Chapter 10. THE SOCIOBIOLOGY HYPOTHESIS

> Culture represents "the cumulative effect of inclusive-fitness-maximizing behavior (i.e, reproductive maximization via all socially available descendant and non-descendant relatives) of the entire collective of all humans who have lived.
>
> Richard Alexander (1979:68)

I. Introduction

A. Recap of Arguments

In this chapter and the two that follow, we will address the question of how Darwin's clever idea of natural selection might be relevant to humans. Think back a bit. We came to an understanding after the five empirical chapters (Chapters 3 to 7) that although the Stewardian notion of a culture core was a useful conceptual peg on which to hang our ideas about how social organization and culture might be related to ecology, the Stewardian method was unable to address adequately the issue of change; that is, the big "WHY" questions were not only still unanswered, but we actually had no tools with which to start tackling them. Then in Chapter 8, you were introduced to the idea of population thinking, which set the groundwork for the important material presented in Chapter 9, the concept of natural selection.

So now we know a little about the fruits of the discovery of natural diversity in human populations, and we have a theoretical tool—natural selection together with population-thinking—with which to start unraveling the question "*Can human evolution and diversity be seen as a product of natural selection and ecological heterogeneity?"*

B. Relevance of Natural Selection Theory to Humans

A number of physiological and morphological[1] *human characteristics are plausibly explained as the result of natural selection*. We talked briefly about skin color: that dark skin seems to be adapted to environments of high light, insofar as it protects from sunburn; pale skin seems to be adapted to low light environments, insofar as it facilitates the critical synthesis of vitamin D. There are plenty of other examples. For example, people tend to be squat and stout in cold climates and tall and lean in hot ones. The compact physiognomy conserves heat, and the slender one helps one to lose heat.

Selection on morphological variation has also been proposed for variations that we know from the fossil record have occurred over time. Thus, large brain size seems to have

1. having to do with the *form* and *structure* of an organism or any of its parts

come under particularly strong selection pressure in the period between 2 million and 1 million BP. Similarly for bidpedalism: evolutionary biologists and paleoanthropologists play endless games trying to guess what the important selection pressures were that may have accounted for some of these dramatic changes in the hominid lineage (we'll go into these more in a later chapter).

Whether natural selection has anything to do with human behavioral variation has been the subject of much controversy from Darwin down to the present day. Using natural selection theory to account for either current variability within humans, or for evolutionary changes that occurred amongst our ancestors, is central to the pursuits of biological anthropologists, paleoanthropologists and primatologists. It is important to remember this because, from this chapter onwards our focus is mainly behavior, and not the less controversial matters of anatomy and physiology. Before delving into a subject where everything seems debatable, it is important to reflect on the main message of the last lecture: biologists have no well verified mechanisms other than natural selection to account for complex, costly organs (Dawkins, 1987, cite in previous chapter). The human brain is a is a very complex, very costly organ. The human brain is the basis for human behavior. Natural selection works directly on phenotype, and only indirectly on deeper sources of variation. Behavior is the phenotypic product of the brain so natural selection could get at the brain only through acting on behavior. Does this mean that natural selection works on human behavior, or at least must have done so over the long haul as the brain evolved? Yes. Scientists are schooled to entertain doubts, but the alternatives to natural selection as an explanation for the evolution of human behavior are much more dubious. Natural selection wins the "least dubious" contest hands down. On the other hand, natural selection is a "big tent." There are many fascinating puzzles to solve in understanding exactly how natural selection has shaped human behavior.

II. Study of the Evolution of Behavior

A. The Beginnings

In biology the study of the evolution of behavior began its "golden age" only in the 1960s. Of course biologists prior to this date, such as the ethologists, Lorenz, Tinbergen, Hinde etc. had recognized this, but the theoretical developments of the 1960s stimulated a growth industry in a new subdiscipline called "sociobiology", from which sprang the modern versions of animal behavior and behavioral ecology. The term was introduced as the title to Edward O. Wilson's (1975) famous book *Sociobiology: A New Synthesis,* which celebrated the even then large body of evolutionary studies of (mostly) non-human animal behavior. Giraffes, for example, were no longer simply interesting to the biologist on account of the evolution of their long necks and long legs, but because of their behavior, for example, keeping offspring in communal daytime creches. How might natural selection have shaped the *behavior* pattern of a giraffe mother so that she takes her offspring to the creche, with one of the mothers staying behind to look after youngsters while the other adults go off and eat all day and then return to collect their young in the evening? Darwin had anticipated that these kinds of questions should come into the purview of the evolutionary biologist, but it was not until the late 1960s that systematic examination of these issues was begun.

