2

What Sociobiologists Study

What Is the Purpose of Behavior?

When a male tarantula hawk spends hours every day of its short adult life perching alertly on a palo verde tree, ever ready to dash out to meet intruders and challenge them to an elaborate aerial contest, the obvious question is, Why? What's the point? As noted earlier, sociobiologists find this kind of question intriguing. They wish to understand why organisms like the tarantula hawk come equipped with special attributes that seem designed to achieve particular social goals. What makes the tarantula hawk male especially interesting is the obvious costliness of its actions, the clear survival *disadvantages* associated with its particular brand of social behavior. Males spend hours and hours on their territories, and yet they almost never encounter females. By the end of a couple of weeks, the males' wings are faded and worn from the wear and tear of their repeated flights out and back to their perches. In two more weeks, if they survive even that long, the wasps are barely able to fly. Why do it this way? What reproductive benefits come from territorial possession that might counterbalance the costs to survival that come with (defending) the territory?

Or take the readiness of female red-winged blackbirds (fig. 2.1) to slip away from their primary partner in order to mate with another male, often one on a neighboring territory [159]. It is not as if the female's main mate has failed to provide her with a suitable nesting site and sufficient sperm, yet off she goes, spending time and energy to secure surreptitious "extra-pair" copulations. In fact, although birds were once believed to be paragons of monogamy, it turns out that paired males and females in many "monogamous" species regularly mate with several individuals in the course of a single breeding season. The central question for the sociobiologist is, Why do pair-bonded females (and males) make time for these extra matings, when they could be doing other useful things, like nest building or foraging for food, thereby avoiding the downside of their extracurricular sexual activities [252]?

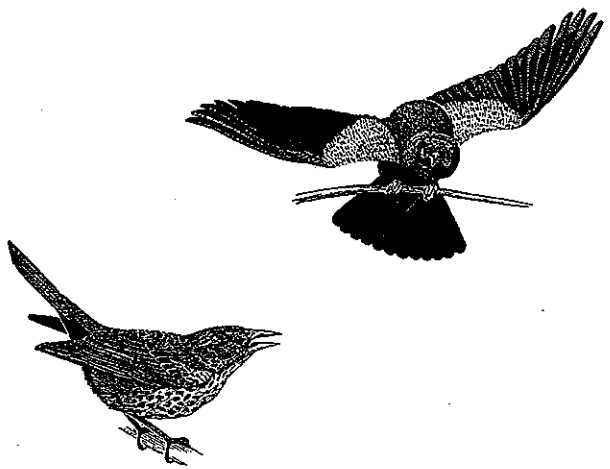

Figure 2.1. A female red-winged blackbird soliciting a copulation from a displaying male. This species is merely one of many songbirds now known to engage in extra-pair copulations with individuals other than their social partner with whom they share a territory and a long-term relationship. Based on a drawing by Gene Christman.

A biologist with an interest in the proximate causes of behavior might try to explain the female blackbird's readiness to engage in extra-pair copulations in terms of her hormonal condition or her physiological response to the songs of various males around her. But sociobiologists try to explain what's going on in terms of how females actually improve their chances of leaving surviving descendants by "cheating" on their partner, even though the behavior has its negative aspects, its *fitness costs*. (In the jargon of sociobiology, *fitness* does not mean muscular strength or stamina but instead refers to an individual's reproductive success as measured by the number of surviving offspring that it produces in a lifetime, or its genetic success as measured by the number of copies of its genes that the individual manages to contribute to the next generation.)

The demonstration that the fitness benefits of extra-pair copulations generally outweigh their fitness costs for today's female red-winged blackbirds would help explain the behavior in ultimate, evolutionary terms. If it could be shown, for example, that the several sexual partners of a nonmonogamous female blackbird tend to provide her offspring with extra food or extra protection from predators, then it could be more plausibly argued that females in the past with the same roving sexual tendencies may have left more descendants, and more of their genes, than others of their species. If so, past differences in sexual fidelity would have shaped the course of evolution in the species.

In addition, if it could be demonstrated that female red-winged blackbirds freely

chose to mate with males potentially able to provide them with useful resources while resisting copulation with other males unable or unlikely to be helpful, there would be another line of evidence that female mating decisions had evolved by natural selection.

On Anthropomorphism

Incidentally, some critics of sociobiology wax indignant if birds are spoken of as being unfaithful or male scorpionflies as raping female scorpionflies (which they sometimes do, by the way). These critics speak sternly of the uniqueness of human behavior and the errors of anthropomorphism, among which is the attribution of human desires to organisms other than ourselves. For example, Derek Bickerton complains, "When a bird practices what zoologists call 'extra-pair copulation,' can we really call this adultery? . . . The intent of the two activities is completely different. Those [birds] who engage in extra-pair copulation usually aim to make babies; adulterers usually try to avoid them" [255].

According to Bickerton, unless blackbirds can be demonstrated to have the same *intentions* or desires as humans, the behavior of the two species should not be given the same label. Embedded in Bickerton's complaint are two major misconceptions: (1) that behavioral biologists regularly commit the sin of anthropomorphism and (2) that to behave adaptively, an individual must have a conscious wish to increase its production of offspring [255].

