 1960s (Parker 1970a,b) and began accumulating for a few other model organisms (e.g., Alatalo et al. 1981, Rowe et al. 1994, Clutton-Brock and Parker 1995). The work by Linda Partridge and coworkers on fruit flies, demonstrating male-imposed costs of mating for females, was particularly influential (e.g., Partridge et al. 1986, 1987, Fowler and Partridge 1989, Chapman et

al. 1995). Despite the accumulating evidence, studies remained relatively rare, and most centered on insect behavior. One notable exception was a laboratory experimental evolution study of sexual conflict in flies (Rice 1996b).

This situation changed noticeably with the publication of a perspective by Brett Holland and Bill Rice in 1998. In this paper, they persuasively laid out the case for sexually antagonistic coevolution and did so with examples from favored taxa for studies of sexual interactions, such as birds and fishes. This paper certainly brought the evolutionary potential of sexual conflict to a much wider audience. Since then, the scope of study has increased not just taxonomically, but also in level of analysis. Molecular studies showing positive selection on, and rapid evolution of, reproductive proteins are now being interpreted as evidence of sexual conflict (see Chapman 2001, Swanson and Vacquier 2002). New theory suggests that sexual conflict has profound implications for the evolution of reproductive isolation and speciation itself (Rice 1998a, Parker and Partridge 1998). These facts reinforce the view that sexual conflict may be playing a central role in evolution within and between species. Today, the field is still rapidly expanding and filled with lively debate (Zeh and Zeh 2003). Hopefully, these accumulating data and debates will enrich our understanding of the biology of male-female interactions, and the evolution of the sexes themselves.

1.2 Sexually Antagonistic Selection and Sexual Conflict

The evolutionary interests of any two individuals are rarely, if ever, identical. This must be true, simply because they do not share the same alleles for all loci, with the possible exception of clones. Where alleles at a locus differ, there will be competition among them. Therefore, the evolutionary interests of any two individuals have the potential to conflict, even if they share much of the same genome. When two unrelated individuals of the two sexes meet to engage in sexual reproduction, conflict intensifies: while one individual needs the other to spread its genes, this dependence may be asymmetric. Further, although both have a shared interest in any mutual offspring, they usually have divergent interests in many aspects of the "economics" of reproduction. Defined as a conflict between the evolutionary interests of individuals of the two sexes (Parker 1979), sexual conflict becomes exacerbated because selection will often be tugging in different directions in the two sexes. Sexually antagonistic selection is symptomatic of sexual conflict. We expect sexually antagonistic selection to be common simply because the "roles" of the sexes in reproduction differ (Clutton-Brock 1991, Andersson 1994), and sexual conflict should be a general feature in the evolution of the two sexes.

Conflict between coreproducing individuals occurs also in isogamous species (gametes of equal size), because increased investment by one partner per-

mits decreased investment by the other. In fact, there are good reasons to believe that "primordial" reproductive conflict in isogamous taxa has led to the evolution of anisogamy, and consequently the sexes (see Parker et al. 1972, Parker 1979, 1984, Bulmer and Parker 2002). Because males and females, by definition, produce gametes of different size (anisogamy), they typically maximize their reproductive success in more or less different ways. A classic example of this is the fact that, over much of the natural range of mating frequencies, the number of offspring produced generally increases monotonically with the number of mates in males but not in females (Bateman 1948). When this is so, there is selection favoring increased mating frequency in males, but not females. The fact that the sexes thus "play" very different roles during reproduction then sets the scene for differences in physiology, morphology, and behavior between males and females. This fact also means that the attributes or trait values favored in one sex are often not those favored in the other. Consequently, there will be sexually antagonistic selection on these traits. As such, some degree of sexual conflict will be ubiquitous in sexually reproducing taxa (Trivers 1972, Parker 1979, Lessels 1999).

The effects of sexually antagonistic selection at the genetic level can be described as intra- or interlocus conflict, depending on whether the target of selection is determined by alleles at one locus expressed in both sexes, or alleles at different interacting loci in the two sexes (Parker and Partridge 1998).