B. An Example of Studying Behavior With Darwin's Theory

Before we examine how sociobiological hypotheses are applied to human behavior you should have some idea of how questions about the evolution of behavior have been investigated in non-humans. You need to know how to start thinking in a selection-minded way.

Consider starlings and how they hunt for insects in the soil in order to feed their offspring. Starlings must feed their ravenous nestlings with small larvae ("leatherjackets") that are found in the soil in the meadows surrounding their nesting areas. At the height of the breeding season a parent has to make about 400 round trips from the meadow to the nest in a single day. The question is how many leather jackets should the parent bring back each time? This might seem like an inconsequential question, but size of load brought back has a critical effect on the parent's overall delivery rate to the nest, which determines whether or not the chicks survive to become healthy fledglings. Juvenile starvation is a serious risk in starlings, so parental feeding skill and efficiency is under strong selection pressure.

Basically, a poor parental strategy would be to bring a single larva back each time; (like going to the grocery store and bringing back one item per trip). A better strategy might be for the parent to bring the largest number of larvae back that it can carry. But, because of the way starlings probe in the soil for leatherjackets with their beak, they become very inefficient searchers once their bills are full of larvae. This diminishing returns curve presents a starling parent with this problem: if it gives up larvae collection early, it spends a lot of time flying back to the nest with only a very small meal. If it struggles on until its beak is jammed full, its larvae collection becomes so inefficient that it would be better to fly back to the nest and feed the nestlings. If you do the math, it turns out that the optimal load depends on how far away the nest is from the leatherjacket meadow: if the meadow is distant the load should be heavier than if it is nearby.

The solution makes intuitive sense. Think how differently you pack and box your possessions depending on whether you are moving to a new room down the hall, or to a new college.

Incidently, Alex Kacelnik (1984, the author of the starling study) did experimental work varying the distance between nest boxes and feeding sites that showed that starlings did just what they should do if they had evolved to forage optimally under the guidance of natural selection. There are all kinds of complications that can be brought into this model, but the important message from this example is that we can make quantitative predictions about what we think the optimal behavior would be (given our knowledge of certain constraints) and then go and test our ideas in the field.

III. Sociobiology—Some Applications to Human Behavior

We now move onto two examples of some very similar kinds of thinking with respect to human behavior. We will consider these empirical cases first, and then finish up with a discussion of what assumptions underlie the studies that we have considered.

A. Birth Intervals, as Studied in the Kalahari !Kung

Deciding how long to leave between the production of each offspring is a major decision that must be made by every potential parent. If natural selection favors individuals who produce as many copies of their genes as they can, the simple prediction would be that parents should produce young in huge litters, and at very short intervals. Some organisms do this, but such a strategy normally entails great costs, both to the parent and to the offspring. The parent gets physically burnt out, and is likely to have a short life-span, and the offspring get little care or nurturance from their parent, and are much less likely to survive.

Human populations are quite variable with respect to the length of time they leave between each child as we discussed in the chapters on human diversity. A group that has drawn particular interest are the !Kung of the Kalahari, who have very long mean interbirth intervals of 4 years. Richard Lee, one of the early ethnographers of the !Kung (whom we discussed in Chapter 4), attributed this long interval to the necessity for mothers to carry their young children on day-long foraging trips. Collecting mongongo nuts, and digging up tubers, and then carrying everything back home to the camp in the desert sun certainly suggests that a mother who had to carry *two* children and all their food would have a very difficult life. Lee thought that having children any closer than 4 years[2] would pose intolerable stress on the mother. This was the first really ecological explanation for the slow population growth of the !Kung.