James Lloyd years ago had something pertinent to say about the charge of sinful anthropomorphism, when he wrote,

> Teleology and anthropomorphism appear rife [in sociobiology]. Bees not only have sisters, cousins and nieces, but crickets and digger wasps have strategies, a bug demands, like some errant macho Californian, proof of his fatherhood before paying out paternity benefits, and rapists and transvestites are described from the Mecoptera. . . . [However] this is but time- and space-saving shorthand, and fun. In the recent past, avoidance of such mild (but technically extravagant) expression has been a fetish in biology. . . . [But] misunderstanding resulting from the present laxity is among the least of [our] worries. What harm is done if I speak of a firefly thinking, or blowing his little mind? If a reader can't translate, and tell from the text what the long story is, then the problem is not one of diction, and it runs too deeply to be bridged in an extra sentence or word substitution. (p. 3 in [206])

Lloyd is saying that the sociobiologist is focused on "the long story," the evolutionary basis of the trait of interest, not the proximate cause per se. Truly egregious anthropomorphism occurs when a person attributes human motivation to

another animal species without realizing that the underlying mechanisms of behavior may well be different for this other species. But as noted previously, when a sociobiologist speaks of a mecopteran rapist or a territorial wasp or a cheating blackbird, it is not to explore the proximate basis for the behavior but to examine its functional (ultimate) consequences. Thus, the territoriality of a tarantula hawk wasp, a white-crowned sparrow, and a human homeowner may have very different proximate bases but in these and other territorial species, individuals may gain genetic success by investing in defense of a useful resource. The word "territoriality" conveys this point nicely without requiring the introduction of new technical jargon for each species.

Of course, one can make finer-grained distinctions between the territorial responses of man and beast, if it is helpful to do so. But references to territoriality in any of a wide range of organisms, are readily understandable, if not to someone who chooses to be perversely pedantic. Likewise, the word "infidelity" is widely understood to include copulations that one member of a pair engages in outside the pair-bond to the possible reproductive detriment of his or her partner. Let's agree not to invent thousands of new labels to be applied one by one to the behavioral traits of each and every species, surely a waste of time. Instead, let's agree that terms such as territoriality, infidelity, rape, and the like are used sociobiologically to refer to functionally similar kinds of behavior in different species without any inferences about the nature of the physiological or psychological mechanisms that control these actions. Readers of sociobiology can also, if they wish, mentally substitute less emotionally charged words for any they find upsetting, as in "forced copulation" for "rape" or "multiple mating" for "infidelity." No loss of meaning would result.

The second misunderstanding encapsulated in Bickerton's complaint—that adaptive behavior requires a proximate drive to behave adaptively—appears often in criticisms of sociobiological research. Here is Michael Rose to illustrate what I mean: "Finally, there is the fundamental problem that, if most people calculate Darwinian plans of action, they certainly aren't aware of it introspectively. Net Darwinian fitness doesn't figure in the great lyric poems, or even in the treatises of political philosophers . . . In total, it would be astonishing if a theory of human nature based on universal, self-conscious, Darwinian motivation should turn out to be correct" [268].

Indeed it would. However, contrary to Rose, neither sociobiology nor evolutionary psychology requires that humans be any more self-consciously desirous of achieving personal genetic success than are red-winged blackbirds. Rose assumes that our proximate mechanisms must provide us with an awareness of the ultimate consequences of our actions if we are to act in ways that will advance the success of our genes. However, animals, ourselves included, need not be alert to the ultimate evolutionary consequences of one's desires in order to behave in ways that

tend to increase the production of offspring. When a blackbird pursues a dragonfly with evident enthusiasm or when a human smacks his lips at the sight of a large hamburger on the barbecue grill, we can be certain that neither individual is motivated to consume these calorie-rich items by a proximate desire to advance his reproductive success. However, variation among blackbirds or humans in the past in their desire to consume high-calorie foods almost certainly had reproductive consequences, thereby affecting the evolution of the proximate food preferences currently present today in these species.

Likewise, a female red-winged blackbird that copulates with a male on a neighboring territory does not have to *want* to advance her fitness in order to behave in ways that have exactly that effect. The proximate mechanisms controlling her behavior doubtless include a host of things, including assorted hormones and neuronal circuits involved in the analysis of the visual or acoustic attributes of male blackbirds. This internal machinery evidently motivates some females under some circumstances to seek out partners other than the males with whom they have pair-bonded. The consequences, intended or otherwise, of these extra-pair copulations are the occasional fertilization of a female's eggs by a male other than her primary partner. The ultimate effects of these fertilizations will determine the success of the female in leaving copies of her genes to subsequent generations relative to other females of her species.

Human adulterers, past and present, have also almost certainly been motivated by a variety of proximate desires, none of which need be at all similar to the "adultery" mechanisms in blackbirds. Nor is there any requirement or likelihood that adulterous humans in the past have been motivated by a desire to make copies of their genes. This point is not grasped by William Kimler when he criticizes the sociobiological claim that adulterous women have sometimes raised their genetic success by cuckolding a social partner on the grounds that the "female cuckold [might] be seeking emotional satisfaction denied by a resource-providing mate, rather than a simple genetic benefit" [185].

