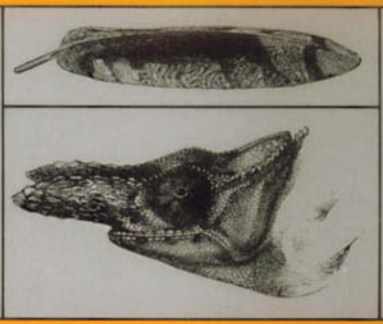
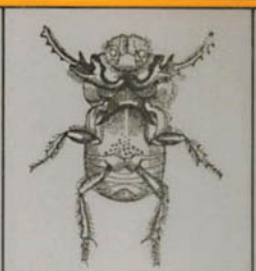
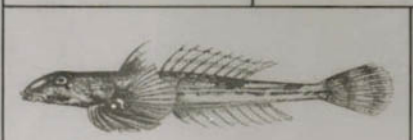




CHARLES DARWIN

THE DESCENT OF MAN,

AND SELECTION IN RELATION TO SEX




INTRODUCTION BY JOHN TYLER BONNER
AND ROBERT M. MAY

CONTENTS

VOLUME II

PART II. SEXUAL SELECTION, *continued*

INTRODUCTION

By John Tyler Bonner and Robert M. May

THE REASON for reissuing Charles Darwin's *Descent of Man* in 1981, one hundred and ten years after its first appearance, is that it addresses an extraordinary number of problems that are, at this moment, on the minds of many biologists, psychologists, anthropologists, sociologists, and philosophers. It is the genius of Darwin that his ideas, clothed as they are in unhurried Victorian prose, are almost as modern now as they were when they were first published.

In this brief introduction, our aims are to indicate the place the book held in its own time, to point out those areas of present-day inquiry where Darwin's comments and questions are particularly relevant, and to identify where his lack of knowledge (particularly in genetics) imposed limitations on his interpretations. The *Descent* (as we shall henceforth refer to it) is unquestionably second only to the *Origin* in the Darwinian canon, and the ground surveyed here is accordingly covered in much greater depth in other works: Gruber and Barrett have given a careful analysis of the development of Darwin's ideas on this subject, especially as reflected in the so-called M and N notebooks; Ghiselin's *The Triumph of the Darwinian Method* is an insightful account of Darwin's general method of working, with Chapter 9 particularly relevant to the *Descent*; and the collection of essays on *Sexual Selection and the Descent of Man*, edited by Campbell, is also helpful.[1]*

* Notes are given at the end of the Introduction.

A separate Note on the Text at the end of this introduction explains why the first rather than the second edition was chosen for reprinting, and why it was not abridged. We also suggest a way of skipping through the book—a *de facto* abridgment—which will enable a reader to encounter most of the basic thoughts and questions, bypassing many of the catalogues of examples.

THE BOOK IN ITS OWN TIME

CONTENT OF *The Descent*

The structure of the *Descent of Man, and Selection in Relation to Sex* is unusual in that, as the title clearly states, it consists of two vast subjects which are cemented together at the end by a discussion of the role of sexual selection in man. The major theme of the first part of the work is simply that man descended from other animals and was not specially created. The book, however, does more than marshal the evidence for the continuity between man and other animals (with all the philosophical materialism thus implied). As observed by Gruber, it also represents Darwin's attempt to "study intelligence as a central feature of adaptive change, and to study it in that organism in which it is most prominent, man."[2] The theme of the second part of the book is that besides natural selection there is sexual selection, so that not only will the general character of a species change over time, but the character of the two sexes may also change, as in, for instance, the peacock and the peahen.

Neither part of the *Descent* can be understood without reference back to the *Origin,* whose three-stranded thread of argument runs as follows. First, there is variation among the individuals in populations of plants and animals, both natural and domesticated, and some of this

variation is heritable. Second, organisms in nature tend to produce more offspring than can survive to reproductive age if the population is to remain, on average, steady over any length of time. There is thus a "struggle for existence," in which individuals with certain variations may be favored (or "naturally selected"); these favored individuals will tend to spawn children and grandchildren possessing their traits, their variations. Third, it can happen that over the span of geological time new species eventually evolve by such processes of natural selection. Darwin saw sexual selection as an important variation upon the theme of natural selection, with certain traits in the male (or, less commonly, the female) making him (or her) more successful in mating; the result is a dimorphism between the sexes. Darwin shows that these two kinds of selection can act in concert, or not, and if the latter, then the structure of the sexes reaches some sort of compromise between the pulls of natural and sexual selection.

As we shall discuss further below, one of Darwin's greatest problems was to understand how variations arise, how variability is maintained, and how and to what extent variations are inherited. Without an understanding of genetics this enterprise was doomed. Not the least of Darwin's strengths was the courage and the sense eventually to base his theory on the observed—but unexplained—fact that variability existed. However, in 1838 when he began the M and N notebooks, upon which much of the *Descent* is based, he still hoped to discover the basis of variability and heritability; ideas and information about man's intellect looked like a promising testing ground for exploring hypotheses about heritable variation. Hence the discussions of South American natives, and particularly of the three Tierra del Fuegans transported into English society.

DEVELOPMENT OF IDEAS IN *The Descent*

Working from the notebooks[3] Darwin kept in the years 1837-1839—the B, C, D, and E notebooks dealing with evolution in general, and the M and N notebooks with "Man, Mind and Materialism"—Gruber and others have shown that Darwin's thinking about man was, from the start, an integral part of his exploration of evolutionary questions: "the subject of man and his place in nature was so woven into Darwin's thoughts that it forms an indispensable part of the network of his beliefs."[4] Specifically, the first passage in the M and N notebooks which clearly enunciates the principle of natural selection and applies it to man appears in the N book around 27 November 1838.[5] An earlier passage in the more general C notebook says, "I will never allow that because there is a chasm between man . . . and animals that man has a different origin."[6] And the M notebook of 16 August 1838 contains a triumphal passage with all the combative ring of contemporary sociobiology: "He who understands baboon would do more toward metaphysics than Locke."[7]

In short, although Darwin in his public utterances was for a long time reticent concerning his opinion about man, his private thoughts are clear. The basic intellectual edifice presented in the *Origin* and in the *Descent* was in place by 1838, and his subsequent actions may be seen as a "strategy involving two grand detours: the first, a long delay before publishing his general theory of evolution, and the second, another long delay before revealing his ideas on the evolution of man."[8] The reasons for the first of Darwin's long delays, until Wallace's independent enunciation of the principle of natural selection precipitated the publication of the *Origin* in 1859, have been much discussed. The *Origin* does have a chapter entitled "Instincts," which deals with some psycho-

logical issues, but the book avoids discussion of higher mental processes, and (as Darwin admits on the first page of the *Descent*) refers to man only through the evasive phrase that "light will be thrown on the origin of man and his history."