2. 4-year-old toddlers can follow their mothers through the desert without needing to be carried.

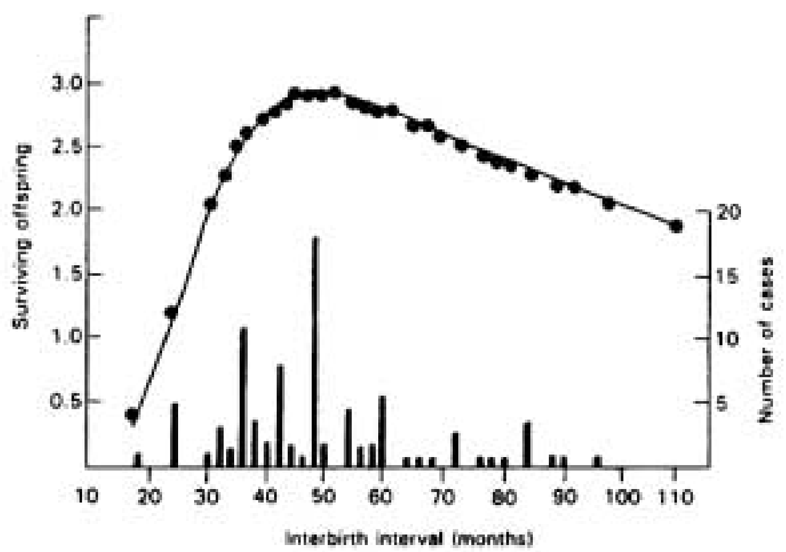
Lee's observations laid the groundwork for a very neat Darwinian model showing that the IBI of 4 years is the optimal birth interval. The thinking behind this is very similar to the starling example we considered earlier. A woman would "like" to have as many children as possible[3], but there is a cost: the cost of carrying and feeding these children.

Nicholas Blurton Jones (1986) examined the relationship between infant mortality and IBIs of different lengths. First he had to investigate the cost of short interbirth intervals to the child. Not surprisingly, he found that children born after very short intervals were much more likely to die, probably for the reasons Lee outlined.

Indeed it was only children who were born at more than 40 months after the birth of a preceeding child who had a greater than 50% chance of survival.

Does birth spacing maximize reproductive fitness among the !Kung? From this diminishing curve, and assuming a reproductive life-span of about 20 years (which is true for !Kung women), Blurton Jones could do a mathematical calculation to see how closely births should be spaced in order to produce the maximum number of *surviving* offspring. In figure 10-1, the curved line shows the results of this calculation. If a !Kung mother spac-

Figure 10-1. !Kung infant mortality as predicted by mother's backload and interbirth interval (IBI). (Source Blurton Jones 1986:99)



es all births at 25 months she can only hope to produce a little more than 1 survivor on average, because the chances of mortality for closely spaced children are so high. If she spaces children at 90 months, she can only produce 2 survivors, because she "wastes" so

3. What do we mean by this?

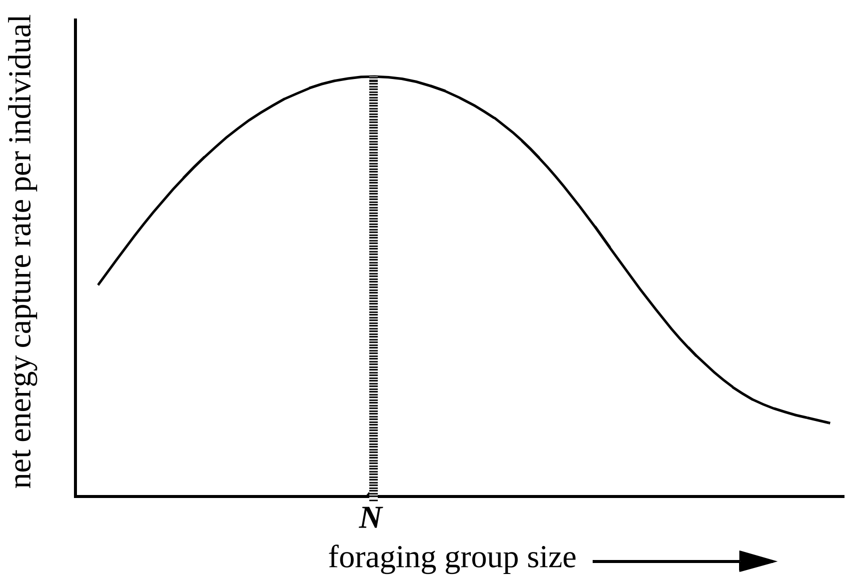
much time reproductively speaking. In terms of maximization of fitness, it turns out that it is best to space children at an average of between 45-50 months, a behavioral strategy that produces 3 surviving offspring. The bars in the figure show the distribution of empirically observed interbirth intervals; notice how these approximate the prediction from optimality theory, although there is an awful lot of scatter in the empirical distribution, In general, however, we can say that !Kung women are behaving more or less optimally with respect to the spacing of their births. By incorporating the weight of food needed to feed children, Blurton Jones developed a somewhat better prediction of the scatter of the real data.

