



OXFORD JOURNALS
OXFORD UNIVERSITY PRESS

Baboons, Space, Time, and Energy

Author(s): Stuart A. Altmann

Reviewed work(s):

Source: *American Zoologist*, Vol. 14, No. 1 (Winter, 1974), pp. 221-248

Published by: [Oxford University Press](#)

Stable URL: <http://www.jstor.org/stable/3881985>

Accessed: 19/10/2012 13:39

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Oxford University Press is collaborating with JSTOR to digitize, preserve and extend access to *American Zoologist*.

<http://www.jstor.org>

Baboons, Space, Time, and Energy

STUART A. ALTMANN

*The University of Chicago, Allee Laboratory of Animal Behavior,
Chicago, Illinois 60637*

SYNOPSIS. How are social organization and ecology related to each other? Yellow baboons, hamadryas baboons, and gelada monkeys are all large, terrestrial African primates, but they have three different patterns of social organization, and they live in three, markedly different habitats: savannah, steppe-desert, and alpine heather-meadowland, respectively. An attempt is made to provide testable hypotheses and heuristic principles that can relate these two classes of phenomena.

“. . . There is an adaptation, an established and universal relation between the instincts, organization, and instruments of animals on the one hand, and the element in which they are to live, the position which they hold, and their means of obtaining food on the other . . .”

—Sir Charles Bell,
Bridgewater Treatises,
1833

INTRODUCTION

There are two complementary, but quite different approaches to “explaining” social organization. One is reductionistic: an examination of immediate behavioral or motivational causes in the individuals that make up the social group. In baboons, this approach has been pursued most vigorously by Kummer, in a series of illuminating papers on the nature of social bonds and repulsions in hamadryas and their relatives (Kummer, 1967*a,b*, 1968*b*, 1971*b*). The alternative approach, and the one that we will pursue here, is to study the adaptive significance or ecological function of group processes. The distinction between what these two approaches seek is essentially that

made by Baker (1938) between proximate and ultimate causes.

Animal species differ in their habitat, and they differ in their social organization. The question is, are these differences related? To what extent do group processes represent adaptations to the exigencies of the environment? To what extent are differences in the success of a species in two habitats—or of two species in a single habitat—attributable to differences in group size, numbers of adult males and females per group, group responses to predators, spatial deployment of group members when progressing or foraging, differential use of parts of home range, simultaneous occupancy—by different groups—of zones of home range overlap, and defense of territories? If a population of animals were transplanted from the habitat in which they live to the kind of habitat occupied by a related species with a different social organization, would they survive? Would their social organization converge on that of the related species?

In the last decade these questions have begun to attract the attention of primate field workers and anthropologists (e.g., Chalmers, 1968*a,b*; Crook, 1967, 1970*a,b*; Crook and Gartlan, 1966; Denham, 1971; DeVore, 1963; Dyson-Hudson, 1969; Eisenberg et al., 1972; Fisler, 1969; Forde, 1971; Gartlan, 1968; Hall, 1965*a,b*, 1966; Kummer, 1971*a*; Rowell, 1967; Struhsaker, 1969; Vayda, 1969). The major tack taken in most previous attempts to relate primate ecology

Based on the Philip J. Clark Memorial Lecture, delivered at Michigan State University, May 18, 1972. Field research on primates was supported primarily by grant GB27170 from the National Science Foundation and MH19,617 from the National Institute of Mental Health. I am grateful to J. Altmann, M. Slatkin, and S. Wagner for a critical reading of the manuscript. I would also like to thank P. Olindo, Director of the Kenya National Parks, and D. Sindiyo, former Game Warden of the Amboseli Reserve, Kenya, for enumerable courtesies.

and social organization has been simple correlation, combined with *post hoc* explanation. First, a correlation is noted between a habitat and certain characteristics of primates living in it. For example, forest frugivores live in small multi-male groups, whereas savannah vegetarian omnivores live in medium to large multi-male groups (Crook and Gartlan, 1966). Then an attempt is made to "explain" the correlation in a pre-eminently reasonable fashion, e.g., greater visibility in open savannah country leads to larger groups. The most ambitious attempt so far to provide such a scheme of classification is that of Crook and Gartlan (1966). They classify primates into a series of five grades representing levels of adaptation in forest (nocturnal or diurnal), tree savannah, forest fringe, and arid environments, respectively. This scheme of classification has been revised by Crook (1970a), by Jolly (1972), and by Eisenberg et al. (1972). The latter make its basis explicit:

"When a group of allopatric species shares the same relatively narrow range of adaptation, then this group begins to exhibit a predictable 'adaptive syndrome' with respect to feeding, anti-predator behavior, spacing mechanisms, and social structure."

While such classifications may help organize large bodies of data, they must fail as explanatory devices. The reason is this: there are many different ways to exploit any habitat. Thus, food in a rain forest may be widely dispersed for one species and markedly clumped for another, as a result of dietary differences. Social communication and group coordination over distance may be easy or difficult, depending on sensory modality used, height of the animals in the forest, the particular plant complex, and so forth. Consequently, as we learn more about primates in the wild, we continue to find exceptions to the classifications. For example, contrary to the correlation noted in the last paragraph, several forest *Cercopithecus* monkeys are forest frugivores that live in one-male groups (Struhsaker, 1969), whereas patas monkeys live in savannahs in large one-male groups

(Hall, 1965a). At this point an attempt is made to change the classification (e.g., grassland species that inhabit partially wooded areas live in multi-male groups, those that inhabit more open grassland live in multi-male groups). The final result of such revisions will be either a classification that continues to lump together species that share some characteristic while ignoring species-specific characteristics, or one that copes with species diversity by describing social organization and ecology in a manner that is unique for each species, so that there is just one species per slot. Even then, there is no assurance that the particular characteristics of the habitat that have been used to make the classification are in fact the ones that are important to the animals.

STRATEGIES FOR COMPARISON

Comparative and correlational studies can be more informative if we take into account the taxonomic relations between the groups that are being studied. When we attempt to relate differences in group behavior to ecological factors, the populations that are compared may be either closely related or distant ("unrelated"), and their habitats or niches may be similar or dissimilar. This results in four basic types of comparison.

