Primate Ecology and Human Origins:

Ecological Influences on Social Organization

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Chapter 14

In Summary

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In the introduction, we presented the viewpoint which we hoped to take in examining the relationship between primate social organization and ecology. We expressed confidence in the scientific method and outlined the premises which have traditionally been used in developing models or theories relating social organization to ecology. In the chapters that followed each of the authors developed specific theoretical approaches to the problem. Some developed the framework of a theory, defining terms and hypothesizing relationships among the constituent elements; others tried specific applications of various theories, whereas others examined relevant data in an attempt to test the explanatory power of a theory, or to suggest additional theoretical elements.

Thelma Rowell, in the first chapter, set the stage by challenging explanations and predictions based on presumed adaptive functions. She strongly suggests that this particular approach would be incapable of identifying data conditions under which the null hypothesis should be accepted, that is, those conditions under which we would accept the null that a behavior was not adaptive. Since we are limited only by our imaginations in the postulation of possible adaptive functions, support of a theoretical formulation on the basis of its "adaptive value" is useless. She concludes that a new look at our theoretical assumptions is required and begins the task.

Our other contributors take up the same task from multiple perspectives and, in the last chapter, Ueli Nagel proposes a new 341 conceptualization of the relationship between social organization and ecology. He uses a systems approach to develop a method for identifying the nature of interrelationships between behavior and ecology. This produces then not a new theory summarizing existing knowledge, nor an explanatory theory to account for what we know, but rather a new tool which can be used to obtain data relevant to the development of such theories. This is perhaps where we should be: collecting data and

testing hypotheses. It is far too early for any grand scheme, for we really know very little about: the elements of social organization or ecology which relate to one another, the causes of variation in social behavior, the evolutionary mechanisms which bring about such changes, the ontogenetic processes which influence social behavior, and the functions of the social mechanisms which we do see. Several authors in this book have examined the sources of variability which influence the expression of social behavior, which is also presumably directed at coping with a particular ecological pressure. Both human and nonhuman societies were examined, and multiple contexts were considered in attempting to gain an appreciation of the extent to which behavioral adaptations are in direct response to ecology. Phylogenetic heritage has to be considered, of course, but in an order noted for its generality and its plasticity of response, problem solving, learning abilities, information acquisition, and retention mechanisms must be closely attended to.

Behavioral adaptation thus may be a result of genetic mechanisms expressing themselves in a species typical environment, or a result of responses modified as a function of experience in an environment. Obviously these two sources of adaptation will interact with one another, and there are several variations of each. In terms of behavioral adaptations acquired during the lifetime of an individual, however, in socially living organisms it is useful to distinguish between responses acquired by direct problem solving experiences and those acquired by some form of social learning. Whether we call the information transmitted from one generation to another traditions, culture, or some less specific term, it is clear that we must consider the mechanisms of such information transfer and compare it to genetic mechanisms of information transmission in order to understand how social behavior may be responsive to ecological situations. The social organization in which social behavior is expressed is itself an outcome of behavioral interaction patterns. Social organization thus not only influences social behavior, but

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is defined by the pattern of expression of such behavior. The possible patterns of expression are limited by the characteristics of the members of the social unit, including their age, sex, and physical condition, and their relative numbers. The composition of the social group, its social structure, thus strongly influences the expression of social behavior and the organization of the unit. As such, we must consider these variables which influence social structure when we consider how ecology may influence social organization.

What began as an examination of existing theories relating ecology and social organization, ended as a major reevaluation of the entire approach to understanding such relationships. It was not a matter of testing, refining, and extending existing models, but rather an examination of basic assumptions. We discarded some premises and specified others and recognized that oversimplifications would be useless in understanding the outcome of the complex interface between behavior and environment.

No one needs to be told that the world is complex. What we need is identification and understanding of the principles which produce regularities consistently enough to permit useful prediction. Simplified approaches accept a level of variability in predicted outcomes, but in the present case, the level of variability remnant after accounting for one or two basic factors makes predictions useless. We shall have to develop more basic theories encompassing several of the major sources of variability.

