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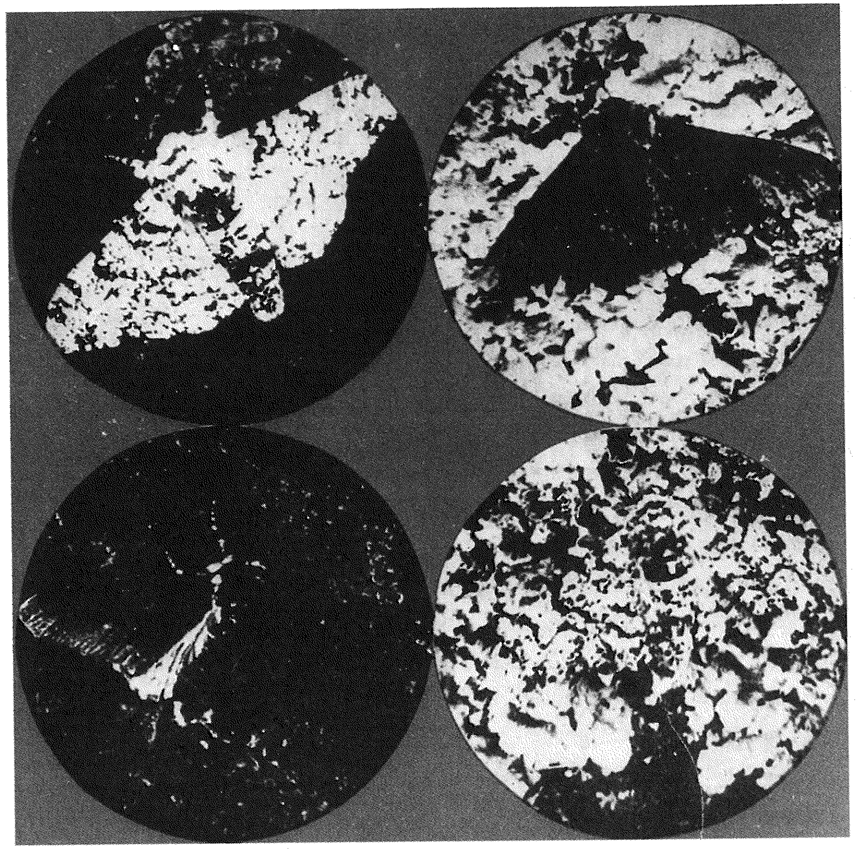
# Evolution, the Eternal Tinkerer

### Pollution and Evolution

Charles Darwin traveled as the ship's naturalist on H.M.S. *Beagle* from December 27, 1831, to October 2, 1836. This gave him an opportunity to observe a tremendous variety of animals and plants and also "to read for amusement Malthus's *Essay on the Principle of Population* (1798)," all of which led over 20 years later to the publication of *The Origin of Species by Means of Natural Selection, or The Preservation of Favoured Races in the Struggle for Life* (1859)—a book that sold out its first printing in one day. It is hard to imagine another book that has so completely changed our view of the world and of ourselves. And yet, perhaps the most remarkable thing about this book is that Darwin never really demonstrates even a single case of evolution in action. Darwin argues convincingly that evolution must have happened, but he never saw it happen. Indeed, he writes that "natural selection is daily and hourly scrutinizing, throughout the world, the slightest variations; rejecting those that are bad, preserving and adding up all that are good; silently and insensibly working, whenever and wherever opportunity offers. . . . We see nothing of these slow changes in progress, until the

hand of time has marked the lapse of ages, and then so imperfect is our view into long-past geological ages, that we see only that the forms of life are now different from what they formerly were." For this reason, the moth *Biston betularia* will always remain a textbook example of Darwin's theory of evolution by natural selection in action. Bernard Kettlewell, an English physician who gave up the practice of medicine and turned to the study of *Biston betularia* and other lepidopterans, writes that "among all living things it has fallen to the Lepidoptera to provide evidence of the most striking evolutionary change in nature ever to be witnessed by man."

In the early part of the nineteenth century, the common form of *Biston betularia,* called *typica,* had a peppered appearance. Its wings were flecked with black and white, and it was well camouflaged in its favorite resting place, the pale and lichen-covered barks of trees in rural England. A dark, or melanistic, form of the moth, called *carbonaria,* was first recorded in about 1848, and presumably had existed in very small numbers before then. But by the middle of the twentieth century, the melanistic form of the moth had come to represent over 95 percent of the *Biston betularia* population, especially in such industrial centers as Manchester and Liverpool. This is among the most rapid of all recorded evolutionary changes. Why was there such a dramatic change in fortunes of the peppered *typica* and the melanistic *carbonaria?* With rapid industrialization, soot came to cover the barks of trees, making them black instead of pale, and also killed the lichens. Now the melanistic form was better camouflaged on the darkened bark, while the peppered form became increasingly less camouflaged and hence more easily detected and eaten by birds. The birds, which had kept the melanistic form at a very low frequency before industrialization, now concentrated their attention on the peppered form. Natural selection, in the form of bird predation, favored the peppered form earlier and the melanistic form later.