Type I: Comparison of unrelated organisms in dissimilar habitats is probably the least informative type, with one notable exception: convergent traits may illuminate constraints imposed by common factors in the two environments. For example, in a wide variety of habitats, large social groups, extending beyond the immediate family, may represent an adaptation to predation. Another class of common traits (e.g., suckling in new-world and old-world primates) consists of patterns that were no doubt present in the most recent common ancestor of both populations. Such ancient patterns (*plesiomorphous characters*, in the terminology of Hennig, 1966) delimit a broad adaptive zone that is characteristic of a major taxonomic group, but provide little information about ecological aspects of behavioral differences in contemporary

species. Distinguishing between these two classes of characters—convergent and ancient traits—must be made on the basis of other types of comparison (see Hennig, 1966).

Type II: Similarities in unrelated populations that occupy similar niches (e.g., behavioral and anatomical similarities in colobus monkeys and howler monkeys in old-world and new-world tropical rain forests) offer essentially the same information as in Type I comparisons, except that the greater number of common niche parameters can be expected to increase the number of convergent traits. Such comparisons are the mainstay of the “grades” of Crook and Gartlan (1966) and the “adaptive syndrome” of Eisenberg et al. (1972). Furthermore, where the species being studied occupy the same biome, one has the opportunity to study interspecific competition, niche separation, character displacement, and related phenomena. Such comparisons sometimes turn up striking cases of convergent or parallel evolution. An example from birds has been given by Cody (1968). In short grass, birds can probe the ground (e.g., meadowlarks, *Sturnella* spp.), launch into the air for flying insects (e.g., larks, *Alaudidae*), or forage from the foliage (most sparrows); and each short-grass area of the world contains probers, launchers, and foliage-gleaners, usually one of each.

Types III and IV: Studies of closely related populations provide some of the most illuminating comparisons. Particularly valuable are comparative studies of closely related species or populations in a group that has recently undergone a major adaptive radiation (Tinbergen, 1960). In such groups, species differences primarily reflect adaptations to the differing characteristics of the habitats,¹ and most species similarities will be homologs. For this reason, the hamadryas/cynocephalus baboon contrast that will be used in this paper is particularly revealing.

Within a single generation of one popu-

¹ One alternative is that they are different solutions to a problem that is faced by every species in the group.

lation, and thus with virtually no genetic change, one can sometimes observe changes in behavior and social organization that can be related to ecological factors. Such studies on a single population have the advantage of minimizing the effects of genetic differences and thus suggesting the extent to which intrapopulation variability reflects the plasticity of the individual animals. The changes in behavior and ecology may occur naturally and repeatedly, as a result of daily, lunar, annual, or seasonal cycles. In some cases, longer range secular changes in the environment occur, such as those that have been observed in our main study area for yellow baboons, the Amboseli Reserve of southern Kenya (Western and Van Praet, 1973). Alternatively, changes in the habitat may be artificially induced for experimental purposes. Planned interventions are of particular value in studies of limiting factors, of the sort that will be described below. If, for example, the spatial distribution of water is believed to limit the area exploited by a group, artificial water sources could be established. Watson and Moss (1971) have altered territorial behavior in grouse by increasing productivity of their heath, through locally applied fertilizer.

In addition to such temporal changes, geographic variability and habitat variations over space may sometimes be correlated with intraspecific variability in group processes. On a large scale, such comparisons involve macro-geographic differences. For example anubis baboons live in rain forests on the slopes of Mt. Meru, in verdant areas of the Kenya highlands, and in arid short-grass savannahs in the northern frontier district of Kenya. An illuminating study could be based on a sample of comparable ecological and sociological data in each of these habitats. On a much smaller scale there often are differences in the ecological conditions in the home ranges of groups in a local population, and these may be related to differences in group behavior and composition. Here again, one has the advantage of populations that have relatively small genetic differences.

Whichever type of comparison is made,

the initial effort will usually be simply an observed correlation of some ecological variable with a biological or behavioral characteristic. Such correlations are more convincing if populations or species that live in an intermediate habitat exhibit an intermediate form of the character. Particularly revealing comparisons can be made by making use of the following principle: A trait that is convergent for two species (or species groups) and that represents, for at least one, divergence from the corresponding trait of its closest relatives is probably an adaptation to distinctive features that occur in the environment of the two convergent species. For example, howlers of the new-world tropics and colobines of the old-world have specialized stomachs that are adapted to digesting high-cellulose leafy diets, and both of these groups of monkeys differ in this respect from their closest relatives. *Douroucoulis*, the only nocturnal primates of the New World, have many traits that diverge markedly from those of other new-world monkeys but are convergent with traits found in several nocturnal primates of the Old World.

Correlation by itself is not adequate. For example, group size in baboons is correlated (inversely) with aridity. But many other characteristics of the environment co-vary with this environmental factor. The test of any putative ecological determinant rests on a demonstration of its mode of operation. As Williams (1966) has put it, adaptation requires a mechanism.

ECOLOGY VERSUS PHYLOGENY

What about those traits of a species that are also found in closely related forms, despite differences in habitats? A recurrent question in recent discussions of the social ecology of primates is the extent to which primate social structure represents the phylogenetic heritage of the species rather than specific adaptations to the local environment. Struhsaker (1969) has emphasized that:

"In considering the relation between ecology and society . . . each species brings

a different phylogenetic heritage into a particular scene. Consequently, one must consider not only ecology, but also phylogeny in attempting to understand the evolution of primate social organization. The interrelations of these . . . variables . . . determines . . . social structure. In some cases, the immediate ecological variables may limit the expression or development of social structure, and, with other species and circumstances, variables of phylogeny may be limiting parameters."

As an example of the latter, Struhsaker points out that heterosexual groups with one adult male seem to be typical of most *Cercopithecus* species (excepting vervets) and of the closely related patas monkeys, despite the fact that there are considerable differences in the habitats and niches of these species.

Any "ecology vs. phylogeny" controversy over determinants of social behavior and group structures may turn out to be as sterile as the "hereditary vs. environment" controversy that has plagued the behavioral sciences, and for exactly the same reason. Indeed, these two controversies seem to be two aspects of the same problem. It can be avoided by asking every question in a way that suggests a verifiable answer, for example: To what extent are observed differences in the social behavior of two populations attributable to genetic differences between them? A number of research strategies can be used to answer such questions, including regression of variance in offspring against parents (Roberts, 1967), cross-fostering experiments (Kummer, 1971*b*), and studies of hybrid zones (Nagel, 1971; Müller, unpublished; Kummer, 1971*a*).

THE STUDY OF ADAPTATIONS

An alternative to this purely correlational approach is to analyze the adaptive aspects of group processes in each species, to propose testable (and thus falsifiable) hypotheses about the relations between specific aspects of social organizations and ecology in primates, and to test these on the basis of data from observational and

experimental research. Such an approach seems to me to be essential if we are to achieve something more than a "species-in-slot" comprehension of the ecology of primate societies.

