KEEP WALKING

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The title of my lecture is derived from an experience that I had while correcting the proof of my *Introduction to Population Ecology* (Yale University Press, 1978). I had just taken several galleys to the press and was walking back to my laboratory when I passed a favorite hawthorn tree that reminded me of Glastonbury in England. As I passed the tree I realized, I know not why, that fabricational noise, discussed in later passages of this lecture, might be of considerable importance in human evolution. I turned round, walked back to the office of my editor and friend, Jane Isay, and asked if I might add to the footnote now on p. 175, a preliminary statement of what I had been considering on my walk. She merely put her arms round my shoulders, kissed me, and said "keep walking." I think that this expresses what I want you of the audience to do. There is clearly a great deal of ground to cover but I believe that it will be unexpectedly productive, if everything that you see is looked at imaginatively.

I want to call attention to five matters concerning human evolution, all derived from thinking about other aspects of biology, all of them suggesting possible lines of advance, all of them incomplete, and some of them perhaps of considerable importance to our species. There is clearly a long but very interesting walk for anyone who wants to embark on it.

K-selection and r-selection

If we express the growth of a population by the simplest kind of equation giving an upper limit, writing as Verhulst (1838, 1845, 1847) did,

$$\frac{dN}{dt} = \frac{rN\ (K-N)}{K}$$

the rate at which the population reaches equilibrium will depend on r, the unrestricted birthrate per individual, and on K, the amount of space of some sort that the environment can supply to the individuals of the species. In so far as the population is tending to fill K at a rate determined both by r and by the proportion of the as yet

unused habitat, which at any moment is given by *(K −N) /K*, we have two processes occurring. These processes have been conveniently called *r*-selection and *K*-selection by MacArthur and Wilson (1967). In the former process any differential survival altering the genetic composition of the species will depend largely on differences in birth rate; in the latter any evolutionary change will depend more on the efficiency with which the environment is used. Those of you who have paid attention to the politics of demography will realize that *r*-selection is primarily involved when simple competition takes place in rapidly growing, food-limited populations. However, populations where human birthrates fall in a way that seems unpredicted by the equation, being lowest where resources are most adequate, are more involved with K-selection. Unfortunately methods of how to secure maximum efficiency are seldom effectively discussed. Differences of this sort, largely unanalyzed, can lie at the bottom of various kinds of racism and other undesirable violence. It is extremely important in arguments of this kind that everyone involved learn as much as they can before they lose their tempers and that they keep a deep understanding of the facts that are freely available before any action is taken prematurely and in an unloving way.

The Genetic Screen

In all problems involving the variability of *Homo* we run into a most curious situation. There are a large number of differences between one specimen of *Homo sapiens* and another. A great many involve skin color or complexion, minor differences in the soft parts and skeleton, texture of hair and the like, which are clearly inherited. Using the kinds of criteria employed by systematic mammalogists for rodents or other small mammals in the early half of the twentieth century. Homo *sapiens* would probably have been divisible into hundreds of geographically well defined subspecies. None of these are really of any obvious adaptive significance at the present time, though under different climatic conditions before the invention of clothing and housing, they well might have been.

A variety of individual differences in temperament and intellectual ability are clearly characteristic of *Homo*. These differences may be explained by experience, by the influences of home life and by formal education. Our species is a difficult one to belong to and intense natural selection has no doubt operated to fit it for adjusting to this difficult role, so that the modal qualities of every population are reasonably

adequate. We may in fact find ourselves postulating that, though the physical variability is very great, the inherited psychological variability is probably much less so. In order to be able to use our overall genetically determined brain we may have some mechanism that screens out casual genetic variability so that the needed variability can be actually learned and not dependent on a slow Darwinian type of natural selection. This is probably implicit in the teaching of most social scientists but the explicit aspects of the process are seldom made clear, at least in a balanced way.