The idea that evolution by natural selection could account for the origin of man was taken up by others as a direct result of Darwin's ideas. The respected T. H. Huxley did this explicitly in 1863 in his *Evidence as to Man's Place in Nature.* So did the flamboyant German biologist Haeckel, who even invented an imaginary missing link between ape and man, *Pithecanthropus alalus,* the speechless apeman. One of the principal dissenting voices was that of Alfred Wallace, who published an essay in 1864 saying that the bodily structure of man could be entirely accounted for on the basis of natural selection, but that the mind of man was created by some "higher intelligence."[9] As a result, Darwin could hardly have expected that his book would create any surprises; rather, he must have wanted to present in detail his own position and publish the great mass of evidence he had accumulated. By 1871 he was a famous person; everyone was eager to know what he had to say of this subject, so central at the time.

A convincing explanation for Darwin's two long hesitations is that he had a lively apprehension of the trouble he was inviting. The *Origin,* doing away with the need for Creation, was bad enough; but (as Wallace and many others showed) its message could be reconciled with a basically religious view of man's place in the world. The frank out-and-out materialism of the *Descent* was worse, leaving no role for the Deity to play. Moreover, as Gruber emphasizes, Darwin knew that he ran real risks, more substantial than the simple storms of public controversy.[10] As an undergraduate at Edinburgh Univer-

sity, he had seen a fellow student's paper formally expunged from the records of the Plinian Society because it argued that "mind is material." Earlier, in 1819, a distinguished surgeon, Lawrence, had published his *Lectures on Physiology, Zoology, and the Natural History of Man*; this work was decried as expounding materialism, and Lawrence withdrew the book and resigned his post as lecturer. When a pirate edition was published in 1822, he lost a suit against the publisher, under a law dating back to the Star Chamber of Charles I whereby an author had no property rights to a "blasphemous, seditious, or immoral" work. Darwin refers to this book in the *Descent.*

The fact that the basic ideas in the *Descent* are contained in the M and N notebooks of 1838 does not imply that fears of fierce controversy alone detained Darwin from producing the book then. Much hard work remained to be done, collecting facts and observations to bind to the framework and testify to its soundness. This work, a lot of which was very original, was done around 1867-1871. The project was initially conceived as having three parts, of which the first two (the descent of man and selection in relation to sex) were realized, while the third (the expression of the emotions in man and animals) grew into a separate and important work, published in 1872.[11]

DARWIN'S SCIENTIFIC METHOD

In this general context, it is interesting to look at the way Darwin went about his work. Gruber gives a particularly fascinating discussion of the disparity between what Darwin actually did, and what he said he did. In his books, Darwin consistently portrays himself as cleaving to the accepted Baconian canons: first marshal the facts, then see what conclusions emerge. Thus on page

one of the *Origin,* he claims to have "patiently accumulat[ed] and reflect[ed] on all sorts of facts which could possibly have any bearing on it. After five years' work I allowed myself to speculate on the subject, and drew up some short notes. . . ." Likewise, on page one of *The Expression of the Emotions in Man and Animals,* he explains that "I arrived, however, at these three Principles only at the close of my observations." The actuality of the B, C, D, E, M, and N notebooks tells a very different story, and one which is more familiar to a practicing scientist. Gruber summarizes this beautifully: "The pandemonium of Darwin's notebooks and his actual way of working, in which many different processes tumble over each other in untidy sequences—theorizing, experimenting, casual observing, cagey questioning, reading, etc.—would never have passed muster in a methodological court of inquiry. . . . He gave his work the time and energy necessary to permit this confusion to arise, at the same time persistently sorting it out, finding what order he could. It was an essential part of this 'method' that he worked at all times within the framework of a point of view which gave meaning and coherence to seemingly unrelated facts."[12] In addition to the evidence implicit in the notebooks, Darwin's correspondence shows the divergence between private views and public pieties: "all observation must be for or against some view if it is to be of any service!"; "let theory guide your observations, but till your reputation is well established be sparing in publishing theory. It makes persons doubt your observations."[13]

Naively simple formulations of The Way to do science—be they Baconian, Popperian, or otherwise—are, if anything, more pervasive today than they were in Darwin's time. We believe that Darwin got it right when he wrote, "The only advantage of discovering laws is to foretell what will happen and to see bearing of scattered

facts,"[14] and that the scrabbling, nonlinear way he pursued this end is typical of most good science. As Ghiselin puts it: "Viewed from without, science appears to be a body of answers; from within, it is a way of asking questions. . . . The 'predictionist thesis' and 'hypothetico-deductive' model seem a bit trivial as clues to what real scientists are trying to do."[15] This struggle toward understanding and "seeing the bearing of scattered facts" is not entirely concealed in the finished products, and the *Descent* is interesting for the persistent questions that underlie the structure of the book.

A criticism often leveled against the theory of evolution by natural selection is that it is little more than a collection of Just So Stories, in which particular facets of behavior or morphology are argued to be "adaptive" or "optimally designed" to fulfill purposes which are tautologically inferred from the behavioral or morphological feature in question.[16] It is true that individual pieces of the evolutionary puzzle, taken one by one without replicates, controls, or comparisons, are indeed each susceptible to one or more *ad hoc* anecdotal explanations. These are the general grounds for Popper's suggestion that evolut onary thinking is metaphysical, and inherently unfalsifiable.[17] Darwin, however, had a fully modern awareness both of this methodological problem and of one answer to it. By deliberately collecting comparative information for large assemblies of different organisms (geographical races, species, or other taxonomic groupings), he showed that it is possible to document broad trends and patterns among behavior, morphology, or biogeographical features. Moreover, these patterns in such phenomena as geographical distribution or vestigial organs can often be correlated with systematic patterns in the differing environmental circumstances of the organisms under study.

Such comparative studies can then permit predictions to be made about as yet unstudied species. Some instances are given below. For example, the relationship between the degree of sexual dimorphism and the socioeconomic sex ratio (females per reproductive male) recently obtained by Clutton-Brock, Harvey, and Rudder for primate species would enable a rough prediction to be made about either one of these quantities once the other is determined for a species not included in the original study.[18] Whatever their philosophical status, these methods are capable of generating testable predictions that are not qualitatively different from those of the physical sciences. The extreme assertion that evolutionary biology can never aspire to more than "thick description" of individual cases, each unique (as advocated on similar grounds in a different context by some social scientists),[19] fails to comprehend the power of the comparative methods employed by Darwin and refined by later workers.