The real point is that as an outcome of their proximate desires, which have not been consciously focused on genetic matters, some women who duped a social partner into caring for another man's offspring may have had more surviving children or grandchildren than they would have had otherwise. If women have differed in the past in their hereditary tendency to seek out extra-pair copulations, for whatever proximate reason, and if these differences affected the genetic success of individuals, then evolution by natural selection occurred in the past. The process may well have shaped such things as the desire of married women for "emotional satisfaction" provided by a husband. Even though the proximate mechanisms underlying the sexual behavior of birds and humans are most assuredly not the same, if we define adultery *in evolutionary terms* as behavior that potentially raises the genetic success of the extra-pair copulator at the expense of another individual, then

we can usefully apply the same term to bird and man. Understanding the difference between proximate and ultimate hypotheses, which are different but complementary to one another, can help us avoid the kind of confusion evident in Kimler's complaint about sociobiology.

Not All Evolutionary Biologists Are the Same

Returning to the main issue at hand, let me now point out that some evolutionary biologists explore questions that do *not* concern the evolved purpose of a trait. Thus, one school of evolutionary researchers attempts to trace the historical steps that converted an ancestral trait in a long extinct species into a modern characteristic of interest in a living species. So, for example, work proceeds on the evolutionary steps that occurred between an ancestral, now extinct species of insect absolutely incapable of flight and those modern species descended from it that possess extraordinarily complex neuronal and muscular flight machinery, which enable these species to fly in a most beautiful manner. Uncovering these steps is not an impossible challenge, and this kind of evolutionary research is full of interest and importance [220]. But it is not directed at the issues that motivate the typical sociobiologist.

The difference between the evolutionary biologists interested in historical reconstruction and those interested in adaptation is, to use an automotive analogy, similar to the difference between someone who wants to know when each innovation in engine design occurred as the Model-T engine was converted by degrees into the one present in today's Ford Escort and someone who wants to know whether the component parts of the modern Escort engine are functionally better than those in their predecessors and if so, precisely why.

Evolved Traits Need Not Help Preserve Species

If the exploration of adaptation in living things is the central goal of the orthodox sociobiologist, then it behooves us to make certain that we understand just what a naturally selected adaptation is and how it is produced. This task can be achieved in part by explaining what Darwinian adaptations are *not* designed to do, particularly because so many people believe incorrectly that traits evolve in order to help prevent the extinction of the species. Although evolutionary biologists have worked diligently for more than thirty years to explain why evolutionary processes have little or nothing to do with the promotion of the welfare and survival of the species as a whole, the idea has tremendous staying power with the general public, social scientists, journalists, and the producers of nature programs made for television.

For example, I read in the *New York Times* that timid and bold individuals can coexist within animal species because the existence of two alternative types "may allow adaptation to changing environments, favoring species survival" [144]. A different article, also appearing in the *Times* in 1998, explained that "natural selection favors whatever chance mutations will allow the species to change and survive" [259]. And had you read about sociobiology in the 1998 edition of the *Encarta Concise Encyclopedia*, you would have found the following: "In attempting to reconcile altruism with natural selection, Darwin foreshadowed the thesis later developed by sociobiologists: that the performer of the altruistic act, if forfeiting its own reproductive opportunity, nevertheless contributes to the survival of the species." Actually Darwin did nothing of the sort in his explanation of altruism and neither do today's sociobiologists, one of whom has since revised the *Encarta* entry on sociobiology; almost no behavioral biologist active today would give any of the hypotheses presented in this paragraph the time of day for reasons that will become apparent shortly.

In fact, overcoming the misconception that evolution's "goal" is to help species avoid extinction was the key development on the road to modern sociobiology. The journey down this road began in 1962 with the appearance of *Animal Dispersion in Relation to Social Behaviour* [354], which interprets almost every aspect of social behavior to be altruistic self-sacrifice that advances the welfare of the species. Thus, for example, the flights of starlings assembling at winter roosts are, according to Wynne-Edwards, displays that permit flock members to judge the size of the local population so that individuals can adjust their production of offspring accordingly, when the breeding season arrives. By reproducing less at times of high population density, the starlings supposedly act together to prevent destruction of the food base needed for their species' survival over the long haul. According to Wynne-Edwards, species that failed to develop population-regulating mechanisms of this sort went extinct relatively quickly while those that acquired these social devices tended to survive, which explained why they were around to be studied by twentieth-century scientists.

As a biology undergraduate in the mid-1960s, I read Wynne-Edwards with great enthusiasm as much for the sweeping panorama of natural history that he assembled in the service of his theory as for the theory itself, although I had no doubt that the theory was correct. His opening chapter presented an utterly compelling (as far as I was concerned) account of the human whaling industry to illustrate by analogy what happened to populations that failed to regulate their numbers properly. Wynne-Edwards noted that in the nineteenth century, the whaling fleet grew rapidly and the take of whales increased correspondingly. But as the pressure on whales steadily increased, the population of whalers failed to realize that by driving their prey toward extinction, they were pushing their own profession toward the same end. Instead of exhibiting restraint in exploiting the resource that supported them all, whalers tried to beat the competition to the remaining remnant populations of prey. Because whalers failed to limit their take, their prey did indeed be-

come scarcer and scarcer, until the whaling industry itself went belly up. By analogy, species that lacked an evolved mechanism for suppressing runaway population growth and overexploitation of vital food resources would march off the world stage, leaving the globe in possession of species whose members managed to act with foresight and reproductive restraint.