In what follows, I shall present a number of organizing principles and hypotheses about relations between group organization and ecology. They are consistent with what is now known about the social ecology of baboons and geladas. I leave it to others to decide whether they have broader application than that.

The basic concept that will be developed here is that of an adaptive distribution of baboon activities:

"For any set of tolerable ecological conditions, the adaptive activities of baboons tend in the long run toward some optimal distribution away from which mortality rate is higher, or reproductive rate is lower, or both" (Altmann and Altmann, 1970, p. 201).

The so-called "principles" that will be presented below are intended to be heuristic guides in the search for such optima. They will be based largely on methods for analyzing intra-specific variations in adaptive behavioral processes.

A more deterministic viewpoint is expressed by Denham (1971, p. 78), who assumes that in energy acquisition, "the most efficient strategy compatible with the structure of the organism is used by members of a primate population in a natural habitat." Similar claims about the perfection of nature have been made by others. Denham's statement is either a tautology (because any other course of action would not be compatible with the structure of the organism) and thus analytically true, or else it is intended to be verifiable, in which case I believe that it is false. It seems more likely that in the efficiency of foraging strategies, as in many other traits, natural primate populations include a wide range of variability, and that there is a genetic component to this variability. Such variability is the raw material on which natural selection works and is a rich source of material for the study of adaptive aspects of behavior.

BABOON SOCIAL ECOLOGY

Baboons are among the best primates for analyzing ecological aspects of social organization. They live in habitats that range from evergreen tropical rain forest, through various types of woodland and savannahs, to semi-desert steppe country. In parts of Africa they are abundant and readily observable. Their groups include one-male harems and multi-male groups. They have been studied at several locales in Africa by a number of investigators.² For no other genus of non-human primates do we have a comparable body of information on behavior, social relations, population dynamics, and ecological phenomena.

Our discussion will center on two markedly different baboon populations, the hamadryas baboons (*Papio hamadryas*) of Ethiopia and the yellow baboons (*P. cynocephalus*) of east Africa. Further contrasts will be provided by gelada "baboons," a large, terrestrial primate of the Ethiopian Highlands, whose relationship to the other cercopithecine primates is uncertain. These three primate species—yellow baboons, hamadryas, and geladas—center on three quite different habitats: savannah, sub-desert steppe, and alpine heather-meadowland, respectively, and there are equally marked differences in their social organizations.

Hamadryas in eastern Ethiopia have been studied primarily by Kummer and his students (Kummer and Kurt, 1963; Kummer, 1968a, b, 1971; Nagel, 1971, unpublished observations by Kummer, Abegglen, Goetz, Müller, and Angst) and were observed by M. Slatkin and me during September, 1971. Yellow baboons have been studied most extensively in southern Kenya by us and our associates (Altmann and Altmann, 1970; Cohen, 1971, 1972; unpublished studies by the Altmanns, Slatkin, G. Hausfater, S. Hausfater, and Fuller). Both populations are still being studied.

² In 1972 alone, no less than 16 people were involved in field studies of baboons: J.-J. & H. Abegglen, S. & J. Altmann, R. & P. Dunbar, M. Fuller, R. Harding, G. & S. Hausfater, S. Malmi, W. Müller, N. Owens, O. Oyen, R. & D. Seyfarth.

Major publications on ecology and naturalistic behavior in other baboons include those by DeVore (1962), DeVore and Hall (1965), Hall (1965*b*), Rowell (1966, 1969), and Aldrich-Blake et al. (1971) on anubis baboons, and by Hall (1962*a,b*) and Stoltz and Saayman (1970) on chacma baboons. A number of other publications describing the results of recent studies are currently in preparation. Our knowledge of geladas in their natural habitat comes primarily from observations by Crook (1966), Crook and Aldrich-Blake (1968), and several recent unpublished field projects by Altmann, Dunbar, Nathan, and Slatkin.

The basic contrast in social organization and ecology between hamadryas and yellow ("cynocephalus") baboons³ have been described by Kummer (1968*b*, 1971*a*) and will only be summarized here. Yellow baboons live in social groups that usually

³ Under *P. cynocephalus*, Kummer includes not only yellow baboons (*P. cynocephalus, sensu stricto*), but the closely related chacma, anubis, and guinea baboons. The difference is immaterial for our present purposes.

contain more than one adult male, several adult females, and associated immature offspring. In the Amboseli Reserve, Kenya, yellow baboon groups ranged in size from 18 to 198 during 1963-64 with a mean of about 51. Mean group composition was 14.8 adult males, 16.5 adult females, 12.7 juveniles, and 10.5 infants. Within each group of yellow baboons a female often mates with any of several males during each menstrual cycle. These groups are virtually permanent: they do not routinely break up, either daily or seasonally. With very few exceptions, only males move from one group to another, and then, only as adults. Females generally spend their entire lives in the social group in which they were born.

Although yellow baboons live in a wide variety of habitats in central and eastern Africa, perhaps the largest area occupied by them consists of moderately arid savannah country, areas with variable tree cover but in which the dominant ground cover is grass (Fig. 1). In areas to the north and to the west, yellow baboons are replaced by