In one important way, however, many predictions in the biological sciences do differ from those we are familiar with in classical physics. In physics and engineering, most simple predictions or tests of hypotheses are crisply and pleasingly deterministic. But in population biology, ecology, and evolutionary biology, many of the predictions are inherently probabilistic (as, for similar reasons, are the predictions of meteorology or portfolio theory). This point is emphasized by Gruber and Barrett, Monod,[20] and others, and it has implications that range from the grand sweep of evolutionary thinking to important practical aspects of fisheries management.[21]

DARWIN'S STYLE OF PRESENTATION

Finally, it is worth commenting on Darwin's style of presentation. The language is simple and vivid, and to

a reader accustomed to the elaborately "objective" circumlocutions of much of the contemporary social sciences it may appear alarmingly anthropomorphic and teleological. Ghiselin analyzes this issue in detail, showing clearly that there is a world of difference between Darwin's "metaphorical use of anthropomorphic expressions and the propositions which he actually asserts." As Ghiselin demonstrates, Darwin "used everyday terminology to convey precise and definite meanings, with elegance and clarity. For instance, Darwin gives two pictures in which he shows the contrasting appearance of cats under conditions involving precisely opposite kinds of behavior. These are entitled 'Cat, Savage, and Prepared to Fight . . .' and 'Cat in an Affectionate Frame of Mind. . . .' Contemporary biologists may regard these captions with amusement, even delight, for the prevailing standards of pedantry are opposed to such expressions, even though nobody ever would take them literally, and even though they could scarcely better express the underlying ideas."[22] Darwin preferred playing with dogs to engaging in ludic activity with canine companions.

Probably the most striking stylistic difference between the book Darwin wrote in 1871 and the one he would write if he lived today lies in his discussion of the races of man and the differences between the human sexes. For his period he is remarkably objective on the matter of race, although he does make it clear that to be civilized means to be like an educated Englishman. Here he was partly influenced by his voyage on the HMS *Beagle* as a young man, where the unspeakable behavior of the Tierra del Fuego Indians impressed him enormously. They had no religion, no care of their hair or their rude clothing, no obvious code of morals, and they ate their grandmothers first when food was short. Yet he sees that

those natives who were taken to be educated for a period in England did appear to become civilized; they were capable of improvement. Darwin had the capacity to see beyond the prejudices and ideologies of his own time and culture—more so, indeed, than many who work in these general areas today.

Those readers who are sensitive to sexism may be provoked to considerable outrage by Darwin's short discussion of "the difference in the mental powers of the two sexes." Here he is reflecting no more than the common view of the time, and this unreflective attitude is somewhat mitigated by a curious and somewhat obscure passage on page 329 where he seems to imply that women could become like men in their mental facilities if they were provided with suitable opportunities and training. (It may be remarked that his diligently kept record of backgammon games with his wife show them roughly evenly matched, with Darwin at one time ahead by 2,795 to 2,490.[23] Did he not realize the highly analytical character of this game? Most likely, he never thought about it.)

Some Scientific Problems Confronting Darwin's Work in the Nineteenth Century

Discussion of the public reception of Darwin's work tends to center around the religious and other broadly philosophical issues. It is often not fully appreciated that the theory of natural selection met with very serious scientific objections.

Without a precise understanding of genetics and the laws of Mendelian inheritance, the causes and heritability of variation among individuals in natural and domesticated populations are bound to be a bit mysterious.

Around 1838, Darwin still hoped to solve this mystery and place his theory on a solid base. As we have seen, the M and N notebooks from which the *Descent* sprang were begun partly in the hope of using man's origins to shed light on the sources and mechanisms of heritable variation, and to test hypotheses about habits becoming hereditary. In retreating to the position of taking heritable variation to be an unexplained premise, Darwin was condemned to a lifelong struggle with two large problems which he never satisfactorily resolved.

The first problem stemmed from the received wisdom of Darwin's time, namely, that inheritance worked by a blending of maternal and paternal characters. As emphasized to Darwin by Fleeming Jenkin,[24] under blending inheritance variation simply cannot be maintained! The essentials of the argument can be grasped by considering a trait (such as height or weight) that can be described by a single variable.[25] Suppose the mother departs from the population average in this respect by an amount x, and the father by an amount y. Then, under a scheme of blending inheritance, the progeny will depart from the mean by $\frac{1}{2}(x + y)$. In the parental generation, suppose the statistical scatter of the variable about its mean value is characterized by a variance σ^2; that is, the expectation values of x^2 and y^2 are both σ^2 ($< x^2 > = < y^2 > = \sigma^2$). In the next generation, the corresponding variance is the expectation value of $(\frac{1}{4})(x + y)^2$ or $(\frac{1}{4})$ ($< x^2 > + < y^2 > + 2 <xy>$), which is equal to $\frac{1}{2}\sigma^2 (1 + \rho)$. Here ρ is the correlation coefficient between x and y. If mating is at random, $\rho = 0$, and the variance of the trait among the offspring is $\frac{1}{2}\sigma^2$; the variance is halved in a single generation. Even if there is a tendency for like to seek like in mating, so that $\rho \neq 0$, the variance will still decrease in each generation (except in the unlikely extreme of perfectly sorted mat-

ing, with $\rho = 1$). In short, the mid-nineteenth-century conventional wisdom of blending inheritance was flatly inconsistent with the observed propensity for natural populations to exhibit variability. Darwin was troubled by this inconsistency. The answer, of course, lies in the fact that genes are inherited in particulate Mendelian fashion, not by "blending." The basic theorem of Mendelian population genetics—the Hardy-Weinberg theorem, proved in 1908—can be rephrased to state that, in the absence of perturbing factors (such as mutation, selection, drift, migration, or nonrandom mating), variance remains constant from generation to generation.

Mendel's paper on the laws of heredity, providing the key to the puzzle, was published five years before the *Descent* appeared.[26] Although in German, the paper was not in an obscure journal, and was accessible to Darwin and his colleagues. Fisher has made the interesting and plausible suggestion that Mendel's work was overlooked because it was cast in a mathematical idiom, which was truly a foreign language to nineteenth-century British naturalists. De Beer notes Darwin's regret for his ignorance of mathematics;[27] if Fisher's explanation is correct, Darwin had more to regret than he realized! It remained for the early twentieth century to rediscover Mendel.[28]

The second problem associated with Darwin's lack of basic understanding of genetics is that he did not fully comprehend the distinction between what we would call gene inheritance and the inheritance of habits, customs, and behavior. In the *Descent* and elsewhere, Darwin repeatedly says that if an animal behaves in a particular way for a number of generations, this will result in the behavior becoming permanently fixed. Today we know there are some sorts of behaviors that do become genetically fixed, but we understand that the mutations

which produce these changes have nothing to do with transmitting the information by teaching and learning. There is a vast difference between behavioral transmission and genetic transmission of information.

In addition to the central difficulty of dealing with variation and heritability in the absence of Mendelian genetics, Darwin had other technical problems when he turned to sexual selection.[29] In general, discussions of sexual selection involve the concepts of sex-linked genes and the role of hormones in producing secondary sexual characteristics. These concepts, whose implications are pursued further below, were not available in Darwin's time.

Another, and quite different, class of difficulties arose because the only fundamental energy sources known to physics in Darwin's day were those associated with the electromagnetic and gravitational forces. Kelvin showed that if the sun's energy source was gravitational, it could not possibly have been burning for more than about 20 million years, and that chemical (electromagnetic) fuels would have given an even shorter life. A different calculation showed that it could not have taken more than around 20-40 million years for the earth to cool from molten rock to its present temperature. These two calculations meant that either the earth was at most a few tens of millions of years old, or that Victorian physics was fundamentally deficient. Faced with Kelvin's arguments, Darwin removed all numerical references to geological time spans in the third and later editions of the *Origin*,[30] and you will look in vain for any explicit chronology in the *Descent.* The discovery of the weak and strong nuclear forces has, of course, shown us that Victorian physics was indeed fundamentally deficient in some respects: the sun has burned nuclear fuel for nearly five billion years; and the heat generated by decay of

radioactive elements inside the earth invalidated Kelvin's calculations about cooling rates. Darwin was nearer our modern view in his first purely geological calculations; there is enough time to account for the evolution of man.