Wynne-Edwards was by no means the only biologist who had come to believe that evolution would produce adaptations beneficial to the species as a whole. But he did everyone a favor by systematically interpreting a great many behavioral traits as group benefitting and species preserving and thus forcing some other biologists to scrutinize the logic of his argument. Among these skeptics was George C. Williams, who wrote *Adaptation and Natural Selection* [339] in response to Wynne-Edwards and the many others who had accepted the thesis that characteristics helpful to the species would spread over time.

Williams forcefully presented the counterthesis that evolved adaptations, including behavioral ones, were extremely unlikely to promote the long-term survival of entire populations or species *at the expense of individual reproduction* [339]. To make his main point, Williams asked his readers to imagine what would happen in a population composed of reproductive altruists along with a few others that did not reduce their personal reproductive output to benefit their species in the long term. Imagine, for example, a population of starlings, some of whose members cut back the number of nestlings reared solely to keep the population below a species-threatening size. If, however, those individuals that held back on reproduction, conserving key resources for future generations, had fewer surviving offspring than those that did not exercise restraint, then the tendency to act altruistically would become rarer in the next generation. The trend toward the replacement of the group-benefitting altruists would be under way, leading eventually to their complete elimination as long as "reproductive maximizers" tended to leave more surviving offspring than the genetically distinctive "species preservers."

Or take the timid and bold personality types that appear in some animal species and that attracted the attention of the science writer for the *New York Times*. If the differences between the two personality types were hereditary, and if their behavioral differences caused one type to leave more surviving offspring on average than the other, then either timidity or boldness would eventually become the standard for the species—whether or not it would be good for the species as a whole to retain both variants in order to adapt to changing environments at some unspecified point in the future.

The logic of this kind of argument as presented by Williams convinced almost every evolutionary biologist active after 1966 that Darwinian natural selection based on unconscious but ruthless reproductive competition among *individuals*, not groups or species, would be more powerful than any other process in shaping the attributes of a species. Thus if Darwinian selection favored reproductive "selfishness" and

species benefit selection favored reproductive altruism, species benefit se... would be relatively impotent and reproductive altruism would disappear. Williams's commentary made it impossible to continue to think sloppily about these matters. Thereafter almost no professional biologist casually proposed explanations for traits in terms of their survival advantages to entire groups or species.

However, some other academics interested in human behavior continue to do so. Thus, "neofunctionalist" sociological theory presumes that "society" imposes its institutions on people in order to overcome the antisocial impulses of humanity, the better to promote cooperation and stability within the greater community [67]. Such a theory assumes that individuals will sacrifice their reproductive chances on behalf of the group to which they belong, provided they receive appropriate guidance. Just how the hereditary basis for truly self-sacrificing traits could be maintained in a species subject to natural selection is rarely addressed by these theorists, most of whom believe that they need say only that human behavior is learned in order to dismiss the need for an evolutionary explanation. But remember that proximate explanations do not substitute for ultimate ones. The capacity for enculturation in response to "societal pressures" surely requires a nervous system of a particular sort, and since nervous systems evolve by natural selection, we can be skeptical of any theory that simply assumes people can be *easily* induced to reduce their fitness *for the general good*.

For evolutionary biologists, any ultimate hypothesis has to pass a plausibility test. If you are going to argue that species benefit led to the evolution of a trait for reproductive self-sacrifice, you better be able to account for its persistence in a world in which reproductively selfish variants will inevitably appear in the species via mutation. This accounting is always a challenge and is only rarely achieved and then only under special conditions. Thanks to Williams, sociobiologists are well aware that natural selection theory predicts that individuals will rarely help other members of their species at genetic cost to themselves, even though the help might increase the smooth functioning of an entire society or the survival chances of the species as a whole. Darwin himself was fully aware of this point, writing that "if it could be proved that any part of the structure of any one species had been formed for the exclusive good of another species, it would annihilate my theory, for such could not have been produced through natural selection" (p. 189 in [88]).

Some evolutionists have continued to explore "group selection" of a more sophisticated sort than the species-benefiting selection proposed by Wynne-Edwards. David Sloan Wilson and Eliot Sober have been especially active in promoting the value of one modern form of group selection, which goes by the label of trait-group or multilevel selection [296, 342]. Indeed, Wilson and Sober are willing to claim that, because of multilevel selection, "at the behavioral level, it is likely that much of what people have evolved to do is *for the benefit of the group*" (their emphasis) (p. 194 in [296]), although they rarely specify precisely what behavioral trait(s) re-

quire multilevel selection if they are to evolve [321]. In addition, some other biologists firmly believe that the origin of modern bacteria and protists also required processes other than classical natural selection [221]. Readers are welcome to explore these matters with their proponents but I will not deal with "multilevel selection" or the evolution of symbiotic microorganisms for the following reason.