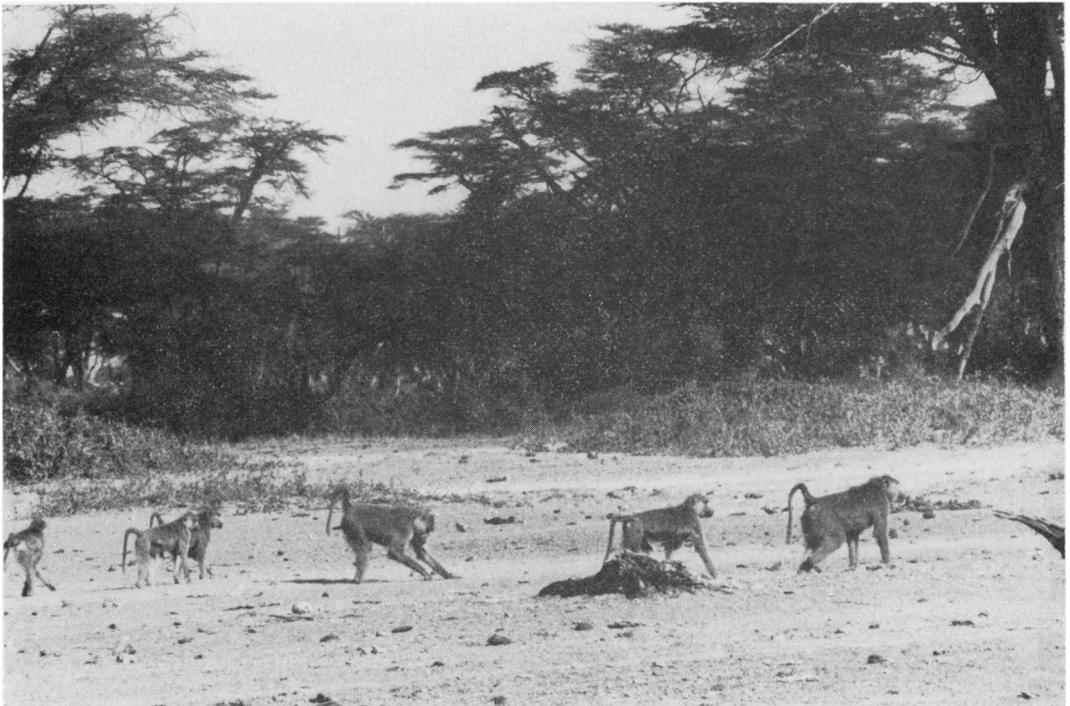


FIG. 1. Yellow baboons (*Papio cynocephalus*) in acacia woodland (Amboseli Reserve, Kenya).



FIG. 2. Arid desert-steppe habitat of hamadryas baboons (*Papio hamadryas*) near Gota, Ethiopia.



FIG. 3. Hamadryas baboons (*Papio hamadryas*).

anubis baboons, which often inhabit areas of higher rainfall and with a larger proportion of non-grass flowering plants as ground cover.

Hamadryas live in a much more arid region. They are sometimes called desert baboons, which I thought to be a misnomer until I observed them in Ethiopia, during a 1971 field trip. Their habitat represents an extreme environment for non-human primates; it is a region of high temperature, low seasonal rainfall, little soil, rapid erosion, and sparse vegetation (Figs. 2, 3).

A hamadryas population has three levels of group organization. Several bands—which in many respects resemble the groups in yellow baboons—join together in using the same sleeping rock, thus forming a large herd or troop. The membership of the band appears to be consistent, whereas that of the herd is not. On the other hand, the band may split into one-male units that forage independently dur-

ing the day (Kummer, 1968a).

Geladas, too, have harems that amalgamate into enormous herds, but for those that we observed in Ethiopia, the daily cycle of fission and fusion was exactly the opposite of hamadryas: the harems slept separately or in small clusters, each on a cliff ledge (Fig. 4), and then amalgamated into herds on the upland feeding ground during the morning. They foraged *en masse* until late afternoon (Fig. 5), then again broke up into harems. The heart of the geladas' range is the alpine meadowland of the Ethiopian Highland. They generally occur well above 7000 feet; my observations and those of Slatkin, Dunbar, and Nathan were made in the vicinity of Sankaber, at about 11,000 feet.

SOME PRINCIPLES OF PRIMATE SOCIAL ECOLOGY

Many of the ideas presented here have grown out of our early field work on



FIG. 4. Gelada baboons (*Theropithecus gelada*) on a sleeping cliff (near Sankaber, Simien Mountains, Ethiopia).

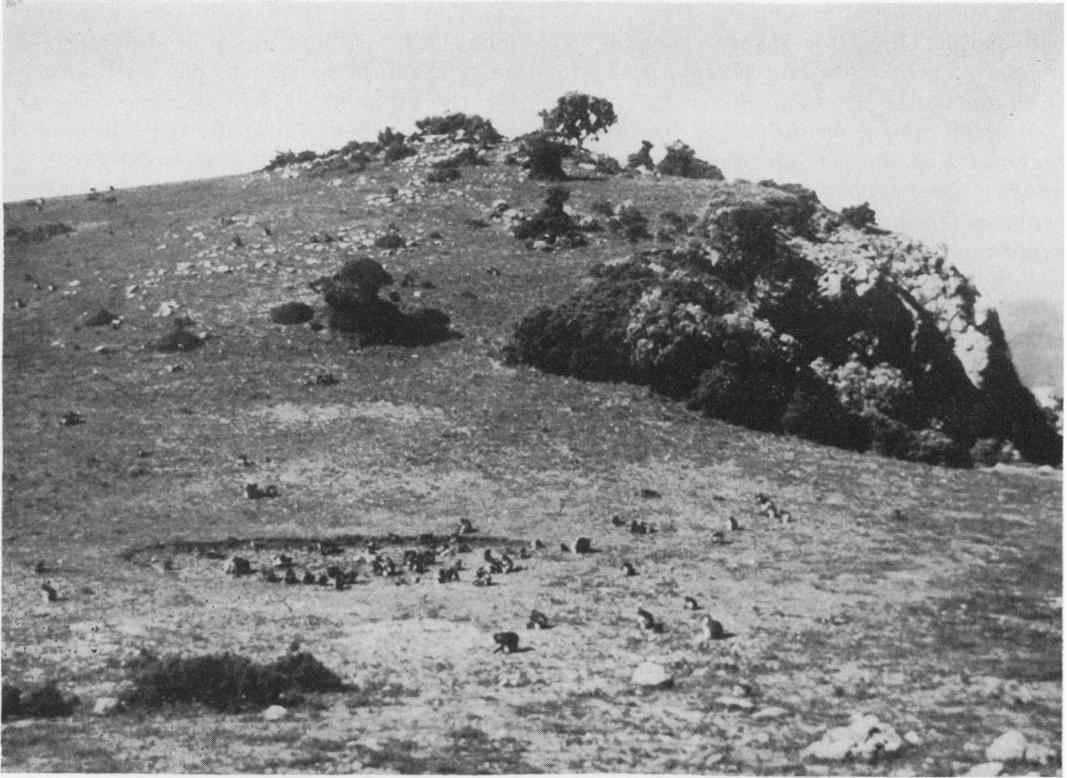


FIG. 5. Gelada baboons on an alpine meadow (same herd as shown in Fig. 4).

baboons, and some were published in *Baboon Ecology* (Altmann and Altmann, 1970). In some cases, similar ideas have been developed by others, including Denham (1971), Kummer (1971a), and Schoener (1971). The section on time budgets was stimulated primarily by a recent study of time budgets in yellow baboons and gelada monkeys by Slatkin (unpublished).