THE BOOK IN RELATION TO RESEARCH TODAY

PART ONE: THE DESCENT OF MAN

In Part One of the *Descent,* Darwin argues from comparative analyses of morphology and behavior that man is basically not different from other animals, and that what differences do exist are simply a matter of degree. His arguments about the bodily structure of man, with the exception of the brain, were relatively uncontroversial in his own time, and are entirely acceptable today.

The real controversy surrounding the relation between man and other animals in Darwin's time was essentially a problem of science versus religion. As we have mentioned, even Wallace wrote an essay saying the morphology of man could be entirely accounted for by natural selection, but that man's "intellectual and moral faculties . . . must have had another origin . . . in the unseen universe of Spirit."[31] Except for a disturbing resurgence of anti-intellectual fundamentalism in North America in recent years, this idea that the Creation must have supervened somewhere along the evolutionary line leading to man is no longer the issue. The idea has, however, been replaced by a doctrine held firmly by many social scientists. They see human culture and civilization as being something so special and so unlike anything elsewhere in the animal world that it can only be analyzed in its own terms, and not in terms of the level below (that is, not in terms of biology). The argument is interestingly similar to that of Wallace and other religious

people in the nineteenth century: the body of man is indeed a biological structure, clearly descended from the apes, but his culture, which stems from his extraordinary and unique mind, is on a new, higher hierarchical level of its own; evolutionary biology has nothing to tell us about this higher level. This resistance to exploring the possibility that principles of evolutionary biology can shed light on human societies is most recently demonstrated in the reaction[32] of some sociologists, anthropologists and others to E. O. Wilson's *Sociobiology: The New Synthesis* when it was published in 1975.[33] Indeed, many people continue to bring to these issues an unseemly degree of dogmatic certitude.

Setting aside the large questions of culture and social organization, there remain other human attributes—consciousness, morals, language, and other mental qualities—that many people, both in Darwin's time and today, believe clearly separate man from the beasts. In recent years, through the rise of the study of animal behavior, these ancient and entrenched views are again being challenged.

The whole question of consciousness has been reappraised by Griffin in his *The Question of Animal Awareness,* published in 1976.[34] This book, which makes full use of modern work in animal psychology and behavior, comes out strongly for the idea that the difference between man and lesser animals is one of degree, and that there is a continuum. The surprising thing is that when one rereads Darwin's *Descent,* although his facts are not the same, his main points seem completely consistent with the modern views of Griffin and those who have followed him.

More broadly, Darwin's M and N notebooks, and particularly those parts distilled into Chapters 3, 4, and 5 of the *Descent,* establish him as a seminal figure in psy-

chology. As discussed by Gruber, in the M and N notebooks "we can see the wide range of psychological topics Darwin touched upon in the years 1837-39; memory and habit, imagination, language, aesthetic feelings, emotion, motivation and will, animal intelligence, psychopathology, and dreaming."[35] The method, as illustrated in the *Descent* and in *The Expression of the Emotions in Man and Animals* (many of the insights of which are only just being rediscovered by contemporary psychologists),[36] is to search for mental resemblances between man and other animals, and to indicate the line that a more fully developed psychology might take. The *Descent* makes good Darwin's boast at the end of the *Origin*: "Psychology will be based on a new foundation, that of the necessary acquirement of each mental power and capacity by gradation."[37]

The more philosophical question of what evolutionary theory, and natural selection in particular, have to say about human morals and ethics has a long history. Most evolutionary biologists, Darwin included, have succumbed to the temptation to put in a word on this subject. These questions have seen a flurry of activity recently, much of it inspired by new studies in animal behavior. See, for instance, Wilson's *On Human Nature,* Alexander's *Darwinism and Human Affairs,* and the proceedings of a conference on *Morality in Animals,* edited by Stent.[38] Again, the surprising thing is that what Darwin has to say about the subject of these books seems so up to date.

On another philosophical theme, essentially all biologists would agree that Darwin's work, and particularly the *Descent,* disposed of the "mind/brain" dialogue once and for all. As Gruber observes, Darwin once expressed how inseparable he thought mind and brain were by bracketing "intellectual faculties" and "cerebral struc-

ture" as equivalent in a passage in the B notebook.[39] It takes much ingenuity and verbal cleverness, plus considerable ignorance of contemporary biological research, to keep this topic alive.

Before going on to take up sexual selection, we return to the general problems of the evolution of culture and social organization in man and other animals, and note some of the directions current research is taking. This survey of contemporary work in sociobiology is necessarily only a very superficial one.

Much of this recent progress stems from a clearer definition of just what it is that is being "naturally selected." Following the rediscovery of Mendelian genetics, the neo-Darwinian revolution of the first half of this century welded together Darwin's basic ideas about natural selection with a rigorous description of the way gene frequencies can change in populations.[40] The upshot was a precise definition of an individual's "Darwinian fitness," which essentially measures the net number of offspring that will, on average, survive to reproductive age. This Darwinian fitness clearly depends on many factors (all of which are therefore susceptible to evolution by natural selection): the probability of successful mating (which can depend in a complicated way on the mating system), the average ratio of males to females among the offspring, along with the more commonly stressed probability that offspring will survive the "struggle for existence," and themselves reproduce. This technical definition of fitness, however, leaves the focus on individuals and their direct progeny. Mainly as a result of the work of Hamilton,[41] it is now realized that the important thing is not how many direct descendants an individual has, but how many of his or her genes get into the next generation. Thus in a diploid sexual system such as possessed by humans, your own offspring share, on average,

half your genes, but your brother's children also share one-quarter of your genes, your first cousin's offspring one-sixteenth, and so on. An individual's input of genes into the next generation thus involves not only his or her own net reproductive success or fitness, but also those of all his or her relations, discounted by the degree of relatedness; this quantity has been christened "inclusive fitness" by Hamilton, and it provides a powerful tool for exploring the evolution of some kinds of social behavior.