This is a book about what might be called orthodox sociobiology, not any of the several other subdisciplines within evolutionary biology. From 1975 to the present, the overwhelming majority of researchers exploring the adaptive value of social traits have employed the adaptationist or sociobiological perspective, which is founded on the premise that behavioral attributes (and their underlying mechanisms) evolve under the primary influence of natural selection acting on individual differences in genetic success. In contrast, relatively few researchers have employed multilevel selection theory in studies of social behavior under natural conditions [145]. Some of those who have done so have also noted that multilevel selection approaches are fundamentally the same as the standard methods based on assessing the relative genetic success of individuals [264]. As Reeve and Keller point out, "Multilevel selection approaches simply partition selection into different components (often into more components) than do classical individual selection models, and which approach is more useful depends on the theoretical aim" (p. S43 in [265]). None of the multiselectionists is attempting to revive the for-the-good-of-the-group selection of Wynne-Edwards. Given that multilevel selection theory is not widely employed and given its essential similarity to the so-called classical or standard approach, I will remain focused on the objections to orthodox sociobiology. After all, the controversy about sociobiology has been directed at adaptationists, not multilevel selectionists.

How to Identify Darwinian Puzzles Worth Solving

Once my undergraduate adviser, Lincoln Brower, managed to convince me that Williams had it right, I too became an adaptationist interested in how individuals might gain genetic success from their behavioral attributes. I accepted Williams's conclusion that natural selection is incapable of taking a long-term view because "it" is not a prescient being but a blind process in which the genetic effects of individual differences in reproductive success add up in the here and now. And then the process repeats itself again, and again, one generation at a time. In place of the notion that what was good for the species would evolve, I and almost all other biologists of my time recognized that what helped individuals leave more surviving offspring or more copies of their genes should become more and more prevalent in all species. This is a theoretical perspective, and like all useful theories, it shapes the expectations of observers in productive ways, so that they can first

identify the surprising features of nature and then develop testable hypotheses to account for these surprises. Someone who understands Darwinian theory is *prepared* to be puzzled by certain things, not others. Someone who, in contrast, believes that group benefit selection may have shaped the evolution of living things will be taken aback by different things and will develop different explanations for these phenomena.

In the era before *Adaptation and Natural Selection*, many biologists operating under a loose kind of species-benefit selection theory did not consider reproductive restraint and self-sacrifice all that surprising. Instead, they believed that these attributes were the expected products of selection among species in the past, leaving in place those species whose members worked for the collective good. Wynne-Edwards gave this approach its formal expression. Williams demolished it.

For the Darwinian biologist, for the sociobiologist, traits that appear to reduce the reproductive chances or genetic success of individuals are inherently surprising, not the kind of thing that "should" have evolved, and very much deserving of investigation. It is the gift of theory that helps us realize what needs explanation. Both Darwin, and later W. D. Hamilton, recognized the importance of explaining the extreme reproductive self-sacrifice of the sterile workers in an ant colony or social wasp nest (fig. 2.2). Indeed, anything that appears to reduce an individual's chances of reproducing successfully, even by a very small degree, becomes by definition a Darwinian puzzle. The social aggregations of those whirligig beetles that we mentioned earlier provide an ultimate problem worth investigating only when one realizes that beetles probably pay a reproductive price of some sort when they cluster in groups (see fig. 1.2, p. 11). For example, males in these groups may interfere with each other's attempts to secure mates. Or beetles, male and female, in large groups may compete more intensely for food, perhaps consuming less than beetles in smaller groups that do not have to outrace so many others to the edible items floating downstream. Beetles that get less to eat may reproduce less well as a result. Finally, large groups may also be more conspicuous to predators than are small aggregations or solitary beetles; group members that are killed by predators attracted to large bands obviously cannot reproduce.

As it turns out, the attack rate on groups of different sizes held in laboratory setting does increase for larger bands of whirligig beetles (fig. 2.3), demonstrating that getting together in nature probably carries a cost for these insects. On the other hand, in the lab experiment, the increased number of attacks on the large groups did not rise as rapidly as group numbers increased, and therefore the risk of attack *per individual* was lower for beetles surrounded by relatively many companions. If this result applies to beetles whirling about on real streams, then highly social individuals are generally safer than solitary beetles or those that prefer to associate in small aggregations. Thus, the disadvantages of living together are actually less