Fabricational Noise

What may well be a very important kind of variation in man, animals and plants has been termed fabricational noise by Seilacher (1973), though his discussion deals with a rather more limited range of cases than is discussed here. At least two aspects of what is fundamentally the same sort of phenomenon can be distinguished. To introduce the subject I would call attention to a very common morphological characteristic easily observed on many pairs of human hands. Here the veins visible from above are clearly very asymmetrical and seem to run from the muscles in a most irregular way; there is in fact little evidence of the fundamental bilaterality that the most elementary knowledge of vertebrate anatomy would lead one to expect. There is some pattern that enables the veins to function, drawing blood from all the fingers. We do not find any area totally devoid of functional vessels, nor is any part of the organ clearly provided with impractical wide channels; there seem to be very definite tolerance limits, as an engineer would say.

If we compare two hands, the seemingly random-looking designs are markedly different, but since their possessors largely live normal lives, the natural limits laid down by natural selection are presumably adequate if not quite geometrically elegant. It is very likely that if it were not for the forces imposed by locomotion more irregularity would be evident. Considering again our pair of hands, it is clear that in some cases a fair amount of fabricational noise may be tolerable. What I want to suggest is that in an organism or a population in which the tolerance limits are not too binding, the noise very occasionally may produce something extraordinary, not transmitted genetically but functional if imitated or copied.

As an essentially hypothetical example of the kind of thing of which I am thinking, I would merely mention some possible exceedingly rare accidental

non-genetic change that might have been, for example, behind Kurt Gödel's being able, unlike any other person, to produce his incompleteness theory. This theory proves that, in any system rich enough to produce a foundation for mathematics, statements can always arise that can neither be proved nor disproved in the system. In an elementary way this means there is always something to do, at least to find out whether we have come upon one of the intractable statements. I chose this example not because there can be anything further known of its genesis but because it has been called the most remarkable intellectual result of the century. Moreover given a fairly good high school course in mathematics, a copy of Wilder's admirable book on the foundations of mathematics, and a fair degree of patience, it is possible for the non-specialist to work through the proof and gain some experience of the beauty of this kind of mathematics.

Helpers and Homosexuals

In the social insects, as Darwin recognized, there is a peculiar kind of natural selection, which would now be called kin selection, I favor of the production of queens that produce enormous numbers of nonreproductive workers, Several genetic situations exist in the various species of these insects. The mechanisms by which this happens depend on the cytology of sex determination in these insects. It is a matter of great satisfaction to me that I had for many years as a colleague and close personal friend the late Professor Alexander Petrunkevitch who, as a young man in Wiesmann's laboratory in the beautiful German city of Freiburg, put the finishing touches on the roles of the queen, males and workers in the development of the honeybee.

In some vertebrates, notably birds and mammals, a certain number of young may act as *helpers* to the reproducing adults which may gain a considerable advantage from the additional help that they receive. There are a number of possible ways in which this may occur. By far the most extraordinary case of this kind in vertebrates, if adequately established, relates to homosexuality in human males. Kallmann (1952a, b) has shown by his study of the incidence of homosexuality among male twins that there is strong evidence of some genetic determination of the condition, though without twin studies this is not easily apparent. The incidence of homosexuality in human males is quite high, about 10% of the population of reproductive age, belonging to Kinsey, Pomeroy, and Martin's groups showing mainly or only homosexual behavior three years prior to interview. Such evidence as has been thought worth collecting supports the

simple-minded theoretical low incidence of paternity in the group. We are therefore faced with a significant problem in population dynamics. It seems unlikely that the condition is disappearing from western populations. The very high incidence suggests that an excessively high mutation rate would have to counterbalance the low fertility and it would therefore seem probable that some sort of kin selection is occurring.

Hutchinson supposed that the helpers are heterozygotes; Trivers (1974), Spieth (in Wilson 1975) and to some extent Wilson (1975) that homosexuals are themselves in effect helpers.