1.2.1 Intralocus Sexual Conflict

Whenever selection favors different values for a phenotypic trait in males than in females, there is the potential for *intralocus sexual conflict*. For example, we could imagine that selection for elongated tails in males of some songbird occurs because females prefer to mate with males possessing long tails. We might then expect males with longer tails to be favored, even if there is some cost to efficient flight. In females, on the other hand, selection favors some intermediate tail length that maximizes flight efficiency (assuming that males are indifferent to female tail length when choosing a mate). In this case, optimal tail length depends upon which sex is assessed. If genes at the same locus (or loci) determine tail length in both sexes, then different alleles at that locus will be favored in females than in males. If expression of a given allele at that locus moves one sex toward its tail length optimum, the same allele expressed in the other sex will move that sex away from its tail length optimum. Alleles at the tail length locus are then under sexually antagonistic selection, and there is intralocus sexual conflict. Intralocus conflict will appear in all those cases where the direction of selection at a given allele depends upon in which sex it resides (i.e., whenever there is a sex x genotype interaction for fitness).

Intralocus conflict has great potential to limit adaptive evolution in both sexes. Because the sexes largely share the same genome (excluding sex chromosomes), and genes at many loci are being pulled in opposite directions by antagonistic selection in the two sexes, selection in one sex will impede adaptive evolution in the other (Rice 1984, Halliday and Arnold 1987, Lande 1987, Parker and Partridge 1998, Rice and Chippindale 2001). In the most general case, neither sex will be able to reach its adaptive peak during these evolutionary tugs-of-war. The resulting average phenotype will represent some evolutionary "compromise" between the evolutionary interests of the two sexes. However, males and females of most species do look and behave differently, they are sexually dimorphic, and this fact demonstrates that the constraint of sharing much of the same genome is not absolute. The evolution of sex-limited gene expression is one way out of the bind (Rice 1984), because it permits independent evolution in the two sexes toward their phenotypic fitness optima.

Although intralocus sexual conflict is potentially common and consequential, its evolutionary importance is debated. On the one hand, one could argue that the optimal phenotype in males and females should be different for virtually every conceivable phenotypic trait. On the other hand, one could argue that sexual dimorphism will evolve relatively rapidly and easily under selection for sex-limited expression of genes, implying that intralocus conflicts will at most have only transient effects on evolutionary dynamics. Thus, our view of the potential evolutionary significance of intralocus conflicts depends on the importance we place on evolutionary constraints in general. Some theory suggests that the evolution of sex-limited expression of sexually antagonistic genes may be slow (Lande 1980, 1987), but debate continues (see, e.g., Badyaev 2002 vs. Lindenfors 2002 for contrasting views on the evolution of sexual size dimorpism).

There is growing empirical evidence suggesting that intralocus sexual conflict may be persistent. Several studies have documented sexually antagonistic selection on traits in a variety of species (e.g., Price and Burley 1994, Merilä et al. 1997, Björklund and Senar 2001) (figure 1.2). Likewise, some laboratory studies have found genotype by sex interactions for adult fitness components (e.g., Vieira et al. 2000, Mackay 2002), and Chippindale and coworkers have provided strong evidence for intralocus conflict in laboratory stocks of the fly *Drososophila melanogaster* (Chippindale et al. 2001, Gibson et al. 2002). These authors used genetic techniques to assay the effect of sets of alleles on the fitness of males and females that otherwise shared the same genotype. When assayed in larvae, before the sexes look or behave differently, sets of alleles that increased fitness in one sex usually increased fitness in the other; good alleles were good whichever sex they were expressed in. However, when assayed in adults, when the sexes look and behave differently, sets of alleles that increased fitness in one sex generally decreased fitness in the other (figure