In particular, the notion of "inclusive fitness" helps explain many apparently altruistic acts observed in nature, such as uttering an alarm call upon noticing a predator, or helping to raise a relative's offspring. Hamilton notes that most of the social insects possess a haplo-diploid sexual structure, whereby females are more closely related to their sisters than to their own offspring, and he suggested that this characteristic may predispose such creatures toward evolving the "eusocial" behavior actually found, in which the sterile female workers help raise more sisters. In the *Origin,* Darwin dwelt at length on the problems posed for his theory by the sterile castes among the social insects, seeing them as "one special difficulty which at first appeared to me insuperable, and actually fatal to my whole theory."[42] With typical insight, he saw that kinship structure within the colony could possibly provide an answer. But, lacking the formal apparatus of modern theory about "inclusive fitness," Darwin could not imagine the fascinating quantitative studies now being done on the social insects as test cases for the evolution of social behavior.[43]

Wilson's *Sociobiology: The New Synthesis* gives a synoptic account of research applying evolutionary thinking to the ecology and behavior of social groups. This research includes field, laboratory, and theoretical studies of territoriality, mating systems, the optimal size of

groups, communication within and between groups, social parasitism, energetic and other aspects of foraging, and a host of other things. Some good recent surveys are *Behavioural Ecology* by Krebs and Davies, the collection of papers edited with a commentary by Clutton-Brock and Harvey, and the proceedings of a Dahlem Conference held in 1980.[44]

Many of the studies are characterized by the sort of comparisons so much used by Darwin in the *Descent* and elsewhere. For example, Short has investigated the way various sexual characteristics (size of penis, breasts, etc.) differ among humans, chimpanzees, gorillas, and orangutans.[45] This general subject is touched on briefly in the *Descent,* and less coyly in the M and N notebooks. Short also shows that the patterns of morphological difference correlate well with the mating habits of the species. In a series of interesting papers, Clutton-Brock and Harvey[46] have compiled information about the ecology and social organization of primate societies, and have documented patterns of relationship between quantities such as population density, degree of sexual dimorphism (male weight divided by female weight), "socioeconomic sex ratio" (number of adult females per adult male in breeding groups), the size of feeding and of breeding groups, the size of the home range, and the daily path length of the feeding group. Bertram[47] has made a similar survey of the relation between the behavioral ecology and the social systems of the major vertebrate predators on the Serengeti (lion, leopard, cheetah, hyena, wild dog). Some of the patterns or "evolutionary rules" emerging from these comparative studies are, moreover, what one would deduce by applying optimality arguments to foraging.

As evidenced by the books by Wilson and Alexander referred to above, there is a current surge of interest

among biologists in the application to man of the principles of sociobiology. Also, many anthropologists are actively seeking correlations between the social activities of different human societies and the predictions of sociobiology.[48] As Barash observes in reviewing Alexander's book: ". . . research on animals can provide propositions about the manner in which natural selection appears to act upon behaviour, even complex social behaviour. Then these predictions—based ultimately on fitness maximization—can be tested cross-culturally. Thus, the world's human societies constitute a global experiment, with many varying cultures and one constant: our biology."[49]

One important aspect of the enterprise of applying to man the principles derived from the study of social animals has been the examination of the relation of cultural change to evolutionary change. If culture is considered the transmission of information by behavioral means, as Bonner has used the term, then, as he shows, one finds many examples of culture among animals that seem to foreshadow the remarkable ability of man to teach and learn.[50] This was understood by Darwin, and in the *Descent* he gives some good examples of behavioral transmission, or culture among animals. Some modern workers are making a bold attempt to understand the role of simultaneous genetic and cultural transmission in evolutionary change and to put the subject in a constructive theoretical framework. For this it is necessary to extend the technical apparatus of population genetics to embrace the effects of learning and teaching. Essentially, this widens the scope of population genetics to include Lamarckian inheritance of acquired traits. The creation of this body of theory has recently been begun by Cavalli-Sforza and Feldman, Lumsden and Wilson, and others.[51] One of the principal reasons we now seem to have pro-

gressed further than Darwin is that, while he appreciated the problems, he lacked one ingredient: genetics.

PART TWO: SELECTION IN RELATION TO SEX

Summarizing passages from the C notebook of 1838, Gruber shows that "in its nascent form the idea of natural selection is suffused with the special notion of sexual selection."[52] This contradicts suggestions that one reason for the extensive treatment of sexual selection in the *Descent* is that Darwin in later life felt impelled to emphasize it to prop up the weakened case for the more general idea of natural selection. Darwin did, however, see "sexual selection" as a mechanism somewhat distinct from "natural selection" (which he often tended to treat as pertaining to survival), and thought it worth pursuing at length in the *Descent.*

A more modern view sees sexual selection as simply one of many particular facets of general questions of natural selection. As we have already pointed out, the current definition of Darwinian fitness deals with an individual's total genetic input into the next generation, and thus includes consideration of mating systems and sex ratios along with simple survival to reproductive age. Thus a species' physical and biological environment is seen as influencing the kind of mating system it adopts (for example, monogamy, polygamy, promiscuity), which in turn influences the evolutionary premium likely to be put on sexual displays and dimorphism. These sexual factors simply have to be weighed along with other factors having to do with foraging, defense, and survival in general; Darwinian fitness is the appropriately weighted sum of all these factors, and it is upon this overall quantity that natural selection acts.

These ideas may be made concrete by considering the evolutionary forces that can bear upon an organism's

color.[53] First, color is influenced by questions of getting your own food and avoiding being food for other animals. This can lead to camouflage, both for prey (zebras; arthropods that look like bird droppings or leaves or twigs) and predators (tigers; mantises; angler fish). Alternatively it can lead to brightly colored advertisement of distastefulness or poisonousness; associated with this is mimicry, either Mullerian (where two distasteful species look the same, so that predators have less to learn) or Batesian (in which an edible species cheats by simulating the coloration of a distasteful one). Second, thermodynamic considerations of keeping warm or cool or (for some desert-dwelling burrowers) changing temperature rapidly are influenced by color. Arguably, large herbivores with no significant predators are likely to have their color determined by thermodynamic efficiency; hence the dull gray of elephants, rhinoceroses, and hippopotamuses. Third, sexual selection may give an advantage to brightly colored males or, less commonly, females.

Which of these several factors will assume predominant influence depends on the ecology of the species. Sometimes the explanation remains unclear; there is still debate as to whether polar bears are white for thermodynamic reasons, or for camouflage as they stalk their prey amid the snow and ice. Some recent studies give beautiful examples of the tensions that exist between coloration for sexual selection and for predator avoidance. To mention one, Endler has shown that male guppies living in the rivers of Trinidad have very bright red spots if they are in a section of the stream where there are no predators, but in sections where there is heavy predation from another fish, the male coloring is much subdued.[54]

A reading of the *Descent* reveals that, basically, Darwin understood all this. Moreover, his ideas about sexual

selection, as such, are essentially correct (which is just one more reason for the general respect in which he is held by biologists today). But the dichotomy between sexual selection and natural selection (usually taken by Darwin to refer simply to survival) is discordant with contemporary usage.