Peppered and melanistic forms of *Biston betularia* resting on lichen-covered and soot-covered backgrounds. Notice the effective camouflage of the peppered form on the lichen background (bottom right) and of the melanistic form on the sooty background (bottom left), and the conspicuousness of the peppered form on the sooty background (top left) and of the melanistic form on the lichen background (top right). *(Reproduced by permission of Oxford University Press from B. Kettlewell, The Evolution of Melanism, 1973.)*

This explanation for the evolution of the melanistic form of *Biston betularia* has been verified in many different ways and found to be reasonably correct. With a few additional minor details, we could recreate the observed changes on a computer. Notice that this means that we are on the right track, because the computer would not reproduce the observed pattern if we input the wrong facts. Of course the ultimate proof would come from demonstrating (in real life, not merely on a computer) that if the environment reverts to its original pristine, unpolluted condition, if the soot disappears and the lichens grow back, the peppered form will regain its dominant position and the melanistic form will gradually disappear. Fortunately, such an ultimate proof has actually been obtained. Strict antipollution laws were adopted in England in 1956 and the countryside became relatively free of smoke. In a mere 20 years, the frequency of the melanistic form dropped significantly, indeed to the levels predicted by the computer models.

More recent research has brought to light strikingly parallel changes in and around Detroit, Michigan, including the near absence of the melanistic form before industrialization, its rise to about 90 percent of the population by 1959–62, and its virtual disappearance by 1994–95, barely 30 years after the clean-air law was adopted in 1963. These parallel and independent changes in England and the United States are like two replications of an experiment with identical results, boosting confidence in our explanation of this phenomenon, which has come to be known as industrial melanism. It must be cautioned, however, that some discrepancies between theoretical expectations and observations remain, suggesting that perhaps we do not know the full story yet; birds that prey on the adult moths appear not to be the only agents of natural selection at work.

### The Blind Watchmaker

It is not difficult to see that some win and some lose in the game of Survival of the Fittest in the struggle for existence. Who wins and who loses is determined by the environment, which alone decides who is fitter. But chance often determines which players in the game are present at any given time. If you are not present at the right time, you don't win even if you are fitter. The melanistic *carbonaria* was present, albeit at a very low frequency in the population, when pollution changed the color of the tree bark and thus the fortunes of the two forms of moths. Natural selection did not produce the melanistic form. It must have arisen by chance, and although it was at a disadvantage in the unpolluted environment, natural selection had been unable to kill it off completely or perhaps enough time had not elapsed since its origin for natural selection to have completed the job.

How then did the *carbonaria* form arise? We know that *carbonaria* is a mutant form of *typica,* differing from the latter at just one gene. Both because of toxic chemicals in the cellular environment and inherent errors in the process of duplication, some changes creep into the DNA molecule—the repository of hereditary information. The cellular machinery has an elaborate mechanism to edit the newly made DNA to correct errors. But even so some errors remain. These are called mutations, and they are the raw material of natural selection. *Carbonaria* thus differs from *typica* in carrying just one error. It follows then that natural selection has no purpose, design, or goal; it merely acts on errors that have been lucky enough to escape elimination. And all that natural selection does is to eliminate some of these errors and retain others. It may also blindly change direction and begin to favor the hitherto "unfit" varieties and to kill off the hitherto "fit" ones, when the environment changes in the opposite direction.

How such a blind process of tinkering can produce the most immaculately designed living organisms is mind-boggling to most of us; for some, it is sufficient to abandon the theory of natural selection altogether. At first glance we may find it improbable that natural selection acting on chance mutations could produce complex entities such as the human eye or kidney but we must realize that natural selection had an enormous amount of time available to it for shaping the final products we see today. More important, natural selection does not begin from scratch every time; there is successive selection at each step. There is a famous saying that, given enough time, a monkey typing randomly on a typewriter can produce all the works of Shakespeare. Richard Dawkins, the author of the famous book *The Selfish Gene,* first employing his daughter and later a computer program in place of the monkey, actually tried this experiment, beginning with the simple 28-character-long sentence METHINKS IT IS LIKE A WEASEL. He soon realized that if you had to start from scratch each time ("single-step selection") it would take his computer program about a million million million million million years to hit upon the correct sequence of characters by chance alone. This is not difficult to appreciate. There are 26 characters in the English alphabet, and counting the blank spaces required between words as the 27th character, there is a chance of 1/27 of getting any letter right by chance alone. The probability of getting all the 28 characters right in the required sentence simultaneously would be 1/27 raised to the power of 28, which is equal to about one chance in 10,000 million million million million million million.