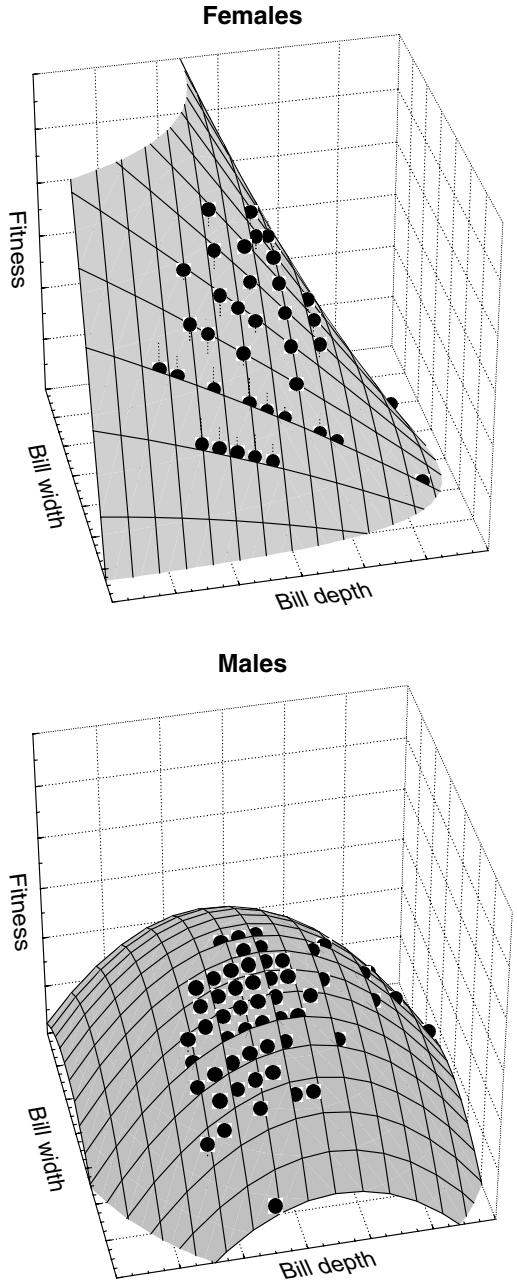

Figure 1.2. Survival selection on bill morphology differs between the sexes in a natural population of the serin (*Serinus serinus*), a carduline finch, presumably as a result of differences in food utilization between males and females. Selection on bill depth and width is directional in females but stabilizing in males. (Reprinted from Björklund and Senar 2001, with permission from Blackwell Publishing Ltd.)

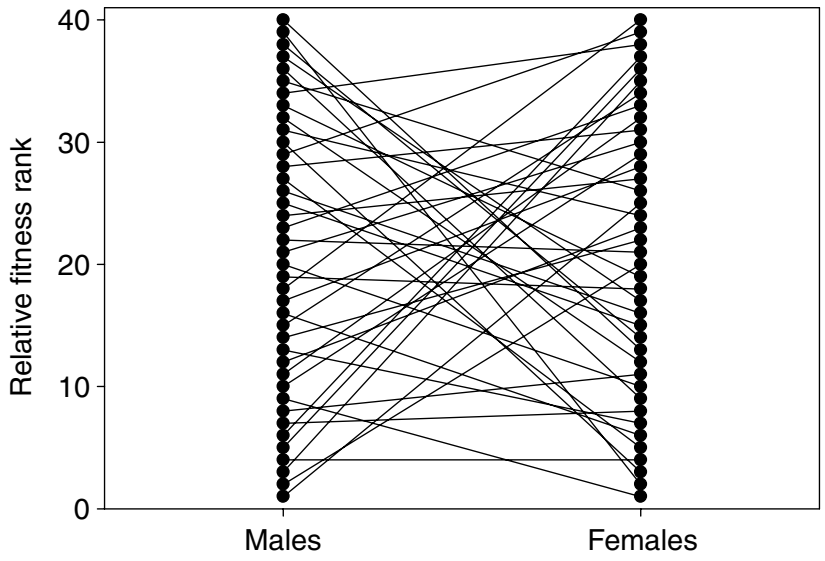

Figure 1.3. Plot of male and female adult fitness in a suite of discrete *Drosophila melanogaster* haplotypes. Note that these haplotypes tend to have opposing effect on fitness in the two sexes: haplotypes that result in high fitness in males tend to result in low fitness in females. These data demonstrate that, for at least some genes in this species, their effect on the fitness of males and females is antagonistic. (Reprinted from Chippindale et al. 2001, with permission from the National Academy of Sciences.)

1.3). These data demonstrate that there is substantial sexually antagonistic selection on these loci, and hence intralocus sexual conflict. At the moment, however, it is very difficult to evaluate how general or important intralocus sexual conflict might be, largely because of a paucity of relevant empirical studies. For this reason, we will refer to intralocus sexual conflicts to only a limited extent in this book.