Many recent studies of sexual selection are in the spirit of Chapter 16 of the *Descent,* in which Darwin uses ecological insights and comparative studies to identify six classes of cases for the color of the plumage of immature birds in relation to that of the adult birds. For example, in *Ecological Adaptations for Breeding in Birds,* Lack[55] compiles information about the percentage of bird species that are monogamous, polygynous, polyandrous, and promiscuous. He relates these mating habits to the diet of the various species, and goes on to discuss the significance of the pair-bond and sexual selection in birds. Orians[56] has widened the discussion to consider the evolution of mating systems in both birds and mammals; he considers the general ecological circumstances favoring the various kinds of mating systems, and shows how this can explain such trends as, for instance, that 92% of all bird species are monogamous, while monogamy is uncommon among mammals. These and other patterns in mating systems and sexual selection are reviewed by Maynard Smith in his recent book, *The Evolution of Sex.*[57]

Male-female dimorphisms are not all necessarily forged by sexual selection. In some cases, the sex differences can be accounted for by ecological factors, usually an expansion of the niche of the species. Thus, on islands, the dimorphism between the beaks of male and female woodpeckers is often significantly more pronounced than for the same species on the mainland;[58] the woodpeckers use this device to broaden their niche, in the absence

of many species that constrain them on the mainland. Another example among birds is the remarkable dimorphism in the beaks of the now extinct New Zealand huia. In discussing the huia and other such cases, Darwin considers them primarily the result of natural selection due to ecological factors, but suggests the possibility that the dimorphism might also be initially affected by sexual selection. For further discussion, see Selander's chapter in *Sexual Selection and the Descent of Man*.[59]

As mentioned above, the discussion of sexual selection in the *Descent* is greatly hindered by Darwin's lack of understanding of the specific biological mechanisms producing differences between males and females. As a corollary to nineteenth-century ignorance of the mode of genetic sex determination in different animals, biologists were ignorant of the whole concept of sex-linked genes. Darwin saw that something of this kind was necessary to explain many of the phenomena he discussed, but there is a noticeable gap that we must close as we read his pages. We know now that in most animals, including vertebrates, which have been intensively studied, the genetic constitution and even the chromosome complement of the sexes differ. This means that the sexes may have different genes which affect their appearance on both the sex chromosomes and all the other chromosomes (autosomes). In humans, for instance, women carry two similar *X* chromosomes, while males carry only one *X* which is paired with a quite different *Y* chromosome. The result is that genes on the sex chromosomes may be expressed differently in the opposite sexes. To give an example, in a woman a single recessive gene at one locus on the chromosome will be suppressed by the dominant gene on the other, homologous *X* chromosome, and as a result she will show the dominant trait. However, in a man the recessive gene will be expressed as there is no homologous *X* chromosome to hold a

dominant gene. This exactly describes the situation of haemophilia where men suffer the disease if they have the mutant gene, but women will not have it if they have only one such copy. More generally, characters connected with the appearance of males and females are carried on both the sex chromosomes and the autosomes.

By the same token, the role of hormones in the growth and divergence of secondary sexual characters was not known in Darwin's time. He came close to seeing the general idea; pointing out, for instance, that castrated males often appeared like the females or the young, But the detailed mechanism remained a mystery, and he could only talk vaguely about all the sexual characters working together to produce the extreme male coloration or structure. Today we know that sex can be genetically determined by genes on the chromosomes. But the way the differences between the adult male and female characters appear in mammals (which have been studied most intensively) is also by means of hormones. At an early age, usually in the foetus, certain genes induce the production of sex hormones in the male; the female, at least according to current evidence, differentiates directly without significant help from hormones. In the male the chemical messengers stimulate the growth of specific tissues so that both the primary and secondary sexual characters are altered from the female mode to the male. These include the characteristic structure of the genitalia and all the other features of bodily structure: hair distribution, absence of mammary glands, increased size, changes in the skeletal structure, some neuronal patterns in certain regions of the brain, and sexual behavior. Again it will be helpful to the reader to keep all this in mind in the appropriate places.

Another matter which was of concern to Darwin in the

Descent is sex ratios. This subject is again under intensive study because, as discussed by Fisher, and carried further by Hamilton, sex ratios at birth should also be considered in any general discussion of sexual selection and mating systems.[60] This is especially true as one moves from the vertebrates to the larger world of invertebrate species. In an elegant series of papers, Ghiselin, Charnov, Leigh, and others have combined theories of sexual selection and of sex ratios to show that it would benefit some kinds of animals to evolve the ability to change from female to male as they grow older.[61] Charnov has further shown in quantitative detail that some shrimp species conform to these theoretical predictions.[62]

Underlying all this is the question of the evolutionary advantage of sex itself. Why should a female produce offspring carrying only half her genes, when by parthenogenesis or otherwise she could produce clones of herself? The simple answer that the variability produced by sexual recombination makes for greater adaptability, and is therefore "for the good of the species," will not serve. Darwinian natural selection, in both nineteenth century and modern forms, has to do mainly with individuals, and selection for group characteristics has no simple place. The reasons for the evolution of sex remain of absorbing interest today, and are the subject of much argument; see, for example, the work of Ghiselin, Williams, and Maynard Smith.[63]

CONCLUSION

It is often said that a big difference between science and letters is that in the former the early works provide a foundation of what is to come, but they are no longer quoted. One never sees the name of van Leeuwenhoek

or Pasteur in the bibliography of a journal article in microbiology today, yet everyone agrees that their contributions were great milestones. But Shakespeare or, more appropriately, Dickens and Trollope continue to be read with interest and pleasure.

Darwin seems to fall into an intermediate category. He is still read and is cited, we suspect, more than any other nineteenth-century scientist. The *Descent*, for example, runs around forty entries annually in the Science Citation Index in recent years, and the number seems to be increasing. The reason, as we have seen, is that the ideas, the questions, and the methods set out in the *Descent* anticipate much of the work now going on at the frontiers of biology, psychology, sociology, and anthropology, as we try to grasp the evolutionary basis of social organization in animals. Darwin's books, and the *Descent* in particular, make it clear that many of our insights of the last few years were part of his thinking over a century ago.[64]

A Note on the Text

The text reproduced here is the first issue of 1871 of which 2,500 copies were printed (retailing for 24 shillings).* Some readers may wonder why we chose to reprint this first issue rather than a subsequent issue of 1871 or the second edition of 1874. The reason is partly that Darwin had an unfortunate habit, in his revisions, of rewriting some of the freshness out of the initial work.

* This is item no. 937 in the standard handlist, R. B. Freeman, *The Works of Charles Darwin: An Annotated Bibliographical Handlist*, 2nd ed. (Folkestone, England and Hamden, Conn., 1977).

He was very sensitive to criticism, and tried hard to satisfy all his critics by making appropriate alterations and accommodating conflicting points of view. This process is far more evident in the *Origin*, where the first edition nowadays seems much superior to the sixth and last edition. But, to some extent, the problem also arises in the *Descent.* Still, the later revisions do include several new examples which Darwin came across after 1871, some of which are interesting. In the 1874 and later editions he included a table of the principal additions and corrections made since the first printing. We reprint this table, taken from the 1913 edition, following the index in the present volume.