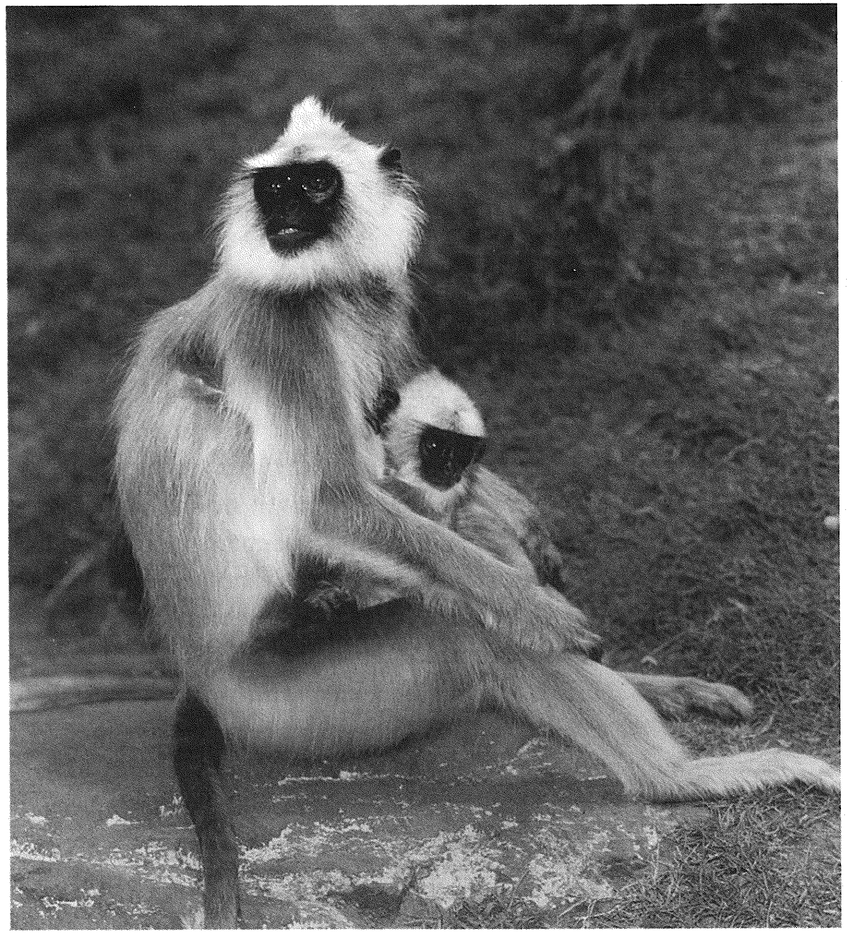
But if the computer program were allowed to select, in each generation, the string of 28 characters most closely resembling the target sentence and then to act on further mutants produced from that "best" variety ("cumulative selection"), the job could be done in just about 30 minutes. In one of Dawkins's trials, for example, the computer program began with the phrase WDLMNLT DTJBKWIRZREZLMOQCO P and "mutated" it randomly. Of all the random "mutants" produced, the one most resembling the target sentence was WDLTMNLT DTJBSWIRZREZLMQCO P, and therefore this was chosen as the starting point for the next generation. After 10 generations, the winning phrase was MDLDMNLS ITJISWHRZREZ MECS P, and after 20 generations it was MELDINLS IT ISWPRKE Z WECSEL. After 30 generations the phrase took the form METHINKS IT ISWLIKE B WECSEL, and after 40 generations it became METHINKS IT IS LIKE I WEASEL. At this stage only one letter was incorrect, and it took only 3 more generations to reach the target sentence METHINKS IT IS LIKE A WEASEL.

In opposition to the eighteenth-century theologian William Paley, who argued that just as a watch is too complicated and purposefully designed to have come into existence by accident, living organisms, which are much more complicated, could not possibly have arisen by chance and must have been purposefully designed, Dawkins argues that if natural selection can be said to be a watchmaker, it is a blind watchmaker. Dawkins points out that although the "monkey/Shakespeare model" is useful for explaining the profound difference between single-step selection and cumulative selection, it is misleading in that it gives the impression that each generation is judged by its resemblance to some ideal target. But natural selection has no ideal target, and it worries only about survival in the immediate present. To overcome this misleading implication, Dawkins goes on to use similar computer programs to create animal-like and plantlike shapes by cumulative selection. Having whetted your appetite, I will leave it to you to read about that and indeed to play with such computer programs. There is yet another aspect of Darwin's theory that many people find hard to grasp and that is best illustrated by recounting the shocking behavior of hanuman langurs.