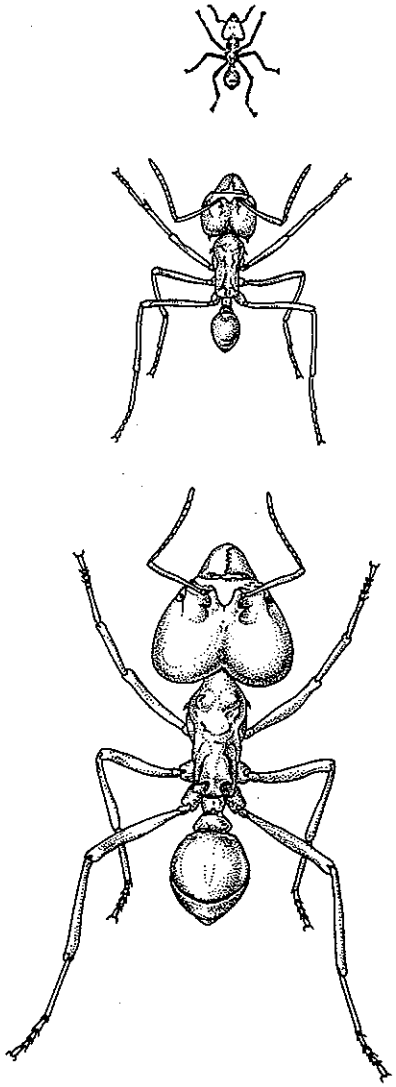

Figure 2.2. The sterile workers of some ant colonies come in a spectacular array of different sizes, with each worker type specializing in a different form of service to the colony, which they perform without ever reproducing personally. From [243].

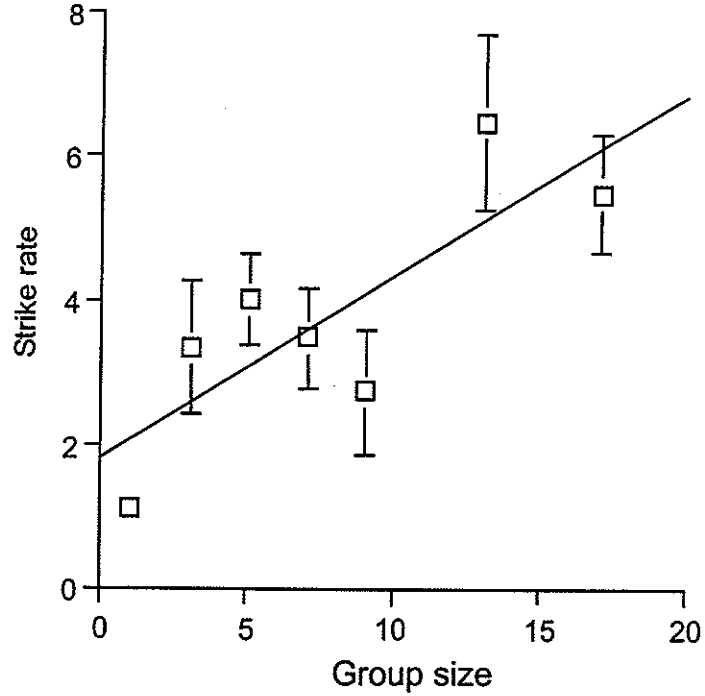

Figure 2.3. A genetic cost of sociality. Large groups of whirligigs were more frequently attacked than smaller aggregations when the beetles were experimentally held in laboratory aquaria stocked with fish predators. From [330].

than one might have guessed in this case, which helps explain why whirligig beetles prefer each other's company. But an awareness of the penalty potential for individuals made it worthwhile to test evolutionary hypotheses on whirligig sociality [330].

Let's consider a rather different case—the widespread occurrence of profound emotional attachments between humans and their pets, especially such creatures as the family Fido (fig. 2.4). I vividly remember the wonderful day about fifty years ago when I went to a neighbor's house to claim a puppy as my own. And I remember just as vividly the awful day somewhat over forty years ago when my dog Fellow, who had taken up chasing cars, was struck by a passing truck and had to be shot by our neighbor Mr. Jones, who was himself crying as he did what he had to do. People of many cultures come to feel almost as strongly about their dogs as they do about their fellow family members. They talk to them, care deeply for them, attempt to cure them if they fall ill, and are convinced that they share mental states similar to their own. In the United States alone, 50 million pet dogs generate some

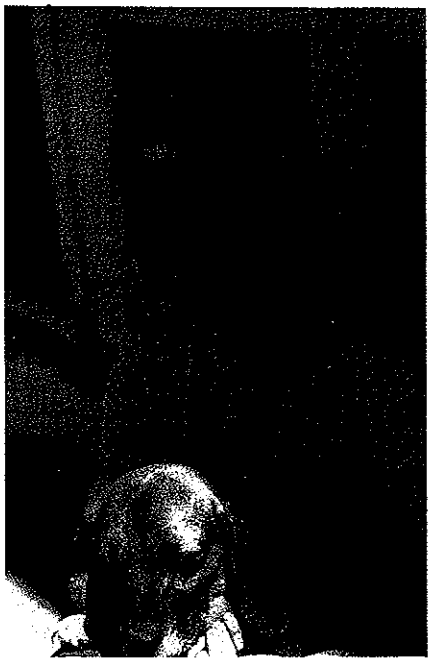

Figure 2.4. The pet dog is a beloved family member in many societies. Why do we invest so much emotional capital in these creatures?

$7 billion in veterinary fees as a by-product of their existence and their caretakers' willingness to attend to their needs [279].