There seems no adequate evidence about this but since my paper (1959) I have had called to my attention at least a single case of an unmarried man exhibiting supposed hints of homosexual behavior and acting in an exceedingly helpful way to a brother who, much too old, had been in the First World War and then suffered from a complete breakdown after very intense responsibility in conditions of great danger. The help that this possibly homosexual brother gave to the soldier, his wife and two children, was very great. It would unfortunately be very difficult to give an adequate statistical estimate of whether this help was more than normally fraternal. At least the observations do not go in the wrong direction. All the principals in the story are now dead. The considerable efforts now begin made by intellectual homosexual men to encourage socially helpful types of behavior are obviously very desirable but may make statistical treatment of this matter somewhat more difficult.

The whole situation with regard to lesbians is clearly of the greatest interest. It may also be noted that the role of parental wishes in the choice of mates, the whole question of artificial modes of sexual decoration and of the mild forms of fetishism which are a normal part of behavior in many societies might have selective effects which are unexplored. If the present speculations have any basis in fact, all sorts of minor selective processes may be happening under our eye. They should not be regarded as too frivolous for investigation but rather as possibly concealing unsuspected aspects of human development.

Knowing What One Is Talking About

At the end of my lecture, I want very seriously to consider what I think is probably the most important kind of practical question with which we are faced in dealing with the interaction of evolutionary and ecological biology with the practical

affairs of daily life. Though much here depends on the kind of political philosophy that we adopt, I take it that all of us will want a society free from war, hunger and disease, a society affording respect to all the kinds of people living in it and full satisfaction of the spiritual wants that are so hard to define but of which any lack is so patently obvious. From the scientific point of view that comes natural to me, I think I am right in saying that at least one primary requirement of such a society is that we should know what we are talking about. The process by which we learn to do this is I think best conceived as education (*educare*, Latin, to lead out), being led out of darkness and error into light and truth. I am happy to live in a house where even the telephone is educated and engaged in propaganda for the subject. At the present time almost every political decision contains some reference to a partially scientific problem. If we take as examples either adolescent pregnancy or the economic paradox of excessive food production in a locally hungry land, we find that basically the solutions involve the properties of the human female reproductive system, or the problems of the ecological succession of crop plants and the economic ethics of their growth. Moreover in all cases the proposed solutions must be carried out in a way that does not produce large-scale ecological changes that prevent the acquisition of new knowledge. I believe that in the next hundred years the results of work by ethologists will make many suggestions towards penetrating the obscurities of ethical and artistic behavior, and that the preservation of stocks of mammals, birds and many other animals can make ultimate contribution to the understanding of such problems as human aggressiveness. It is for this reason that I feel strongly about the preservation of whales since their songs appear to be the most complicated animal productions—shall we call them animalifacts—available for study.

I will formally close with a most curious problem. Our initial approach involved reproduction and selection by some population, human, animal, plant or protist. We know that in the production of domestic varieties, now usually called cultivars, the process of artificial selection has been extremely important. Until recently the variations selected have been mainly the results of random cytochemical events. The extraordinary advances made in molecular genetics in the past decade suggest that a directive kind of change already active in some plants and protists will ultimately be available throughout the living world. We shall not only have artificial selection but also artificially directed variation and thus a whole artificial evolutionary process. Whether we shall be wise enough to handle this may be problematic. What is curious about the case is that we will

have reached a technical position from which direct interference with evolution, human or otherwise, will be possible in some parts of a culture in which politically powerful people, notably the fundamentalists of North America, can maintain that the evolutionary process does not exist in a serious from. Unfortunately, I have not found out how far this situation may exist outside North America.

From my student days in England, I remember seeing posters outside a newspaper stand about the Scopes Traial in Tennessee. This seemed highly absurd, indeed quite laughable. That the issue should now be widely propagated electronically in several other states sixty years later would then have appeared incredible. The matter is one of importance because the general approach of the fundamentalists involves a position as antipathetic to any valid religion as it is to science.

It is obvious that whatever our personal religious and scientific beliefs may be, they cannot be both valid and opposed. My own feeling is that extreme anti-intellectual fundamentalism is primarily doing an immense disservice to religion as well as to science. From the phrasing of the purposes of your foundation, I suspect that I am here in sympathetic hands.