## *Infanticide among Hanuman Langurs*

*Presbytis entellus,* the hanuman langur, with its black face, gray hair, and long tail, is a spectacular-looking monkey. Its populations range from the Himalayas in northern India to the southernmost tip of the Indian peninsula, extending into Sri Lanka and other land masses on either side of the Indian subcontinent. The epithet "hanuman" comes from the name of the monkey god who helped retrieve Rama's wife, Seetha, from the clutches of Ravana, the king of Lanka, in the Hindu epic *Ramayana.*

Hanuman langurs live either in bisexual troops or in all-male bachelor troops. The bisexual troops consist of several adult females, juveniles of both sexes, and either a single adult male or several adult males. The one-male troop, or harem, is particularly interesting. The male in control of a harem is periodically driven out by an invading bachelor troop. If the invasion is successful, the males of the bachelor troop usually fight among themselves until only one of them retains control of the harem—until he is ousted in a subsequent invasion. Upon taking over a new harem, the male typically kills most or all unweaned infants. How could this behavior, which seems clearly bad for the species, have possibly been favored by natural selection? Not surprisingly, many naturalists have described such infanticide as rare and pathological, and as possibly induced by conditions of overcrowding. Then Sarah Blaffer Hrdy undertook a field study of hanuman langurs in Mt. Abu in Rajasthan, India, from 1971 to 1975, and concluded that infanticide by male langurs taking over new harems was neither pathological nor maladaptive. Even more provocatively, she concluded that it was of great advantage to those males who practiced it and thus could easily have been favored by natural selection. Why this profound difference between Hrdy's attitude toward infanticide and those of previous naturalists?



A hanuman langur mother with her infant. *(Photo: E. Hanumantha Rao.)*

## *For the Good of the Species?*

For over a hundred years following the publication of Darwin's theory, biologists consistently misunderstood an important element of his reasoning, and the "theory of natural selection" they promulgated, which was accepted by both professional biologists and the lay public, was actually a misrepresentation of Darwin's theory of natural selection. Biologists came to substitute for Darwin's precise statements about natural selection their own imprecise version, which may now be called "the good of the species" concept. It became implicit in virtually all discussions of natural selection that evolution works for the good of the species.

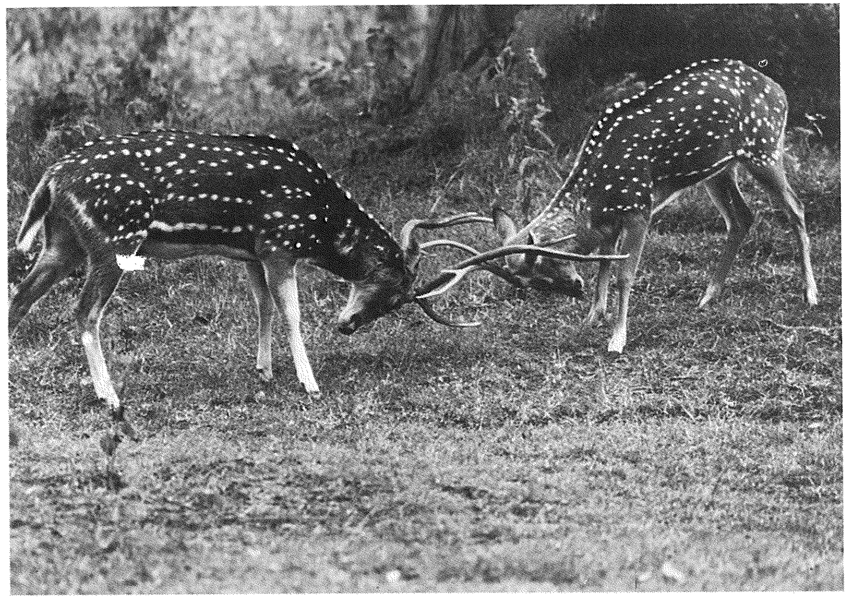
The idea that natural selection favors what is good for the species came to an abrupt end in the mid-1960s. The major credit for this complete change in the way we view natural selection must, ironically, go to one of the foremost champions of the idea of the good of the species. This was V. C. Wynne-Edwards, who in 1962 wrote a book, nearly as massive as Darwin's own, in which he attempted to explain a variety of behavior patterns in animals as being designed to promote the good of the species. So far most biologists were interpreting natural selection as promoting the good of the species only in an indirect and vague manner. Wynne-Edwards stuck his neck out and explicitly developed what he believed to be a unified theory of animal behavior and ecology based on the idea that individuals will always be selected to sacrifice their own interest for the sake of the good of the group. It is this clarity and explicitness in Wynne-Edwards's book that immediately made several biologists sit up and realize that there was a major flaw in what had passed for the correct interpretation of Darwin's theory of natural selection.

I once had the good fortune of attending a conference in which the famous evolutionary biologist John Maynard Smith was participating.