1) *Resource distribution and group size.* A group of vertebrate animals can grow as a result of just three processes: births, immigrations, or amalgamations with other groups. It can decrease in size as a result of deaths, emigrations, or group fission. Thus, any attempt to account for the immediate causes of the group size distribution in an area must be made in terms of these processes. This approach has been very successfully pursued with data on primate populations by Cohen (1969, 1972). However, such an account tells us nothing about the adaptive significance of group

size. What would happen, for example, if there were twice as many groups of baboons in Amboseli, but each was half as large? Why is it that so many primates live in groups that are considerably larger than an immediate family?

Primate group sizes appear to be adaptations to two major classes of selective forces: the distribution and density of essential resources, such as food, water and sleeping sites, and patterns of predator attack and anti-predator behavior. These factors will be discussed in this and the next section.

A resource will be referred to as *sparse* if it occurs at a low density both locally and throughout the home range. Thus, if a food resource is both sparse and has a patchy or clumped distribution, no clump or patch will contain an abundance of food. Each will be small relative to the daily food consumption of the animals. We can now state a relationship between re-

source distribution and group size:

Principle One. *If a slowly renewing resource is both sparse and patchy, it can be exploited more effectively by small groups. Conversely, large groups that are simultaneously using a single resource will occur only if the supply is adequate, either because of local abundance, or because of rapid renewal of the resource. Large groups will be more effective if a resource has a high density but a very patchy distribution and the patches themselves occur with low density, so that the resources tend to be concentrated in a few places ("super-markets").*

In several cases, when the abundance of food that is available to a primate population has been artificially increased, the average group size has increased. This has happened, for example, with the rhesus monkeys on Cayo Santiago, Puerto Rico (Koford, 1966), and the Japanese macaques on Mt. Takasaki, Japan (Mizuhara, 1946; Itani, 1967). Conversely, in the Amboseli Reserve, Kenya, recent marked changes in the habitat, including the death of many of the fever trees (*Acacia xanthophloea*) and the transformation of the plant community from a hydrophytic to a xeromorphic form (Western and Van Praet, 1973), have been accompanied by a decrease in the mean group size of vervet monkeys (Struhsaker, 1973) and of baboons (personal observations). A decrease in food abundance probably was a major contributor to these changes in group size. Unfortunately, in none of these cases can one separate out the relative importance of food density and food dispersion. We predict that group size will increase or decrease according to the dispersion of the food, and independent of its abundance. This does not rule out the possibility that food density *per se* is a major factor controlling mean group size.

If some resources are abundant but only locally and others have a sparse and patchy distribution these can be effectively exploited by a population that aggregates at the concentrated resources and breaks up into small units to exploit the sparse resources. Hamadryas baboons provide an

excellent example of such a social system. The small feeding units probably represent an adaptation to sparse, patchy resources. On the other hand, safe sleeping rocks are few and far between in the Gota Region of Ethiopia, but those that do occur can hold hundreds of baboons. Thus, the night-time sleeping aggregations on these rocks enable large numbers of individuals simultaneously to utilize an essential resource that it abundant locally.

Geladas, too, alternate between large herds and much smaller clusters of animals, but contrary to the hamadryas system, geladas sleep in small groups, consisting of one or a few harems. In the Simien Mountains, sleeping ledges are abundant, but each is fairly small, and they tend to be scattered along the cliff faces; of course, new ledges are formed very slowly. Thus, they are a sparse, slowly renewing resource that is best exploited by small, dispersed groups. The immense herds that we observed in the Simien at the end of the rainy season were feeding on luxuriant alpine meadowland that was continuous over large areas of the geladas' range.⁴ I believe that these herds are an adaptation to occasional predation (Principle Two), rather than to the resource distribution.

We will argue below that predation selects for baboon groups with at least one male. Sparse resources may select groups with *at most* one male, or very few males, because male baboons, with their greater food requirements and their ability to displace other members of the group from food, compete with adult females and other members of the group for already scarce resources. Thus, both males and females can reduce competition by associating in groups that include a single fully adult male.

2) *Predation and group size.* Predation on baboons affects the size and composition of their groups: for baboons, there is safety in numbers and safety in proximity to adult males. There are several reasons

⁴ Our observations on geladas were made possible by the hospitality of Patricia and Robin Dunbar and Elizabeth and Michael Nathan, to whom we are most grateful.

for this. Any member of a baboon group that sees a predator gives an alarm call to which all other members of the group respond. This means that each individual takes advantage of the predator-detecting ability of all other members of his group. As a group of baboons forages across the open grassland, each individual glances around occasionally. But if the group is large the total rate of such visual scans is high. "To live gregariously is to become . . . the possessor . . . of eyes that see in all directions . . ." (Galton, 1871, quoted in Hamilton, 1971). Thus, in open terrain it is almost impossible for a predator to approach a group of baboons undetected. The importance of this predator-detection system probably overrides the disadvantage of the predator's increased ability to locate baboons in large groups.

Another advantage of affiliation with a large group is protective hiding (Williams, 1966). If a predator appears at a random position in the area and strikes at the nearest individual, those individuals that are near other animals are less likely to be preyed upon (Hamilton, 1971), regardless of any predator detection, evasive action, or anti-predator behavior. In fact, the benefits to sociality accrue to animals that are subject to any pattern of predator attack in which the predator neither selects prey animals with equal probability, nor favors those that are near others, i.e., have a higher-than-average density of neighbors. Baboons are preyed on almost entirely by terrestrial predators, seldom by raptors. Thus, a solitary baboon, one in a small group, or one on the periphery of a group probably is not as safe as one in the midst of a large group.

For baboons, another predator-selected advantage of living in large groups is that the baboons of a group sometimes react *en masse* to predators, similar to the mobbing reactions that are given by many passerine birds to owls and other raptors. The effectiveness of such mob responses probably depends on the size of the group. In addition, they are probably more effective because of the presence in the group of adult males: Baboons are highly di-

morphic, and many of the special characteristics of the adult males make their anti-predator behavior particularly effective. In these highly dimorphic primates it is very rare to find females without a male, though the converse is not the case. Doubtless it is no coincidence that even the small minimal foraging groups of hamadryas baboons virtually always contain an adult male.