In asking how ecology influences social organization, Bourlière begins by asking what are the relevant features in the environment which influence the individual. Parameters relating to energetic and nutrient sources, resource distribution and requirements, toxins, predator pressures, temperature limits, and so on are surely all relevant, but they cannot be studied in isolation from the individuals they impact upon. The quality of the habitat is assessed by the individual inhabitant who must be able to recognize and respond to resources. Mere presence is not enough to insure availability to the inhabitant. The individual's perception of the environment is thus crucial, rather than our "objective" measurement of the environment. It matters less what is theoretically available than what the individual accepts and utilizes. Our task in identifying the relevant ecological parameters is thus twofold, identification of the requirements of the individuals and assessment of the individual's responses to the available resource parameters. Neither task will be easy, but it is how the individual perceives and responds to the habitat

which will determine its success or failure in that environment.

Altmann and Altmann then remind us that ecological constraints will act through differential selection on life history processes. The outcome of reproduction in a single year will tell us little about differential genetic fitness of primates. A particular breeding strategy can only be evaluated in terms of reproductive success calculated over the lifetime of an individual. Selection operates on life history processes to influence ontogenetic rates, longevity, fertility, and reproductive strategies. It is these processes which account for demographic rates, such as age specific mortality and fertility, which are determinant of population compositions. The information contained in a life table reflects the product of demographic rate information and represents the population composition which may be organized into social units. The actual structure of a social unit influences the types and frequencies of social behavior and the pattern of social behavior expressed defines the social organization. Selection for social organization will thus be indirect and there will be a long feedback loop from social behavior to the influence on life history processes which will then feedback to influence social

The identification of the patterns of social behavior which may be influenced by ecology will, in and of itself, be insufficient to explain any particular expressed instance of social organization or social structure, for many variables may influence life history processes, in addition to the selection operating on social organization. Dunbar presents us with a specific example of a social organization influenced by demography. The social structure of gelada units strongly influences social behavior, but social structure is influenced by several random processes in addition to any selective pressures which modify life history processes. In relatively small populations the number of individuals of each sex born in any particular year may depart from mean equilbrium rates as a result of random events. The effects of a simple departure from equilibrium in a single year, however, will persist for many years into the future. Given differential ontogenetic rates for the two sexes, even if the ratio of births in the following year were exactly opposite, the long-term effects on social structure would not be balanced. Dunbar shows how departures from equilibrium may persist in a population for more than a generation, even if all but the first year were idealized equilibrium years. Random processes thus can have profound consequences for demography.

Perturbations in age-sex ratios can be demonstrated to have significant consequences on the social organization of gelada

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groups and appear to be responsible for some major shifts in the social behavior patterns of adult males. Moreover, the frequency of perturbations from mean rates in small populations, such as most primate social units, will be of sufficient frequency due to random processes such that idealized stationary life tables may never be achieved. As a consequence, we may expect social structure to vary over time in primate groups, and to the extent that social structure limits and influences social organization, we may find different social patterns described not only for different troops of the same species but also for the same troop at different times.

The implications of this conclusion for primate field work are profound. Not only will we have to contend with variability due to species differences and habitat differences, but we will have to recognize that the usual tenure of field studies, a year or two, is insufficient to describe the "average" social patterns, even for our sample of one. It is hard enough to gain recognition for the fact that each troop, no matter how large, is still a sample of one in studying social organization. Now we will also have to consider the variability of the obtained measure even in that sample of one.