A case can be made for abridging the *Descent.* In the leisurely Victorian tradition, it is an enormously long work. Much of it consists of an overwhelming accumulation of all the evidence Darwin could bring to bear; in particular, Part Two, on sexual selection, includes some 400 pages in which all the instances of sexual dimorphism in the animal kingdom of which he was aware are described, one after the other. A good deal of this could be pruned without losing any of the ideas or the essential flavor of the book. Nonetheless, although such abbreviation could have produced a more crisply readable text, it was decided—for reasons of archival value and service to those who, with Darwin, enjoy the details—to reprint the original in full.

A do-it-yourself abbreviation is, however, easily accomplished. We suggest reading all of Part One on the descent of man (the first seven chapters). Then, after reading the introductory chapter of Part Two on sexual selection (Chapter 8), the reader may skip the next ten chapters (Chapters 9 through 18) which comprise the catalogue of examples of sexual dimorphism. Chapters 19 and 20, on sexual selection in man, should then be

read, as should the concluding and summarizing Chapter 21.

NOTES AND REFERENCES

1. H. E. Gruber and P. H. Barrett, *Darwin on Man: A Psychological Study of Scientific Creativity* (by H. E. Gruber), *Together with Darwin's Early and Unpublished Notebooks* (transcribed and annotated by P. H. Barrett), Dutton, New York, 1974. (Hereafter cited as GB.) M. T. Ghiselin, *The Triumph of the Darwinian Method,* University of California Press, Berkeley, 1969. B. Campbell (ed.), *Sexual Selection and the Descent of Man, 1871-1971,* Aldine-Atherton, Chicago, 1972.

2. GB, p. 179.

3. Gruber and Barrett (GB) give the chronology of the notebooks as follows: The notebooks on transmutation of species: B, July 1837-February 1838; C, February-July 1838; D, July-October 1838; E, October 1838-July 1839. The M notebook on "Metaphysics—Morals and Speculation on Expression," 15 July 1838-1 October 1838). The N notebook on "Metaphysics and Expression Selected for Species and Theory," 2 October 1838-1 August 1839.

4. GB, p. 10. The designation "Man, Mind and Materialism" is Gruber's, not Darwin's.

5. GB, pp. 338 and 370.

6. Quoted in GB, p. 252.

7. Quoted in GB, p. 243.

8. GB, p. 24.

9. T. H. Huxley, *Evidence as to Mans Place in Nature,* Williams and Norgate, London and Edinburgh, 1864. E. Haeckel, *Die Naturliche Schopfungsgeschichte,* 1868 (referred to on p. 4 of the *Descent*). A. R. Wallace, The Development of Human Races Under the Law of Natural Selection, *Anthropological Review,* May 1864. Reprinted in his book *Natural Selection and Tropical Nature,* Macmillan, London, 1895.

10. GB, pp. 203-208.

11. Charles Darwin, *The Expression of the Emotions in Man and Animals*, John Murray, London, 1872.

12. GB, p. 122.

13. Quoted in GB, p. 123.

14. Quoted in Ghiselin (see note 1 above), pp. 235-236.

15. Ghiselin, p. 236.

16. See, e.g., S. J. Gould and B. C. Lewontin, The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptionist programme, *Proc. Roy. Soc., B205*, 581-598 (1979), and references therein.

17. K. R. Popper, *Unended Quest*, Open Court Publishing Co., LaSalle, Ill., 1976. For an excellent critical analysis of Popper's position see B. Halstead, Popper: good philosophy, bad science?, *New Scientist, 87*, 215-217 (17 July 1980).

18. T. H. Clutton-Brock, P. H. Harvey, and B. Rudder, Sexual dimorphism, socioeconomic sex ratio and body weight in primates, *Nature, 269*, 797-800 (1977).

19. See C. Geertz, *The Interpretation of Culture*, Chapter 1 ("Thick Description, Towards an Interpretive Theory of Culture"), pp. 3-30, Basic Books, New York, 1973.

20. J. Monod, *Chance and Necessity: An Essay on the Natural Philosophy of Modern Biology*, Knopf, New York, 1971.

21. See, e.g., J. A. Gulland, The stability of fish stocks, *J. Cons. Int. Explor. Mer., 37*, 199-204 (1975) and B. M. May, J. R. Beddington, J. W. Horwood, and J. G. Shepherd, Exploiting natural populations in an uncertain world, *Math. Biosci., 42*, 219-252 (1978).

22. Ghiselin, *op. cit.*, pp. 188 and 189.

23. H. Litchfield (ed.), *Emma Darwin: A Century of Family Letters*, Appleton and Co., New York, 1915, Vol. II, p. 221.

24. The history of this problem is discussed, e.g., by G. De Beer in *Charles Darwin: A Scientific Biography*, Doubleday, New York, 1964, pp. 174-175, and more fully in D. Hull, *Darwin and His Critics: The Reception of Darwin's Theory of Evolution by the Scientific Community*, Harvard University Press, Cambridge, Mass., 1973, pp. 302-350. The basic scientific issues are lucidly set out by R. A. Fisher in *The Genetical*

Theory of Natural Selection, Oxford University Press, Oxford, 1930, Chapter 1.

25. The technical details here follow R. A. Fisher, *op. cit.,* pp. 4-5.

26. G. J. Mendel, Versuche über Pflanzen-Hybriden, *Verh. Naturf. Ver. in Brunn,* Vol. X, 1865 (the 1865 issue of this journal actually appeared in 1866).

27. G. De Beer, *op. cit.,* p. 179.

28. See. e.g., E. Mayr and W. B. Provine (eds.), *The Evolutionary Synthesis: Perspectives on the Unification of Biology,* Harvard University Press, Cambridge, Mass., 1981.

29. For an introduction to the quantitative theory of sexual selection, see, e.g., P. O'Donald, *Genetic Models of Sexual Selection,* Cambridge University Press, Cambridge, 1980.

30. See front matter of the third edition (1816) of the *Origin.*

31. Quoted in GB, p. 31, from A. R. Wallace, *Darwinism: An Exposition of the Theory of Natural Selection with Some of Its Applications,* Macmillan, London, 1889.

32. See, e.g., M. Sahlins, *The Use and Abuse of Biology: An Anthropological Critique of Sociobiology,* University of Michigan Press, Ann Arbor, 1976 (a critical review of this book is by N. Humphrey, *New Scientist, 75,* 30 [7 July 1977]); A. Montagu, *Sociobiology Examined,* Oxford University Press, Oxford, 1980; C. Geertz, Sociosexology (review of D. Symons, *The Evolution of Human Sexuality,* Oxford University Press, Oxford, 1979), *New York Review of Books, 26* (nos. 21 and 22), pp. 3-4 [24 January 1980]); G. W. Barlow and J. Silverberg (eds.), *Sociobiology: Beyond Nature/Nurture?,* Westview Press, Boulder, Colo., 1980; A. L. Caplan (ed.), *The Sociobiology Debate,* Harper and Row, New York, 1978.