The conference was held in the picturesque hill resort of Mahabaleshwar, near Bombay. Perhaps the most vivid impression that I have of that and other Mahabaleshwar conferences I have attended since is the synchronous calls of hundreds of male cicadas, repeated every 30 to 40 minutes. Right in the middle of Maynard Smith's lecture and just when he was describing Wynne-Edwards's theory, there erupted a loud burst of cicada singing. Nonplussed, Maynard Smith said, if Wynne-Edwards were here he would have surely argued that the cicadas are singing in unison so as to assess their population density and adjust the rate of their reproduction so that they do not overexploit the habitat and eventually drive their species to extinction. Indeed, Wynne-Edwards had argued that almost all aspects of animal behavior and ecology were designed to limit their populations so as to avoid destruction of their habitat and their eventual extinction; species that lacked such self-regulating mechanisms would soon go extinct from overexploiting their resources.

The Nobel laureate Konrad Lorenz appears to have fallen into the same trap. He wrote, for example, that "Darwin had already raised the question of the survival of fighting and he has given us an enlightening answer. It is always favorable to the future of the species if the stronger of two rivals takes possession of either the territory or the desired female." Wrongly believing that the killing of conspecifics (other members of the same species) is rare in nature, Lorenz attempted to explain the supposed rarity by arguing that animals either are incapable of killing another of their own kind or must possess "sufficiently reliable inhibitions [to] prevent self-destruction of the species."

Today we know that this reasoning is incorrect and that natural selection is rarely, if ever, concerned with the good of the species. Natural selection almost always acts at the level of individual organisms and selects those that are best adapted to their environment, even if that



A sparring match between male spotted deer *(Axis axis)*. The dominant male will have first access to resources. *(Photo: E. Hanumantha Rao.)*

hurts the group or species as a whole. Most of the natural phenomena that Wynne-Edwards imagined could be explained only by *group selection* are better explained by *individual selection.* Hrdy's individual selection explanation for infanticide in hanuman langurs is that if a male kills unweaned infants immediately after taking over a harem, the females that were hitherto suckling will come to estrus sooner and consequently the male will have higher reproductive success. If he does not kill the infants and waits for them to be naturally weaned, he may sire many fewer offspring. And he often has precious little time before he is ousted by another male. Ideally, he needs to have his own offspring weaned before his ouster so that they are not killed by the next male. Males that practice infanticide under such circumstances will be fitter than those that do not practice infanticide and will increase the representation of their genes in future generations of hanuman langurs. If the propensity to practice infanticide has even a mild genetic component, the noninfanticidal males will eventually disappear and the infanticidal males will come to dominate the population. In many cases we now know that the stronger of two rivals takes possession of the territory or the desired female not because the subordinate male gives up voluntarily for the good of the species, but because accepting the subordinate role is better for him than the risk of injury from a prolonged fight; he will copulate with the desired female as often as possible when the dominant male is not looking (quite unmindful of the good of the species).

One of the arguments made by Wynne-Edwards was that animals will be shaped by natural (group) selection to produce fewer offspring than they can potentially produce so that they do not overexploit their food base. Christopher Perrins studied the swift *Apus apus*, which normally lays two to three eggs but is capable of laying many more, and asked what would happen if more eggs were laid. To answer his question, he artificially increased the number of eggs in some nests to four by adding an extra egg. In each of the four years that he did this, the maximum number of surviving offspring was produced by nests that had three eggs and not by nests that had four eggs. When the parents tried to feed four chicks, they apparently fed each so little food that mortality was higher. Natural (individual) selection thus favors the swifts that lay that number of eggs (three) which results in the largest possible number of surviving offspring, in obvious disregard of the possibility of overexploiting their resource base. Thus the assumption that birds produce fewer offspring than they possibly can is wrong; they seem to lay fewer eggs than they possibly can because the largest possible number of eggs does not lead

to the largest possible number of surviving offspring. In other words, they produce as many offspring as they possibly can.

Lorenz's assumption that animals will not kill other members of their species is also wrong. Hrdy writes in the book based on her study of the hanuman langur that "by the time I had concluded my research, I had learned . . . [that] the langur males compete fiercely for possession of females, and that in the process, conspecifics are sometimes killed. Furthermore, langurs are far from unique in this respect. A host of species has been recently added to the list of creatures known to kill conspecifics for motives other than eating them. These include such diverse groups as lions, hippos, bears, wolves, wild dogs, hyenas, rats, rabbits, lemmings, herring gulls, storks, European blackbirds, eagles, and more than fifteen types of primates—or sixteen, counting man."