Is it possible to analyze the enthusiasm for dogs from an evolutionary perspective? You may believe that spending time with the family pooch and paying for dog food or an occasional trip to the vet's office cannot possibly have any effect on the reproductive success of the pet owner, as measured by his or her production of surviving offspring, and you are probably correct, if you think only in terms of people living today in modern Western societies. However, even today, dogs maul and maim young children, who compose the bulk of the dozen or so deaths caused by dogs each year [253]. Moreover, nonlethal bites can easily become infected, since the mouths of dogs are far from hygienic. In one recent study, the average infected wound resulting from a dog or cat bite contained five species of harmful bacteria [253]. Since nearly 5 million Americans are bitten by dogs each year and since about [illegible] of all dog bites become infected, the health risks of dog ownership are [illegible] not the only health hazard that Fido poses for its devoted

human companions. Even good middle-class American dogs sometimes deposit feces in the backyard that contain parasites transmissible to humans, such as the protozoans *Cryptosporidium* and *Giardia* [289]. In traditional societies, where hygiene is less fastidious and contact with dog fecal material more frequent, dog-transmitted diseases can be prevalent. In one African tribal society, 220 persons out of every 100,000 were infected with a potentially fatal tapeworm that passed from dog to man, and this is merely one of about fifty diseases that people can get with a little assistance from the family canine [21, 34]. All of which suggests that some penalty, albeit very small on average, accrues to persons living today with a dog.

The downside of dog ownership must have been much more pronounced in prehistoric times, when food was presumably sometimes very scarce for hunter-gatherers, so much so that sharing even a small amount with an ancestral Rover may have harmed the pet owner or his offspring. And in an environment without antibiotics or other forms of modern medical treatment, an infected dog bite or an intestinal parasite acquired from contact with dog feces surely had far more serious consequences for the pet owner than is the case today.

If we accept that there are or were reproductive costs associated with pet ownership, then we have in effect identified an evolutionary problem worthy of at least some attention. The pet problem caught the eye of John Archer, a British psychologist who employs the sociobiological approach in his research. In his paper "Why Do People Love Their Pets?" Archer writes, "From a Darwinian perspective, it is a puzzling form of behavior, as it entails provisioning a member of another species, in return for which there are no apparent [reproductive] benefits" (p. 237 in [23]). In fact, this case resembles the one that Darwin felt would be fatal to his theory because it is almost as if our "pet-loving mechanism" exists solely for the benefit of a member of another species.

So what are the possible solutions to the puzzle? One basic sociobiological means of producing ultimate hypotheses for Darwinian puzzles is to propose that the mean reproductive costs associated with a trait, such as pet love, are outweighed on average by certain specified advantages. Thus, when the dog was first domesticated from wolves, early dog owners may have gained a net reproductive advantage from certain benefits that their pets provided, such as assisting in the hunt, warning of intruders, and almost certainly by sometimes becoming a main course in the evening barbecue [218]. Even in historical times right down to the present, dogs have been eaten with gusto by many peoples, especially in Africa, the Americas, and the Pacific Islands [288]. The utilitarian exploitation of pets could, however, have provided these benefits without requiring a deep emotional attachment between wolf-dogs and their owners. Indeed, pet love could create difficulties for persons who might otherwise gain by converting a favored mongrel into a high-protein meal.

The real puzzle is provided by those psychological mechanisms that result in

our love of pets. How can we explain the evolution of these mechanisms in a manner consistent with natural selection? Well, on the one hand, a great fondness for a pet might stimulate the formation of a strong companionable bond between owner and dog, with beneficial health effects for the owner. Interactions with friendly dogs have been shown to have a variety of positive effects especially in terms of stress reduction [23]. In other words, gradual evolution by natural selection might have produced a specific psychological mechanism that generates "pet love" today because in the past such a mechanism promoted healthful feelings of companionship with pets.

On the other hand, however, the psychological mechanisms that foster love of pets may have evolved in a totally different context, namely the promotion of affiliative relationships between human relatives or between unrelated humans who might cooperate on fitness-enhancing endeavors. According to the second hypothesis, dogs happen to have attributes that enable them to take advantage of friendship mechanisms that evolved because they promoted good relationships among humans, not because they enabled humans to love dogs per se. Even if the love of dogs had some modest negative effect on human fitness, humans might still become fond of them simply because dogs by coincidence activate certain psychological mechanisms of their owners, mechanisms that evolved in the context of human sociality because of their adaptive effects on interactions among ourselves [23].

In other words, pet love could be a maladaptive side effect of proximate mechanisms that evolved because of some other beneficial consequence. Evolutionary biologists regularly entertain the possibility that evolved psychological systems can sometimes reduce, rather than increase, an individual's chances of passing on genes to the next generation. For example, thanks to the intense drive that people have to be parents and care for babies, many humans have adopted genetic strangers into their families and have treated them with great affection, even though they received no genetic payoff for their actions. For example, thanks to their powerful sex drive, many men have engaged in risky extramarital affairs, and some have paid with their lives at the hands of enraged husbands. For example, although it may once have been advantageous for our ancestors to find small quantities of ethanol stimulating to the appetite, because such a psychological mechanism would encourage the consumption of ripe fruit, which contain some ethanol and much sugar, modern humans with this mechanism may run the risk of becoming alcoholics because they live in a novel environment in which highly alcoholic beverages are now abundantly available [110].