B. Group Size

A simple sociobiological hypothesis would predict that people should select group sizes for foraging that maximize their own individual energy returns. Smith tested his hypothesis in a study of optimal group size among the Canadian Iniut. The Inuit hunt for different species of mammal, bird and fish in groups of very different sizes.

Essentially, while hunting efficiency might increase with number of hunters, the prey must be shared among a greater number of people. It is a very simple mathematical problem to calculate what group size is optimal for the individual in any particular hunt type, if you know the relative hunting success of different sized groups, and the amount of edible flesh on the carcass (Figure 10-2). Note, that in line with the Darwinian model, we are talking about *individual* energy capture; remember the emphasis on individuals kin Chapter 9..

Figure 10-2. Optimal foraging group size ($\hat{N}$) for any type of resource is described by the curve below. (Source: Smith 1981:42.)



Smith (1985) tested this idea, using data he collected on Inuit men engaged in 10 different kinds of hunts. These hunts include taking seals at breathing holes, winter caribou hunting, canoe seal hunts, spring goose hunts, ocean netting, lake jigging, etc. We show three examples. (See Figure 10.3)

Figure 10-3. Hunting group size in three different kinds of Inuit hunts. Note that in all cases, foragers often hunt in groups larger than that which gives the best returns, even when most hunts are undertaken by optimally sized units. Beluga hunts are apparently regularly undertaken by larger-than-optimal groups, but the sample size is small (From Smith, 1991).

(This image not scanned in, pasted up, 1994). Is your copy good enough to use for the paste-up, or do you need an original? Pete R

Ocean netting is the main form of fishing in the summer. Gill nets are set in coves and at river mouths for arctic char. Travel to and from nets is in canoes powered by outboard motors. Very high efficiencies are obtained by individual fishermen, but these decline rapidly as more men join in. (This is presumably because one man can do the job just as well as two or more, but has to share the catch). The data show that single hunting is almost always the most efficient group size, and also the most common. Smith therefore shows that with respect to this one area of Inuit foraging, people were behaving optimally.

If we look at ptarmigan hunting, the picture is very similar. In the late winter and early spring men go off on snowmobiles with.22 rifles to look for ptarmigan. Again both efficiency and group size frequencies peak at groups of one.

For beluga whale hunting, the picture is not so clear. For these hunts men go off on special purpose long distance canoe trips to known concentrations of beluga at estuaries in the early summer. Efficiency drops off markedly above groups of size 5 or 6, but larger groups were observed in 4 out of 6 cases.

Of the 10 different kinds of hunts Smith looked at, the model (most common) group size was also the optimal group size in 4 types, as with the ptarmigan and ocean netting. In two types, the results were equivocal, and in 4 others there were clearly other factors influencing how many people go out hunting together. In a later article (Smith 1985) some of these other factors are investigated.