These factors, in combination, lead to the following principle for baboons:

Principle Two. *Predation selects for large groups and for groups containing at least one adult male.*

No claim is made here that aggregations are the only predator-defense responses that are available to primates, or that the above factors are the only predator-induced sources of aggregation. (For example, patas monkeys live in relatively small groups and rely for defense on crouching in the grass while the one adult male of the group puts on a "distraction" display [Hall, 1965c]. For animals that hide in this manner, large groups may actually be disadvantageous.) What is maintained here is that in animals such as baboons that retain conspicuous aggregations in the presence of a predator, the size of a group and the responses of its members to a predator contribute to the safety of the animals in it.

3) *Localized resources and home range size.* The maximum distance that an animal can go from an essential resource without replenishment will be referred to as the animal's "cruising range" for that resource. At about half the cruising range, the animal reaches a "point of no return" beyond which he must locate a different source if he is to survive. An upper limit on the size and location of home ranges and the maximum length of day-journeys is established by the distribution of resources and the animal's cruising range for each. The relationship may be stated as follows:

Principle Three. *Home ranges are limited to areas that lie within cruising range of some source of every type of essential resource.*

However, for many baboon resources, such as grass, resource points are sufficiently

close together that natural variations over space in nearest-neighbor distances never approach the distance beyond which baboons can walk. Such resources are therefore irrelevant for our present purpose, which is to establish an upper limit on *habitable* areas—though the density of grass or other dispersed resources vis-à-vis the animals' foraging strategy may be significant in determining the *inhabited* areas. In contrast, other resources have a more restricted distribution, and thus the foregoing principle may be sharpened as follows:

Home ranges are limited to areas lying within cruising range of the essential resources with the most restricted distribution. Such resources act as limiting factors determining home range size and site.

For many baboon populations in arid regions of Africa, water is the essential resource with the most spatially restricted distribution. Baboons are probably obli-

gate drinkers: No baboon group that we have observed or that has been described in the literature lives in an area without some source of permanent water. (It is possible that in some rain forest areas, baboons can obtain enough moisture from succulent foods.) This dependence of baboons on permanent water sources was strikingly demonstrated to us in September 1972 near the end of the dry season, when J. Altmann and I traveled over many miles of the arid Northern Frontier District of Kenya, without seeing a single baboon. The few places where baboons (anubis) were observed during that trip all have some permanent source of water, sometimes nothing more than a pit in a sandy wadi.

For hamadryas baboons, too, water sources are essential and scarce. During September 1971, Slatkin and I observed hamadryas in the arid region near Gota, Ethiopia.⁵ The rainy season had just ended,



FIG. 6. Hamadryas at water holes in wadi (same locale as Fig. 2).

yet the porous alluvial soil retained virtually no moisture. There was surface water only in the larger rivers. Elsewhere, hamadryas obtained drinking water from holes in sandy river beds (Fig. 6). In 1960-61, Kummer studied hamadryas baboons in this same area. He writes:

"During the dry season, each troop had 2 to 4 permanent watering places within its range, mostly at pools under small chutes in the otherwise dry river beds. The hamadryas frequently dug individual drinking holes in the sand of the river bed . . ." (Kummer, 1968a, p. 164).

In Amboseli, the yellow baboons occur only in the vicinity of the permanent water sources—a series of waterholes and swamps that are fed by underground water from Mt. Kilimanjaro. One might ask, why don't the baboons in Amboseli conform to the seasonal pattern of many large mammals in Amboseli and elsewhere in East Africa (Lamprey, 1964), and move completely out of the woodland/waterhole region during the rains, when drinking water is widely available in rain pools and food is abundant elsewhere, then move back in as peripheral areas dry out? Such a migratory pattern would minimize the risk of over-utilizing the woodland area, which must sustain a large population through the dry season on the standing crop available at the end of the rains. Perhaps the explanation is this. During the rains, when the home range size and location is no longer restricted by water sources, sleeping trees become the essential resource with the most restricted distribution. In Amboseli, baboons sleep in fever trees (*Acacia xanthophloea*), which occur only where there is adequate year-round ground moisture, i.e., in the vicinity of permanent water sources, but for reasons that are not known to us they do not sleep in umbrella trees (*Acacia tortilis*), which occur in more arid parts of the Reserve, and this despite the fact that at certain times of the year the baboons may spend many hours of the day in umbrella trees,

feeding on the green pods. (A large umbrella tree that is contiguous with one baboon group's favorite sleeping grove of fever trees is used by that group for feeding but not for sleeping. In the morning the group has been observed to move from the sleeping grove to the adjacent feeding tree without first descending to the ground.) These two species of trees are the only ones in the Reserve that are large enough for baboons to use as sleeping trees.

4) *Sparse resources and home range size.* Unless the size and location of a home range is such that it includes an adequate supply of every essential resource, it will not sustain the animals in it. We can therefore state the following principle:

Principle Four. *The essential, slowly renewing resources whose distributions are sparsest relative to the needs of the animals set a lower limit on home range size and site.*

Principle Four can be made clearer by citing some resources to which it does *not* apply. Oxygen is an essential resource for baboons and is sparse—the amount available in, say, a cubic meter of air could not sustain a baboon for long—but it renews rapidly through diffusion and convection. In Amboseli, water is locally abundant, and if baboons only had to satisfy a water requirement, they could spend the entire day in the vicinity of the waterholes. Thus, neither of these resources sets a lower limit on home range size.

Food in the semi-desert area inhabited by hamadryas baboon populations is the most striking case of a sparse, slowly renewing baboon resource. In the Gota region, the abundance of their food is severely limited by a combination of factors: (i) an unconsolidated alluvial upper horizon from which soil or other fine particles readily erode, leaving a barren, rocky terrain; (ii) ground of high porosity and low water-retaining ability; (iii) strong slope combined with a short, but torrential rainy season, thus making erosion even more rapid; and (iv) hot, dry climate the rest of the year. The area appears to be a recent sediment basin which is now an area of rapid erosion, as water from the high plateau to

⁵ These observations were made at the study site of J.-J. and H. Abegglen. We are indebted to the Abegglen's for their hospitality during our visit.

to be determined primarily by available food. In such a situation, the hypothesis can be checked by observing changes in the home range that result from naturally or artificially induced changes in food productivity (cf. Watson and Moss, 1971).