Such considerations make attempts to relate the social behavior of a troop of one taxon in one ecology to the social behavior of a troop of another taxon in another ecology seem naive indeed. Baldwin and Baldwin, however, state that the process may not be the primary influence on primate social organization since, in the order Primates, ontogenetic processes may have enormous impacts on social relationships. In accordance with Rowell, and several other contributors, the Baldwins note the importance of traditions in primate social organization. but rather than considering tradition drift per se, they look at the mechanism of transmission itself. Socialization and other learning processes may be seen in terms of differential reinforcement of variable response systems. With the extreme plasticity of primate behavior, the Baldwins suggest that ecological influences on social behavior will most importantly be a function of individual histories in response to the environment, with only a small genetic component influencing behavioral adaptations to ecology. Phylogenetic inputs may therefore be virtually totally overridden by ontogenetic processes, and the impact of ecology upon primate social organization may best be studied in terms of direct reinforcement for particular responses.

From this perspective, primate social organizations may be very finely attuned to ecological situations. One might expect that responses patterns would be direct expressions of the

differential reinforcement individuals received for responding to ecological pressures with various available responses. In considering the primate with the greatest ability to modify behavior as a function of experience, Birdsell indicates that this is not so. A great deal of the learning that takes place is not a result of individual problem solving, but rather a consequence of the transmission of traditions. Traditional life-styles can be maintained even in the face of massive changes in the habitat; in fact, traditions are sustained not because they are optimal solutions to ecological problems, but because they are tolerable. Thus, no matter if social organization is adapted to ecology through genetic or traditional mechanisms, it is unlikely that we will see either one particular solution, or that we will see optimal solutions for any situation. A range of variability is to be expected with multiple tolerable patterns in any environment and the most prevalent and successful patterns will be those that are tolerable under the widest range of conditions. So much for the precision of adaptation.

Suzuki demonstrates this principle nicely in describing multiple nonhuman primate taxa living in the same habitat and the social organization of chimpanzees living in multiple habitats. The chimpanzee social organization can best be understood not by how it adapts the unit to any particular environment, but rather by how it succeeds in functioning across the range of environments in which the chimpanzee may be found. Even the same troop may drastically alter its environmental setting across the time span of a single year, and the social organization of the chimpanzee must include the flexibility to make the absolute changes required while still retaining the continuity of social organization under all conditions, such that troops may be organized and reorganized periodically without major disruptions.

Coelho et al. further elaborate on the theme of the tolerable in primate social organization by examining two New World primate species with dramatically different social organizations that live in the same habitat. Not only are the howler and spider monkeys at Tikal sympatric, but they apparently exploit much the same food resources and display only minor differences in econiches. Coelho et al. demonstrate that this condition can persist at Tikal, despite theoretical restrictions on competing species in the same niche, by showing that the aspects of habitat attended to normally, food distribution and abundance, are not the limiting factors at Tikal. In the face of superabundant food resources, the manner of exploitation of this resource matters little so long as it permits a sufficiency of resource to be collected and used. Whatever determines the carrying capacity at Tikal, it is apparently not caloric availability. Whatever it is though, it will be the primary selective pressure and we might expect niche differentiation between sympatric species only in regard to critical resources in short supply.

At the moment, however, it is not clear what the limiting factors are at Tikal and we can only speculate as to how the two different social organizations seen relate to features of the ecology. Clutton-Brock and Harvey develop a list of attributes which relate to ecology and hypothesize that where the distribution and density of food is crucial, certain consequences should be forthcoming. If food is generally the limit on primate carrying capacity, then home ranges, day ranges, population densities, and biomass should be lawfully related to food availability. They test this hypothesis by running correlations of these measures with all of the available data they could collect from the literature on all known primates. Their analysis is, by and large, restricted to the generic level and many of the values used are admittedly estimates, but they nonetheless find evidence supporting their hypotheses. Thus, food availability may be the major factor limiting the carrying capacity for primates in most habitats. Dietary strategies and phylogeny also influence the correlations, but the authors are encouraged by the results of this correlational approach.

Eisenberg looks at some of these same factors but develops the most all-encompassing approach to an understanding of primate social organization that we have seen. His perspective includes phylogeny, geology, and distributional data as well as the more usual measures. He covers the New World species in depth with a scope that is perhaps unique and no doubt reflects his interests in mammalogy as well as his special concern for broad principles of New World ecology. A massive amount of data from diverse sources is summarized to yield a comprehension of the problem which perhaps foreshadows the efforts that must be made to eventually understand the relationship of social organization to ecology.