IV. Discussion of Applications of Darwinian Models to Humans

A. Does Culture Make a Difference?

There are problems with a simplistic application of ideas developed in the study of animal behavior to humans. When we moved away from starlings and started thinking about the !Kung and the Inuit, you will may have been getting progressively more uneasy. The most prominent problem is one which was introduced in the first two chapters of this course—the fact that humans are probably unique with respect to the amount of information that is transmitted by non-genetic means, that is through cultural transmission, such as learning and imitation of the behavior of others. Cultural information can be transmitted laterally, can be borrowed and passed on between relative strangers, can be deposited in manuals, resurrected from history books, and can be invented and forgotten. This form of transmission is very different from the strict mendelian inheritance of genetically based traits. This is explored further in Chapters 11 and 12. Many social scientists argue that cultural transmission means that the effect of natural selection is completely obviated in the human case, and that quite other processes guide our cultural evolution.

Sociobiologists counter this objection by claiming that culture itself be explained from pure and simple natural selection thinking. Thus Irons (1979:39) argues that "Most forms of [human] behavior will either be biologically adaptive or will be expressions of evolved tendencies that were adaptive in the past." How could an elaborate capacity for culture have arisen in the first place unless this was true, so that directional selection could favor our big, complex, culture-managing brain?

This quote, and the one from Alexander in the epigraph, rests on two foundations, a deductive argument from Darwinian theory, and the empirical claim that most human behavior does indeed fit the theory. We have already considered some of the empirical evidence for this claim (birth intervals and hunting group size), and will turn to one more classic example, before investigating the assumptions of the sociobiological hypothesis.

B. The Yomut: A Classic Example of the Sociobiological Hypothesis

If culture is a product of natural selection, people who are viewed in their culture as particularly successful individuals should also be the people who have the greatest reproductive fitness. If successful people are the most likely to be imitated, then cultural success-will be a means of perpetuating cultural behaviors that make us successful in fitness terms as well. William Irons proposed this idea, and tested the proposition that cultural success might contribute to genetic success among the Yomut Turkomen pastoralists of Iran. He found strong correlations between wealth and culturally defined prestige, and genetic fitness[4]. Irons interpreted this to mean that culturally defined goals and objectives are actually those that favor genetic fitness.

Similar findings come from studies of hunter gatherers (the Ache of Paraguay), horticulturalists (the Yanomamo of Venezuela), agropastoralists (Kipsigis of Kenya), and many historical populations. Such studies can be seen as at least a step in the direction of showing that cultural differences reflect, at least in part, the behavioral strategies of people in different populations all over the world to maximize their genetic fitness. This is what Richard Alexander was getting at in the quote at the front of this chapter. Look at it again! Alexander is suggesting that everything in human culture is, one way or another, directly or not so directly, a consequence of individuals striving for reproductive success. A bold hypothesis!

C. Deductive Argument From Natural Origins

The capacity-for-culture must have arisen under the influence of natural selection, and thus culture must ordinarily result in adaptive behavior in the usual sense that evolu-

4. Measured as number of surviving offspring.

tionary biologists use the term. Practically no one familiar with modern evolutionary biology can doubt that humans are descended from non-cultural ancestors. Nor do most scholars have much doubt that natural selection is the most important directional force in organic evolution. The capacities that humans use to acquire, store, and use culture (large brains, hands, speech) are based on ordinary anatomical traits underlain by genes. If culture regularly resulted in maladaptive behavior, selection would have reduced or altered the capacity of culture to ensure that more adaptive cultural traits would be favored. The capacity for culture must be an adaptation, hence cultural variation must be adaptive in the usual Darwinian sense of increasing survival and reproductive success.

The standard sociobiological argument therefore depends on the "argument from natural origins" outlined above, and it can be caricatured as follows:

THE STANDARD SOCIOBIOLOGICAL ARGUMENT:

Forget about this business of culture being so terribly special. To a tolerable approximation, we can treat culture and any other mode of phenotypic flexibility, such as ordinary learning or conscious strategizing, as a mere means to an end—optimizing the number of copies of their genes that individuals pass to the next generation. The important thing is which behaviors maximize fitness in a given environment, not the details of whether (or in what proportions, or by what devious and complex interactions) such behaviors are produced by learning, tradition, or genetic influences. What counts is the bottom line—reproductive success, fitness. The evolutionist can depend on this maxim to generate interesting testable hypotheses, and eventually the broad answers to behavioral questions in any species will follow. The dull dogwork of describing all the proximal details of how this is accomplished can safely be left to pedantic psychologists; evolutionary reasoning will get us the ultimate answers straightaway.