There are many areas in the Amboseli Reserve, Kenya, which are not occupied by baboons, but in which grass and other baboon foods are more abundant at the end of the dry season than they are in those parts of the Reserve that the baboons occupy; however, these areas are without permanent water and are beyond cruising range of permanent water sources. A shortage of suitable sleeping sites may also restrict utilization of these areas. Another example of the limiting influence of spatial distribution of water in arid regions is the following. In October, 1963, which was the last month of the dry season, the home range of one group of yellow baboons in the Amboseli Reserve was a relatively small circumscribed area. But at the beginning of the next month, the group moved far beyond the limits of their October range (Fig. 7). We offered the following explanation for this expansion:

"The onset of the rains on November 1 of that year brought about a major ecological change: thereafter, the baboons could get drinking water almost anywhere and thus were no longer tied to the vicinity of permanent waterholes. That this change in range size cannot be attributed to alterations in vegetation is evident from the fact that the change was apparent as soon as the rainy season began, during the first week of November, before the new grass had a chance to grow" (Altmann and Altmann, 1970, p. 116).

5 and 6) *Resource distribution and home range overlap.* The spatial distribution of resources also affects the extent to which home ranges of adjacent groups overlap. The natural tendency of animals to occupy all available parts of the habitat while minimizing competition with conspecifics, combined with the advantages of an established, familiar area, tends to produce a mosaic distribution of home ranges, with contiguous or minimally overlapping

boundaries. Such a situation cannot prevail, however, if one or more essential resources are not well distributed throughout the habitat. When this is the case, we propose the following two general hypotheses to explain home range overlap.

Principle Five. *Home range overlap depends primarily on those essential resources with the most restricted spatial distribution: it will be low in relatively uniform habitats and will be extensive if several essential resources have very restricted distributions.*

Under the latter conditions, overlap zones will include a local concentration of essential resources that are not readily available elsewhere.

Principle Six. *The amount of time that groups with overlapping ranges will simultaneously be in the shared portion of their ranges depends primarily on those essential resources in the overlap zone that can only be utilized slowly and whose availability is most restricted in time.*

As a result, simultaneous occupancy of overlap zones will be long wherever slowly utilized resources have a restricted period of availability, and conversely, will be brief if those resources that require longest to utilize are continuously available.

"Thus an essential natural resource is a restrictive factor in home range separation, in time or space, to the extent that increasing its dispersion in time or space will reduce home range overlap" (Altmann and Altmann, 1970, p. 202).

In the Gota region of Ethiopia, overlap of home ranges of the one-male hamadryas units was imposed by the small number of available sleeping cliffs in the region and resulted in large aggregations or herds (Kummer, 1968a, 1971). During our 1963-64 study of the yellow baboons in Amboseli, Kenya, numerous groups used each waterhole, though usually at different times of the day. In the evening, several of these large groups converged on areas of the woodland in which sleeping groves were particularly abundant; each group moved into a separate grove (Altmann and Altmann, 1970). During 1969, when there was a drought in Amboseli, the Masai tribes-

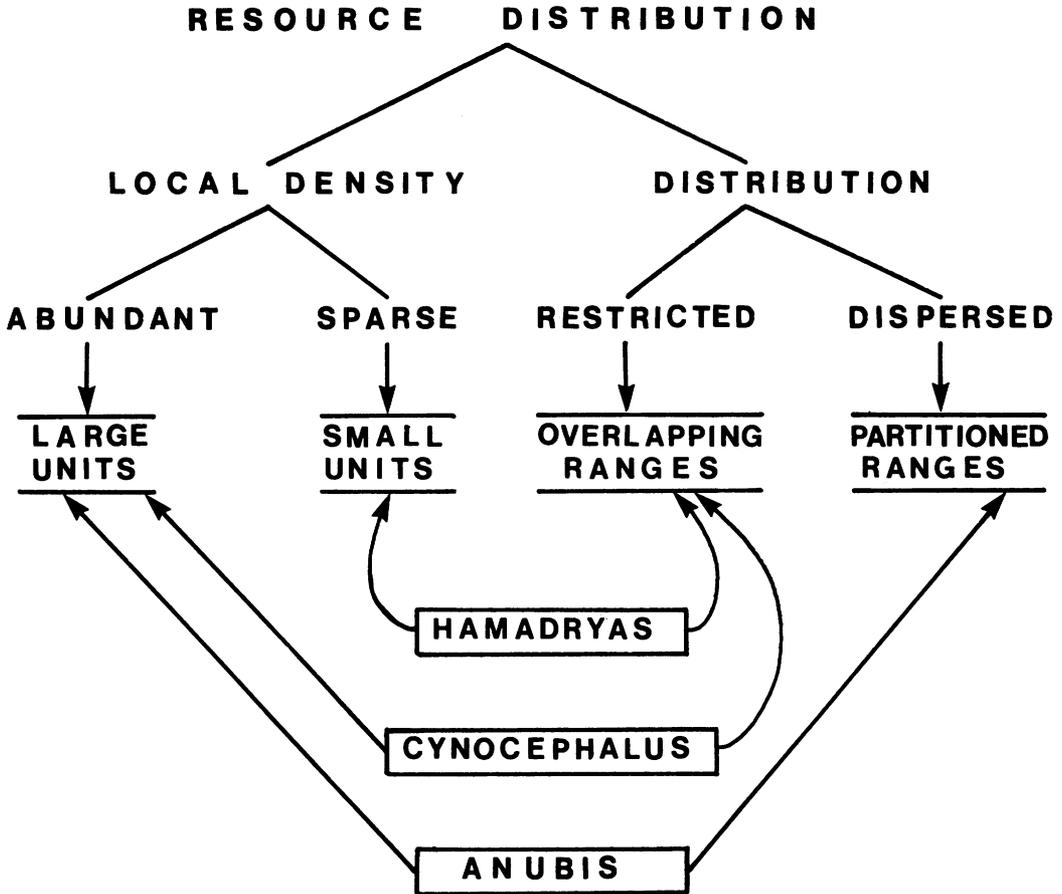


FIG. 8. Some resource correlates of home range overlap and group size.

men had large herds of livestock in and around the waterholes during most of the day. In the late afternoons, after the livestock left the area, several baboon groups simultaneously converged on a waterhole. At such times, intergroup conflicts were frequent.

Such aggregations at waterholes, sleeping cliffs and tree groves illustrate the effects on home range overlap of essential resources that are spatially and temporally restricted. In contrast, during DeVore's 1959 study of anubis baboons in Nairobi Park, Kenya, home range overlap was much less extensive (DeVore and Hall, 1965). In that area, water sources and sleeping sites were much more widely dispersed than in either Amboseli or the Gota region, and no other resource in Nairobi Park is known to have a comparably restricted distribu-

tion. Some of the effects of resource distribution and abundance on group size and home range overlap in hamadryas, anubis, and yellow baboons (Principles One, Five and Six) are summarized in Figure 8.