Citing nobel laureates is an irresistible way of pointing out fallacies that are by no means restricted to their writings; hence the repeated choice of Konrad Lorenz. But it would be wrong to leave the impression that all that Lorenz did was to mix up levels of natural selection. Konrad Lorenz was one of the founders of ethology, the science of the study of animal behavior, and is best loved and remembered for his discovery of imprinting in birds, a discovery he made when birds that he had hand-reared began to treat him as their mother—one bird even tried to court him.

## *Cheaters Take All*

The underlying theoretical reason why Wynne-Edwards's theory will not usually work is that it takes just one cheater to ruin an elaborately laid plan designed for the good of the group. Consider a population of birds in which all members have actually been programmed to produce fewer offspring than they are capable of, so as to ensure sustainable use of their food base. All will be fine until one selfish mutation arises in the population and reproduces as fast as it can. The selfish individuals benefit from the prudence of the altruists and benefit from their survival plan without paying the associated cost of limited reproduction. Eventually the selfish will outnumber the altruists and thus drive the altruists to extinction. In technical parlance, a selfish strategy is stable against invasion by altruists, but an altruist strategy is unstable against and susceptible to invasion by selfish individuals; thus all populations eventually are converted to stable groups of selfish individuals. A cartoon by the famous Gary Larson, showing a band of lemmings on a suicide mission, with one of them wearing an inflated rubber tube around its waist, captures the essential fallacy of Wynne-Edwards's group selection theory better than any verbal description.

It is worth trying to explore the reasons why "the good of the species" idea became nearly universally accepted. There are at least three kinds of reasons that may be adduced. The first is a philosophical one. The idea that individual parts are just slaves in the hands of the master design of nature just seemed more satisfying and correct to people. The idea that the larger unit of organization (the species) ultimately decides the fate of its subcomponents (the individuals) implied a certain harmony in nature. The second reason is a social one. Fairly soon after the publication of Darwin's theory, there began to develop a pseudoscience, often known as Social Darwinism. Proponents of Social Darwinism used their own version of the theory of natural selection to justify human social systems such as capitalism and racism. For example, they argued that there is nothing wrong in the rich getting richer and the poor getting poorer because this is the law of nature—it is natural selection operating for the good of the species. Obviously the good of the species idea came in very handy for such arguments. The third reason is a purely scientific one. Early evolutionary studies concentrated mainly on nonsocial traits, where the good of the individual often coincides with the good of the species. For example, the perfection of the human eye and kidney over evolutionary time is good both for the individuals who possess good eyes and kidneys and for the species as a whole. It was only when social traits, where the good of the species and the good of the individuals do not always coincide, began to be studied, that the fallacy of the concept of the good of the species became clear.

But is it not true that many social animals exhibit altruism, which must benefit their species? Don't honey bee workers sacrifice reproduction and inflict suicidal stings on marauders who invade their nests? Don't stalk cells in the cellular slime mold kill themselves to enable the spore cells to disperse to better habitats? Can all such altruism be explained by individual selection, by the "good of the individual" idea? Could the honey bee worker possibly be selfish and be merely ensuring the propagation of her own genes? The triumph of modern evolutionary biology has been the successful interpretation of nearly all known cases of altruism as a manifestation of some form of individual selection without recourse to Wynne-Edwardian group selection.

## *Levels of Natural Selection*

In describing the triumph of modern evolutionary biology, I deliberately spoke of explaining *nearly* all known cases of altruism on the basis of individual selection because it is not true that natural selection cannot ever act at levels other than the individual. In principle, natural selection can act at any level of biological organization—DNA, genes, cellular organelles, cells, organs, individual organisms, family units, larger groups, populations, species, and even communities of species. Of course the question of where natural selection acts arises only when there is a conflict of interest between different levels of biological organization. If a character (any observable property) simultaneously benefits or harms two levels, then natural selection acts at both levels. For example, if the mitochondria (spherical or rod-shaped bodies inside cells that effect cellular respiration) become more efficient at producing energy, that will simultaneously benefit the mitochondrial genes, the mitochondria itself, the cells and the organs bearing the mitochondria, and the individual organism. The problem arises only when the character in question creates a conflict of interest between different levels of biological organization. If one gene in a cell starts to reproduce faster than necessary for the well-being of the cell and drains the cellular resources, this is good for the gene concerned (at least in the short run) but bad for the cell, the organ, and the individual. Natural selection will then usually act at the level of the cell or individual and suppress such selfish behavior on the part of a gene.