1.2.2 Interlocus Sexual Conflict

Whenever there is conflict over the outcome of male-female interactions, such that the optimal outcome is different for the average male and female, there is the potential for *interlocus sexual conflict*. Conflict can occur over any interaction between the sexes, including mating rate, fertilization efficiency, relative parental effort, remating behavior, and female reproductive rate. For example, imagine that there is selection for higher mating rate in males, and selection for lower mating rate in females. If mating rate is determined at the same locus, then intralocus conflict will result (Halliday and Arnold 1987). If, however, mating rate is instead determined by an interaction between a locus A expressed in males and a locus B expressed in females, the result will be very

different. Alleles that are favored at locus A are those that increase the mating rate of their male bearers, and these will, therefore, spread in the population. These alleles, and their consequences for the phenotype, are adaptive for males (they increase male mating rate), but at the same time they are detrimental to females (they increase female mating rate). Consequently, their spread exerts selection at locus B for alleles that effect a decrease in female mating rate. Spread of such alleles at locus B can then affect selection among alleles at locus A. You can see that this intersexual interlocus conflict may be continuous and thereby affect a continuous stream of allelic replacement at one or many interacting loci in both females and males (see Rice and Holland 1997). Interlocus conflict is thus mediated by interactions between different loci in the two sexes and is of great interest because of its potentially central role in male-female coevolution.

When there is conflict over the outcome of any interaction between males and females, we expect intersexual interlocus conflict to result in suites of interacting and sexually antagonistic adaptations, in both sexes, that function to bias the outcome of interactions toward the evolutionary interest of their bearer (Parker 1979, Rowe et al. 1994, Rice and Holland 1997, Gavrilets et al. 2001). Parker's early work (e.g., Parker 1979, 1983a) suggested that interlocus sexual conflict should lead to complex, dynamic, and even unresolvable evolutionary chases between the sexes, and more recent theory has confirmed this. The predicted result is a coevolutionary "arms race" between the sexes, known as sexually antagonistic coevolution (figure 1.4). During these coevolutionary episodes, one set of traits in males (persistence adaptations) interacts with a different set of traits in females (resistance adaptations) in determining the outcome of a given interaction.

It is this sexually antagonistic coevolution that makes interlocus conflicts a particularly interesting field of study with important potential ramifications for diverse topics, including the evolution of gamete interactions, mate choice, social interactions, genomic imprinting, parental care, sexual dimorphism, and speciation. This book is primarily about this form of sexual conflict.

1.3 Aims and Scope

In this book we aim to illustrate the wide diversity of adaptations in both sexes that we believe are related to sexual conflict. The bulk of this book is then a series of chapters dealing with the major components of male-female interactions. These chapters highlight the ways in which the interests of the sexes differ in an interaction, and the adaptations in both sexes that have resulted from this conflict. For each component of male-female interaction, we discuss examples that we believe are particularly compelling, illuminating, or otherwise interesting. Our hope is that this survey of the natural history of sexual