If all of this information is needed to relate ecology to social organization, then what can we hope to achieve in understanding how a fossil taxon might have responded socially in the face of its now unobservable ecological situation? The first problem will be to discover what the behavior of the extinct taxon was, and the next to discover what the ecological pressures were for that taxon. Relating these two to each other will be no simple task, as indicated in the previous chapters, but the discovery and description of the data themselves will be the more serious obstacle to understanding in the case of extinct species.

If it were not for our interest in understanding our own origins, this task might be regarded as merely a formal exercise in extrapolating from models. As it is, however, the application of techniques is of intense interest to students and investigators trying to piece together the evolution of our own species. Loring Brace begins with detailed measures of a single anatomical feature, the cross-sectional area of the dentition, and shows us how much information can be obtained from this one measure and how this can be used in conjunction with other less exhaustive measures to piece together the story of our own origins. Although much ingenious speculation is required, and many of the details of social organization may never be known, certain broad limits on the social organization of early hominids can be deduced. These deductions are based on both measured data and theoretical premises. The basis for these premises lies in our understanding of the broad principles which govern the relationship between primate social organization and ecology. Tests of these models using extant forms thus strongly influence the premises found to be acceptable in deducing the social behavior of early hominids.

A more extensive model based on presumed ecological inputs to social behavior is provided by Campbell when he considers more recent hominids for which much more detailed information is available concerning both anatomy and the artifacts that relate to their activities. The existence of tools, shelters, and similar objects, consequent to activities, may be regarded in this case as "fossil behavior." When we understand the functions of artifacts we can reconstruct the behavior of their makers to a large degree, and thus bridge the time gap that might ordinarily separate us from a study of the impact of ecology upon the social organization or social behavior of extinct forms.

In conclusion, then, this conference may be regarded as laying the foundation for future studies relating social organization to ecology, including considerations of multiple factors. The mechanisms by which such influences may be expressed are presented and the expected limitations of methodology are discussed. Two major themes are developed by the contributors. In Summary

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First, we stress the importance of considering life history processes as they influence demography and the impact of demography upon social structure and ultimately social organization. Any narrower perspective is considered likely to have serious shortcomings. The implications for field studies should be clear. No single study of even two or three years duration will produce data which will characterize a species nor necessarily reveal a social organization which will be typical of the study group through time. Due to the time duration of primate life history processes, and the time course of demographic perturbations, the same society may show alternative social patterns as social structure changes. In the absence of stationary life tables, one must expect social change.

The second major point we should like to make is that evolutionary processes do not invariably produce optimal adaptations. Even where selection may operate to favor the best available social adjustment to a particular ecology, the critical word is "available." Neither mutations nor social innovations are produced on demand. The biological and social processes which produce variability in social organization are essentially random processes. As environments change, selective pressures change. Social organizations which are tolerably adapted to the new conditions may survive. Although the best of these may have some advantage, none may be optimal since neither biological nor social evolution is teleological. In fact, both genetic and ontogentic processes may be remarkably conservative in the face of changing conditions.

The major dichotomy of genetic and ontogenetic inputs to social behavior was examined in detail and the primacy of "traditional" input in ontogenetic processes was noted for socially living primates. The incredible similarity of function and consequence of mechanisms of genetic transmission and tradition transmission was revealed in detailed presentations of field studies of human and nonhuman primates. The mechanisms which modify and transmit information using the two modalities are essentially parallel and the same processes apply, although the specific mechanisms differ, and the time scales of effect are at least theoretically dissimilar. The process of change in both is one essentially of evolution, with genetic behavioral propensities and traditional modes persisting in so long as they are tolerable solutions to the problems of survival and reproduction in any particular environment. n the stant ional ty in

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