These and other maladaptive actions presumably occur because we possess proximate mechanisms that are good, but not perfect, at manipulating our behavior to serve the interests of the genes involved in the development of those mechanisms. Genes do what they do without supplying us or any other organism with a conscious desire to advance their welfare. Nor do our genes have a clue about what

is happening and why. DNA is an insentient chemical; the sequences of bases that make up our DNA simply happened to be better than other variant sequences in getting themselves copied and passed on as a result of their developmental influences. Genes do not have direct control over our behavior or that of any other organism, but have to work indirectly by affecting the developmental process (chap. 3). The proximate mechanisms whose development they happen to promote rarely, if ever, work perfectly from the genes' perspective. Instead, we and every other organism possess jury-rigged apparati that generally have substantial positive effects on genetic success but can also have some negative side-effects as well, especially when our proximate mechanisms of behavior have to operate in novel environments quite different from those of the past.

Now some persons have argued that it is not legitimate to consider as alternative hypotheses the notion that a trait is (1) the beneficial product of an evolved adaptation *or* (2) an incidental, or even maladaptive, by-product of an evolved adaptation that has some other beneficial consequences. Jerry Coyne, for example, claims that these propositions when taken together are so encompassing as to be all-explanatory and therefore untestable [76]. But if the two alternatives are treated as separate explanations, as they always are by evolutionary researchers, and if predictions taken from each are examined in turn, then evidence can force the rejection of one or both of the hypotheses. In other words, nothing prevents us from testing whether affection for dogs directly advances the genetic success of dog lovers or whether the trait is merely the byproduct of a psychological mechanism that spread through the human population for other reasons.

For example, one way to evaluate each pet-love hypothesis in turn is to consider how much time has been available for the evolution of psychological traits relevant to this emotion. The longer the time that dogs and humans have been living together, the more likely selection could act directly on the attribute of pet love. By some accounts, the first domesticated dogs appeared only 12,000 years ago, although one molecular genetics study suggests that domestication began as much as 135,000 years ago [325]. If the 12,000-year figure is correct, it would afford only a relatively modest opportunity for selection to operate directly on human–dog bonding capabilities.

The "pets-exploit-humans" hypothesis also produces the prediction that the degree to which humans generally develop loving attachments to pets will be a function of the ease with which it is possible to treat these animals as human surrogates. In other words, favored pets are expected to be those that respond to nurturing and affection in much the way that our children and friends do, when they are in a good mood. Dogs fill the bill beautifully because they do respond readily to commands, they appear to enjoy bodily contact with their owners, they possess fur that can be stroked with pleasure, and they do not talk back to their masters (although admittedly they can bark at the wrong times). Reptilian pets, say large lizards or

pythons with the same body mass as an average dog, should rarely inspire the same degree of attachment as the typical family dog.

This prediction and others could be tested rigorously, but the main issue here is not whether Archer's "pets-exploit-humans" hypothesis can be accepted with complete confidence, but rather to illustrate how one's theoretical orientation can help raise evolutionary questions worth answering. An awareness that pet love has at least some costs and no obvious benefits, as measured in the currency of reproductive or genetic success, helped Archer realize that this phenomenon deserved analysis. Darwinian theory also guided his initial speculations, shaping the hypotheses that he eventually presented, by pointing him toward hypotheses on the factors that might overcome the mild reproductive costs of caring so much for a member of another species. The pet love issue shows why selectionist theory is considered central to all of modern biology, not just sociobiology. Here is a theory of vast scope and immense utility for working biologists, an idea that gives structure to one's research [301], whether it concerns the social tendencies of whirligig beetles, the sterile castes of ants, or the ability of the family dog to inspire great love and affection in its owners.

3

Sociobiology and Genes

The Myth of the Genetic Determinist

For the sociobiologist, explaining the behavior of the whirligig beetle, the worker ant, and the pet-loving human being involves figuring out how these creatures' behavior, or the proximate mechanisms underlying their behavioral abilities, generate higher net gains in genetic success than other possible behaviors or different underlying physiological systems. The fact that genes get mentioned rather often by sociobiologists has led some critics to focus on the sociobiology-genetics connection. A considerable number of these critics think, or would like you to think, that sociobiologists have their genetics all wrong—because if sociobiology were founded on a fundamentally flawed version of genetics, dismissing the entire discipline would be relatively easy. To this end, some opponents of sociobiology have claimed that the discipline is founded on "genetic determinism," which also goes by the label "biological determinism."

Both terms refer to the same thing, namely, the view that an individual's genes can guarantee the development of a particular trait without reference to the environment in which the individual develops. Because genes do *not* single-handedly control the development of organisms, it would be a devastating criticism if sociobiology were indeed "another biological determinism," the original charge laid by Science for the People following publication of *Sociobiology* [17] and repeated by Gould at intervals since then (see [9]). Other critics have continued to portray sociobiology in the same light. For example, the feminist biologist Zuleyma Tang-Martinez writes that "traditional feminists contend that human sociobiology is biologically deterministic and serves only to justify and promote the oppression of women by perpetuating the notion that male dominance and female oppression are natural outcomes of human evolutionary history" (p. 117 in [304]). Likewise, from the neuroscientist Steven Rose, "The prevailing fashion for giving genetic explanations to account for many if not all aspects of the human social condition . . . is the ideology of *biological determinism*, typified by the extrapolations of evolutionary