How then do we decide where natural selection will act in a given situation? Can we develop a general theory about this? Perhaps. When two levels of biological organization are competing, as it were, for the attention of natural selection, the strength of natural selection on each level will depend on the relationship between the two levels of organization—how independent the unit at the lower level of organization is of the "clutches" of the higher level of organization, how much short-term gain the units at the lower level can achieve by working against the higher level before they themselves begin to suffer, how much "discipline" the higher level of organization can impose on the lower level. Take for instance a conflict between individual organisms and groups of organisms. The units at the lower level, the individual organisms, are usually pretty free of the clutches of the group; they have a life of their own and can go a long way by revolting against the group. Hence natural selection usually acts at the level of the individual rather than the group. Now consider a conflict between an organism and its constituent cells. The units at the lower level of organization here are the cells. But the cells are pretty much under the control of the higher level of organization, the individual organism. The cells can do precious little to revolt against the whole body and hence natural selection will usually act at the level of the individual organism rather than the cells. We have seen and we will keep seeing examples of natural selection acting at the level of the individual organism. But now let's take up some examples of natural selection acting at other levels, such as the chromosome (DNA), the cell, and groups of organisms.

## *Selfish DNA*

*Nasonia vitripennis* is a parasitoid wasp that is distributed throughout the world and has a fascinating life cycle. The males have only vestigial wings and cannot fly; they therefore die after mating with females that emerge in the vicinity of their birth. The females, however, can fly, and mated females therefore go off in search of new hosts on which to lay their eggs. Their hosts consist of the pupae of flies that breed in carcasses and in bird nests. Like all insects that belong to the order Hymenoptera, *N. vitripennis* is haplodiploid, meaning that males are haploid, with only one set of chromosomes, while females are diploid, with two sets of chromosomes. The females can lay both fertilized and unfertilized eggs. The unfertilized (and therefore haploid) eggs develop into haploid adult males, while the fertilized (and therefore diploid) eggs develop into diploid adult females. This means that sons have no fathers and fathers have no sons. An equally interesting consequence of this mode of sex determination is that females can decide the sex of their offspring. All they need to do is to release sperm (received at the time of mating and stored in special organs called spermathecae) into their oviducts to produce daughters and block the flow of sperm to produce sons. There is good evidence that females actually utilize this ability to choose the sex of their offspring because they do alter the ratio of haploid to diploid eggs they lay in response to environmental conditions. But there are other genetic and nongenetic factors, not under the control of the females, that can rather drastically alter the sex ratio of the offspring. For example, a bacterial infection can be transmitted from mothers to daughters that kills nearly all haploid eggs, resulting in an all-female line. Such an infected strain cannot survive in the wild unless infected females can find males from other, noninfected families of wasps to keep them going. It is of course easy enough to keep such strains in the laboratory, where one can supply healthy males to each generation of infected daughters.

Another strain of *Nasonia vitripennis* has been found where the opposite happens—only sons are produced. Again it is easy to maintain such a strain in the laboratory by supplying healthy females for every generation of mutant males. John Werren has made headlines with these discoveries, announcing son-killing factors that are passed down from mother to daughter and daughter-killing factors that are passed down from father to son! It is the daughter-killing factor that is of interest here. It is now quite clear that mutant males produce normal sperm with normal-looking chromosomes and that these sperm successfully fertilize eggs. The problem begins after that. For reasons that were not clear earlier, the paternal chromosomes in the sperm disintegrate in the fertilized zygote (the cell formed by the union of two gametes, or sex cells), leaving only the maternal chromosomes. But since the zygote is now haploid it develops into a male rather than into a female. This is how the daughters are killed—or rather converted into sons. How and why do the paternal chromosomes disintegrate? Even more puzzling is the question of how the resulting haploid males get the mutant character so that they will in turn convert potential daughters to sons in the next generation when their sperm fertilizes eggs. Such transmission is not expected because the paternal chromosomes all disintegrate. The only possible conclusion is that the factor that causes the daughter-to-son conversion is extra-chromosomal and comes to the zygote along with the paternal chromosomes and does not disintegrate with them. Careful prying into the structure of the mutant sperm has revealed that mutant males carry a small chromosome (a piece of DNA, if you like) over and above the usual 5 chromosomes that normal males carry. This is called a B chromosome.

In the early days when cytologists were describing chromosomes of various species of plants and animals, they found unusual chromosomes in some species. In addition to the normal sets of chromosomes that are present in pairs in the adult stage and that become haploid in the gametes (sex cells—sperm and eggs) and reunite with another chromosome of their kind during fertilization to restore diploidy, there may occasionally be odd chromosomes that are not usually paired and whose transmission is erratic. They may not be present at all or may be present in variable numbers of copies. Most cytologists did not quite understand the significance of these supernumerary chromosomes and simply labeled them B chromosomes, retaining the label A chromosomes for the apparently normal ones. *Nasonia vitripennis* mutants that show the daughterless phenotype have a B chromosome that reaches the zygote along with the paternal chromosomes and appears to produce a factor that destroys all the paternal chromosomes. But obviously the B chromosome itself is resistant to such destruction, so that it stays on in the resulting haploid cell, which will develop into a male when the B chromosome can do its trick all over again.