D. Plausible Mechanisms

Our decision-making rules come from sensations, motivations, desires, etc. that insofar as they promoted survival and reproduction have been shaped by natural selection over our evolutionary past. The assumption underlying Irons' and Alexander's hypothesis is that individuals must chose amongst a variety of strategies, some of which are already in the cultural repertoire, some of which they must learn for themselves. These decision-making forces require preexisting rules for making decisions. The rules that guide these decisions must come from somewhere. It is plausible that selection on genes arranges the rules of human choice so that we tend to invent and imitate those cultural variants that do indeed have a tendency to enhance our fitness. For example, senses of pleasure and pain are by and large arranged to encourage behavior that promotes survival and reproduction. This is demonstrated by the fact that people who lack a sense of pain in some parts of their bodies because of various diseases are prone to serious injury of those parts. If your hand has no sense receptors, you are less likely to drop the hot pan. This, incidently, is a serious side effect of leprosy. (Of course, not all senses of pain and pleasure are completely trustworthy, as the prevalence of addiction to pleasurable, but harmful, substances testifies.) Our enjoyment of sweet things may be another important force guiding our decisions. A food that is sweet tasting probably lacks dangerous tanins, and certainly provides part of the necessary daily intake of carbohydrate. In the environment of our hominid ancestors, a genetically based enjoyment of sweet things was very likely to have been selected, as against a genetically based enjoyment of eating two-week old rotting carcases. (Again, the very cheap sugary foods in our modern grocery stores, can lead to pathological overeating of sugar). Now we get an inkling of how selection must have worked backwards from behavior to structures in the brain.

One of the essential things to keep in mind when thinking about sociobiological hypotheses is that the environment in which humans evolved genetically was quite different from the environment in which most contemporary humans live. For all but the last blink of human time, hominids were hunters and gatherers. The genetic adaptations we see today may therefore be expected to be consistent with a hunting and gathering environment. this lies at the root of one of the sociobiological hypotheses put forward for the modern demographic transition described in Chapter16.

Note that the sociobiologists' argument is not simple genetic determinism. People like Irons agree with the standard criticism of genetic determinism. There is little interesting genetic difference between, say, Turkomen and Anglo-Americans. Our standards of prestige differ from theirs for cultural reasons (a pilgrimage to Mecca carries no weight with us for example), not because Turkomen carry a Moslem gene and we do not! But, under the guidance of decision-making rules that are ultimately rooted in genes, cultural evolution is bent in fitness enhancing directions. (Some varieties of the sociobiological hypothesis, for example Lumsden's and Wilson's, imagine a larger role for genetic variation, see Boyd and Richerson, Ch. 5 for an analysis of various sociobiological positions.)

V. Conclusion

In our opinion the sociobiological hypothesis is a good argument. You will note that the mechanism (individuals choosing to do things as a result of basic genetic propensities that guide them in their decision-making towards the behavioral strategy that is most fitness enhancing) is what, in the next lecutre, will be called *guided variation* and *direct bias*[5]**.** Thus the sociobiological hypothesis is a first and important step in our attempt to develop cultural evolutionary models for human diversity. Be warned though, the next two chapters are going to dispute too literal a use of it. Treat it as something to build on and amend, not as something to reject out of hand, as some of its harsher critics have tried to do, perhaps because it threatens the "splendid isolation" of "Man" from the "beasts"!

In the next two chapters, we are going to do a bit of population thinking, and build a model to see how the processes we have been considering lead to evolutionary change. We are also going to consider under what circumstances it pays not to experiment with new forms of behavior: that is, under what circumstances it pays to follow culturally transmitted information blindly, irrespective of consequences on fitness.

VI. Bibliographic Notes

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5. Daly and Wilson (1988) provide a good example of how one can go about testing for the existence of this mechanism.