33. E. O. Wilson, *Sociobiology: The New Synthesis,* Harvard University Press, Cambridge, Mass., 1975.

34. D. R. Griffin, *The Question of Animal Awareness,* Rockefeller University Press, New York, 1976.

35. GB, p. 221.

36. P. Ekman (ed.), *Darwin and Facial Expression: A Century of Research in Review,* Academic Press, New York, 1973. P. Ekman and H. Oster, Facial expressions of emotion, *Ann. Rev. Psych., 30,* 527-554 (1979).

37. Charles Darwin, *On the Origin of Species*, John Murray, London, 1859, p. 488.

38. E. O. Wilson, *On Human Nature*, Harvard University Press, Cambridge, Mass., 1978. R. D. Alexander, *Darwinism and Human Affairs*, University of Washington Press, Seattle, 1979. G. S. Stent (ed.), *Morality in Animals* (Report of a Dahlem Workshop), Verlag Chemie, Weinheim, 1979.

39. Quoted in GB, p. 21, from the B notebook, about September 1837.

40. For an introduction to the revolution wrought by Fisher, Haldane, and Wright, see e.g., J. F. Crow and M. Kimura, An *Introduction to Population Genetics Theory*, Harper and Row, New York, 1970.

41. W. D. Hamilton, The genetical evolution of social behaviour, *J. theor. Biol., 7*, 1-52 (1964).

42. Charles Darwin, *On the Origin of Species* (see note 37 above), p. 290.

43. R. L. Trivers and H. Hare, Haplodiploidy and the evolution of the social insects, *Science, 191*, 249-263 (1976). R. D. Alexander and P. W. Sherman, Local mate competition and parental investment in social insects, *Science, 196*, 494-500 (1977).

44. J. R. Krebs and N. B. Davies (eds.), *Behavioural Ecology: An Evolutionary Approach*, Blackwell, Oxford, 1978. T. H. Clutton-Brock and P. W. Harvey (eds.), *Readings in Sociobiology*, Freeman, San Francisco, 1978. H. Markl (ed.), *Evolution of Social Behaviour* (Report of a Dahlem Workshop), Verlag Chemie, Weinheim, 1980 (there is an account of this conference by R. M. May and M. Robertson, *Nature, 286*, 327-329 [1980]). See also H. S. Horn, Sociobiology, in R. M. May (ed.), *Theoretical Ecology*, 2nd ed., pp. 272-294, Blackwell, 1981.

45. R. V. Short, Sexual selection and its component parts, somatic and genital selection, as illustrated by man and the great apes, *Adv. Stud. Behav., 9*, 131-158 (1979).

46. T. H. Clutton-Brock and P. W. Harvey, Primate ecology and social organization, *J. Zool., Lond., 183*, 1-39 (1977). T. H. Clutton-Brock and P. W. Harvey, Evolutionary rules and primate societies, in P.P.G. Bateson and R. A. Hinde (eds.),

Growing Points in Ethology, pp. 195-237, Cambridge University Press, Cambridge, 1976; see also note 18 above. See also J. G. Fleagle, R. F. Kay, and E. L. Simons, Sexual dimorphism in early anthropoids, *Nature, 287*, 328-330 (1980).

47. B.C.R. Bertram, Serengeti predators and their social systems, in A.R.E. Sinclair and M. Norton-Griffiths (eds.), *Serengeti: Dynamics of an Ecosystem*, pp. 221-248, University of Chicago Press, Chicago, 1979.

48. See, e.g., the collection of papers on this subject put together by N. A. Chagnon and W. Irons (eds.), *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective*, Duxbury Press, North Scituate, Mass., 1979.

49. D. P. Barash, Human behaviour: do the genes have it? *Nature, 287*, 173-174 (1980).

50. J. T. Bonner, *The Evolution of Culture in Animals*, Princeton University Press, Princeton, N.J., 1980.

51. L. Cavalli-Sforza and M. W. Feldman, *Cultural Transmission and Evolution: A Quantitative Approach*, Princeton University Press, Princeton, N.J., 1981. C. Lumsden and E. O. Wilson, *Gene-Culture Coevolution*, Harvard University Press, Cambridge, Mass., 1980. R. M. May, Population genetics and cultural inheritance, *Nature, 268*, 11-13 (1977).

52. GB, p. 167.

53. W. J. Hamilton III, *Life's Color Code*, McGraw-Hill, New York, 1973.

54. J. A. Endler, A predator's view of animal color patterns, in M. K. Hecht, W. C. Steere, and B. Wallace (eds.), *Evolutionary Biology*, Vol. 11, pp. 319-364, Plenum, New York, 1978.

55. D. Lack, *Ecological Adaptations for Breeding in Birds*, Methuen, London, 1968.

56. G. H. Orians, On the evolution of mating systems in birds and mammals. *Amer. Natur., 103*, 589-603 (1969). G. H. Orians, *Some Adaptations of Marsh-Nesting Blackbirds*, Princeton University Press, Princeton, N.J., 1980.

57. J. Maynard Smith, *The Evolution of Sex*, Cambridge University Press, Cambridge, 1976.

58. R. K. Selander, Sexual dimorphism and differential niche utilization in birds, *Condor, 68*, 113-151 (1966).

59. R. K. Selander, Sexual selection and dimorphism in birds, in B. Campbell (ed.), *op. cit.*, pp. 180-230.

60. R. A. Fisher, *op. cit.*, Chapter 6. W. D. Hamilton, Extraordinary sex ratios, *Science, 156,* 477-488 (1967). G. C. Williams, The Question of adaptive sex ratio in outcrossed vertebrates, *Proc. Roy. Soc., B205,* 567-580 (1979). E. G. Leigh, *Adaptation and Diversity,* Chapter 3, Freeman, San Francisco, 1971.

61. E. L. Charnov, Simultaneous hermaphroditism and sexual selection, *Proc. Natl. Acad. Sci. USA, 76,* 2480-2484 (1979). E. L. Charnov, J. Maynard Smith, and J. J. Bull, Why be an hermaphrodite? *Nature,* 263, 125-126 (1976). J. H. Werren and E. L. Charnov, Facultative sex ratios and population dynamics, *Nature, 272,* 349-350 (1978). E. G. Leigh, E. L. Charnov, and R. R. Warner, Sex ratio, sex change and natural selection. *Proc. Natl. Acad. Sci. USA, 73,* 3656-3660 (1976). M. T. Ghiselin, The evolution of hermaphroditism among animals, *Q. Rev. Biol., 44,* 189-208 (1969).

62. E. L. Charnov, Natural selection and sex change in Pandalid shrimp: test of a life-history theory, *Amer. Natur., 113,* 715-734 (1979). E. L. Charnov, D. W. Gotshall, and J. G. Robinson, Sex ratio: adaptive response to population fluctuations in Pandalid shrimp, *Science, 200,* 204-206 (1978).

63. M. T. Ghiselin, *The Economy of Nature and the Evolution of Sex,* University of California Press, Berkeley, 1974. G. C. Williams, *Sex and Evolution,* Princeton University Press, Princeton, N.J., 1975. See also note 57 above.

64. We are indebted to G. Geison, M. Ghiselin, and H. Horn for their helpful comments on an earlier version of this introduction.