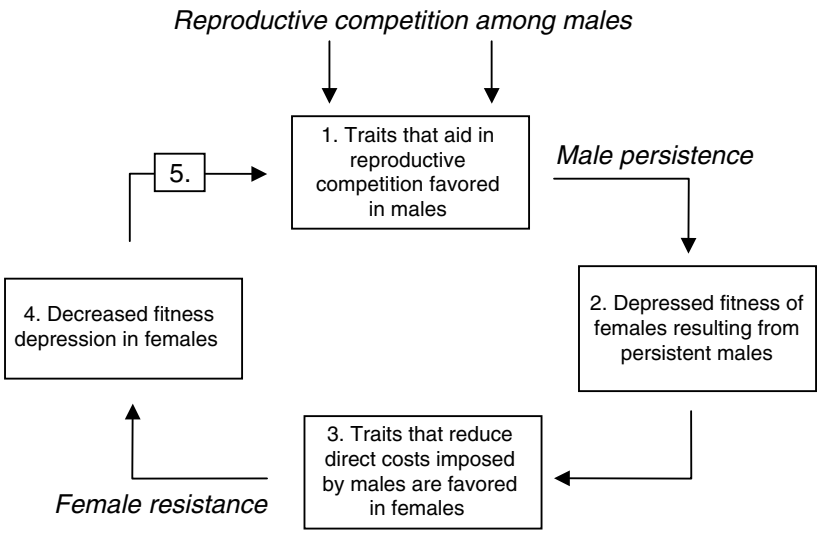

Figure 1.4. Interlocus sexual conflict can result in perpetual cyclical or escalating coevolution of reproductive traits in the two sexes, in a process known as sexually antagonistic coevolution. This process is generally seen as being driven by reproductive competition among males, by male-male interference and/or exploitation competition, simply because males have a higher potential reproductive rate in most taxa. Selection thus continually probes males for new mutations that are beneficial to their bearers in this competition (1). A subset of novel male adaptations will depress fitness in females that interact with the bearers of these adaptations (2). Such traits are referred to as male persistence adaptations. The spread of male persistence adaptations will result in selection among females to reduce the direct costs imposed by persistent males (3). Female traits, or alleles, that in any way reduce such costs are referred to as female resistance (4). The evolution of female resistance adaptations may then feed back and change the strength or form of competition among males (5), causing selection for altered persistence.

conflict will convince readers that sexually antagonistic coevolution may be, or has been, involved in the evolution of a great variety of these traits that distinguish the sexes.

A second aim is to set sexually antagonistic coevolution into the well-established theoretical framework of coevolution between the sexes. There has been a great burst of empirical research into sexual conflict in the last decade. Yet, as in any young and rapidly expanding field, there is a risk that collection and interpretation of data gets beyond the development of a solid theoretical foundation. At present, there is considerable variation in how these new data are being interpreted with respect to competing theories of coevolution between the sexes. Documenting coevolution between the sexes has been relatively straightforward, but distinguishing among alternative mechanisms that may be responsible for this coevolution has been much more difficult. For example, there is still little consensus among students of sexual selection about

the extent to which females choose mates on the basis of the vigor their offspring will have or the sexiness of their sons, despite more than two decades of intense research (Kirkpatrick and Ryan 1991, Andersson 1994, Kokko et al. 2003). Addition of a new mechanism, sexually antagonistic coevolution, certainly does not make this task any easier. Yet we hope that by providing evidence for sexually antagonistic coevolution in nature and setting this newer idea within the established framework of sexual selection, some progress can be made.

Finally, in this emerging field, conceptual ambiguities and inconsistent terminology are holding back progress. Ambiguities include finer distinctions (e.g., what is indirect selection?) but also extend to the core of the field (e.g., what is sexual conflict?). Much of the ambiguity results from the distinct lexicons and conceptual backgrounds of contributing scientists. We hope to bring this field a bit forward by being more precise in discussing concepts, or at least by identifying concepts that remain fuzzy.

We first review the development of the theories of sexual selection and sexual conflict, and attempt to integrate them (chapter 2). This chapter necessarily assumes some background in evolutionary biology, and consequently will be of more interest to students of evolutionary biology than to the general reader. The next four chapters constitute the natural history of conflict in male-female interactions among animals. These interactions are broken into those occurring between individuals prior to mating (chapter 3) and those occurring after mating (chapters 4 and 5). In chapter 6, we discuss a series of interesting issues that fall somewhat outside the three previous chapters. For example, we discuss conflict in hermaphrodites and in plants, and the consequences of conflict for divergence of lineages. Finally, in chapter 7 we discuss some ambiguities that have arisen as a consequence of the rapid growth of this field, and the merging of concepts and terminology from game theory, evolutionary genetics, and behavioral ecology.

It is not our intention to present a complete treatise on sexual conflict, an endeavor that is probably better left for a time when the field has matured. We have also emphasized some aspects over others (e.g., interlocus over intralocus conflict), in part because these are richer in examples, but also, admittedly, because of our own research interests. If our presentation comes across as being biased, speculative, and/or promotional at times, it is because our aim is to make the case for the ubiquity of sexual conflict rather than provide a balanced review of all aspects of male-female coevolution. We hope to encourage many readers to think in novel ways about those interactions involved in reproduction.