The B chromosome confers no benefit to the male that harbored it but instead destroys all the male's chromosomes to ensure its own survival and transmission to future generations. Not surprisingly, the *Nasonia* B chromosome has been dubbed "the most selfish genetic element" known. But obviously this B chromosome can only go so far, because if it invades all males in the population then there will be no females left for the mutant males to mate with. The survival of the B chromosome depends on its ability to use normal females for its onward transmission. Natural selection will therefore restrict the prevalence of the B chromosome to a level low enough that the whole population does not go extinct for lack of females. If the B chromosome does increase in frequency in any population, that population might go extinct, and we can therefore assume that in all surviving populations the B chromosome has been kept under reasonable control. Nevertheless, the *Nasonia vitripennis* B chromosome is an excellent example of how natural selection can sometimes act at levels of biological organization other than the individual organism.

## *Are Cancer Cells Selfish?*

When there is a conflict between cells and the body they reside in, natural selection usually favors the body, which can usually discipline the errant cells, especially because the cells don't have a life of their own outside the body. A well-known exception to this principle is that of cancer cells, which can be thought of as selfish cells attempting to reproduce faster than is good for the health of the whole body. In the end, of course, the cancer cells perish with the individual, but that does not explain why natural selection has not eliminated cancer all together. A common objection to the interpretation of cancer cells as selfish is that they are abnormal and perhaps infected with a virus, that cancer is a disease, and so on. All this is true and pertinent to the proximate answer to the question of why cancer cells reproduce faster than is good for the body. But the ultimate, evolutionary answer must be that natural selection in this case is acting in favor of the cell rather than the individual. The fact that cancer is typically an old-age disease lends further credence to this interpretation; in old age it's no longer critical for the individual to suppress the selfish designs of the cells because the individual has probably already completed its task of reproduction. The very phenomenon of senescence and the prevalence of various other old-age diseases may also be interpreted as resulting from the relaxation of the body's strict control over the selfish tendencies of its organs, tissues, cells, and genes as a person ages.

## *Altruistic Myxoma Virus in Australia*

Australia evolved its own unique mammalian fauna of marsupials and for millions of years did not have the same mammalian fauna as the rest of the world. Rabbits, for example, were unknown in Australia until Europeans introduced them in 1859. But since they did not simultaneously introduce foxes, the rabbits multiplied merrily until they became pests. To control the rabbits, a highly virulent form of the myxoma virus was introduced. This virus was very effective in killing the rabbits, but it went extinct itself whenever the number of rabbits became too small for the virus to travel from one rabbit to another. (The virus depends on mosquitoes to get from one rabbit to another, much like the malarial parasite.) A fresh stock of the virus had to be imported every time the virus became extinct and rabbit populations grew large.

In the course of time a mutation seems to have arisen in the virus population that may be described as an altruistic form. The mutant form of the virus is relatively avirulent and grows rather slowly. This form we may call altruistic because it allows many more virus particles (of its own kind as well as those of other genetically distinct kinds) in the rabbit body to mature before it kills the rabbit. The altruism of course is toward other viruses, not toward rabbits. By contrast, the virulent form of the virus may be described as selfish because it reproduces very fast and uses the resources of the rabbit before the other viruses do so. Here the altruist seems to have defeated the selfish individual. The selfish virulent strain of the virus lost out because it killed the rabbit before the progeny viruses had a chance to be transported by mosquitoes to healthy rabbits. The avirulent viruses kept the rabbit alive for a long time, and consequently mosquitoes efficiently transmitted them from one rabbit to another. Natural selection therefore favored the altruistic avirulent strain over the selfish virulent one.

But such examples are not very common. The simple reason is that the selfish strains usually invade the population and multiply at the expense of other strains. In this particular case, the selfish strain of virus could not easily invade the altruistic population because the selfish viruses killed their host rabbits rapidly and since mosquitoes do not bite dead rabbits they were unable to carry the selfish viruses from one rabbit to another. When there is a conflict between individuals and the group, natural selection usually acts at the level of the individual and promotes selfishness, but the myxoma virus example shows that it can occasionally act at the level of the group and suppress selfishness on the part of the individuals. But this, as we have seen, requires very special conditions indeed.

Before the 1960s, biologists blindly applied the idea of group selection without realizing that natural selection will promote selfishness on the part of individual organisms except under very special circumstances. In mid-1960s and the 1970s, the phrase *group selection* became a term of opprobrium. I have sat in many seminars where a question from a member of the audience was loudly dismissed by other members of the audience shouting "but that's group selection!" even before the speaker

had a chance to understand the question. Today the dust has settled down and we recognize that natural selection can, in principle, act at various levels of biological organization and that we must examine the circumstances carefully before pronouncing a judgment about the level of natural selection. This has brought back a level of credibility to mathematical models of group selection that I hope will permit the discovery of more genuine examples of group selection and natural selection at other unexpected levels of biological organization.