7) *Time-limited resources.* As constituents of the body, many essential resources can be characterized by (i) a critical minimum below which the animal is incapacitated or dead, and (ii) a limited "reservoir" or storage capacity. Such a resource can be referred to as "time-limited." Energy is one of the most important time-limited resources, and we can immediately state an energy limitation: No animal's energy expenditure can exceed its energy input for very long. Because of ongoing metabolic processes, energy resources must be renewed before degradation either kills the animal or renders it incapable of meeting

the metabolic requirements of foraging and other vital activities. (Animals that become dormant, e.g., by hibernating, postpone the problem, but they cannot avoid it.) This suggests the following ecological principle:

Principle Seven. *Energy will place constraints on the time budget whenever it is the essential resource with the shortest exhaustion time.*

Clearly a similar restriction applies to water or to any other vital body component that has a critical minimum and a finite reservoir. For each such time-limited resource, the basic restriction on "foraging" for that resource is that access to the resource must occur before exhaustion of reserves. Critical time allocation decisions involve resources for which reserves are small compared to the rate of use, so that the time to exhaustion is small. The requirements of some time-limited resources, such as oxygen, are readily met by baboons. Others, such as water, present much greater challenges.

Time budgets are further shaped by "scheduled" activities, that is, activities that must occur at a particular time, place, or other contextually defined situation (Hockett, 1964). Examples from Amboseli baboons include the necessity to get into sleeping trees before darkness, and the special alerting reactions given when the baboons go through a critical pass in dense foliage (Altmann and Altmann, 1970).

8) *Resource distribution and time budgets.* Consider a record of an animal's activities that (i) is obtained continuously over one or more time periods and that includes (ii) the time (real or lapsed) between transitions from one activity state to the next and (iii) the state that the animal is in between each transition and the next. Each such sample of the time course of activity states is a focal-animal sample, in the sense of J. Altmann (1974).

Such a record explicitly or implicitly includes at least the following five types of information: (i) rate and relative frequency at which each state is entered, (ii) distribution of the durations of "bouts" in each state, (iii) percent of time spent in each state, (iv) transition probabilities: for all

states i and j , if the animal is in state i , the probability that the next state it enters will be state j ; and (v) the time correlation functions: the probability that if the animal is engaged in activity i at time t , it will be engaged in activity j at time $t+\tau$, for all i, j, t , and τ . We will attempt to provide ecological interpretations of some of these parameters and provide a single analytic framework for them. The third item, proportion of time spent in each activity, is often referred to in the literature as a "time budget," though one or more of the other types of information may also be included under that rubric. Some of this information can be obtained from other types of samples. For example, repeated instantaneous samples can be used to estimate proportion of time spent in each state (J. Altmann, 1974). Slatkin (unpublished) used both of these sampling methods in his comparative study of time budgets in gelada monkeys and yellow baboons.

Many food items (berries, grass plants, etc.) and some other essential resources occur in small discrete packets whose positions in space can be regarded as points. Because the "processing" or utilization of food items and the movements of an individual from one resource point to another each take a certain amount of time, the spatial distribution of resource points that are utilized is reflected in the time budgets of the animals. For example, at various places in the Amboseli grassland, there are patches of a special soil type on which few plants except *Leucas stricta* grow, and those are not eaten by the baboons. When the baboons encounter such a patch while foraging, they stop feeding, walk across the patch, and resume feeding on the other side. Thus, the spatial array: *edible grass* → *Leucas stricta* → *edible grass* is reflected in the time sequence: *feed* → *walk* → *feed*.

Some feeding activities (chewing, reaching, etc.) can be carried out while the animal is moving to the next food item, but if the next food item is too far away, a period of progression (for baboons, walking) will occur between feeding bouts. We define *food patches* as the most inclusive sets of food items that are situated in such

a manner that it is possible for an animal to go from one to another without interrupting his feeding activities. Clearly, the maximum possible distance from any food item to the nearest other food item in the same patch will depend on the animal's processing time and the rate at which the animal travels from one food item to the next. If the latter is relatively constant, or at least, if it has a non-zero minimum, then the length of foraging bouts will be limited by the number of food items per patch. Bout length will be further reduced by the presence of other individuals that feed concurrently on the same patch, by the failure of the animals to utilize all of the items in a patch, and by activities that interrupt feeding.

The proportion of time spent feeding probably reflects relationships between several factors, including the richness of the food sources, their spatial proximity, the processing time required to utilize them, and the metabolic requirements of the animals.

Suppose that we plot a conditional probability function for feeding activities: for all moments t at which an animal was observed feeding, we plot the probability that the animal will be feeding at each subsequent moment $t + \tau$, plotted as a function of the lapsed time τ , regardless of whether feeding is continuous between t and $t + \tau$ (Fig. 9). This time correlation function must begin at 1 (where $\tau = 0$) and converges on a limit which is the proportion of time spent feeding. Slatkin (unpublished) has pointed out that the "rate of decay" of

this function for feeding may reflect aspects of food distribution and has suggested some possible ecological correlates. A somewhat different interpretation is as follows: The function should decay slowly under any of the following conditions: (i) very large food patches, so that the animals can feed continuously; (ii) medium or very small patches that are sufficiently close together that they form a "super-patch," in which the time required to move from patch to patch is small; (iii) medium sized patches that are far apart, so that the animal is better off staying where he is and utilizing some of the less accessible food items in the patch. The function will decay more rapidly if each patch is very small, so that the animal quickly exhausts the local supply, and if the patches are over-dispersed, so that when the animal does move to another patch, he must move a considerable distance.

The first systematic analyses of primate time budgets that has included time correlation functions and length of feeding bouts, as well as the conventional proportion of time per activity, was carried out by Slatkin (unpublished). In a comparative study of adult male time budgets in yellow baboons (Amboseli Reserve, Kenya) and geladas (Simien Mountains, Ethiopia), he discovered that gelada males spent more time feeding than did yellow baboon males, that their feeding bouts were longer, on the average, and that the correlation function for feeding decayed much more slowly than did that of yellow baboons. The fact that geladas spent more time feeding per day, "reflected the fact that during the study periods, the geladas were eating low nutrient food items (grass, leaves, flowers) while the yellow baboons were eating higher quality foods (seeds, rhizomes, berries). The average duration of a feeding bout was greater for the geladas because the food items tended to be closer to each other in the geladas' habitat, thereby allowing an individual to feed continuously for a longer period of time without moving to another feeding site." The amount of time for the function to drop by 90% "was much greater for the yellow baboons

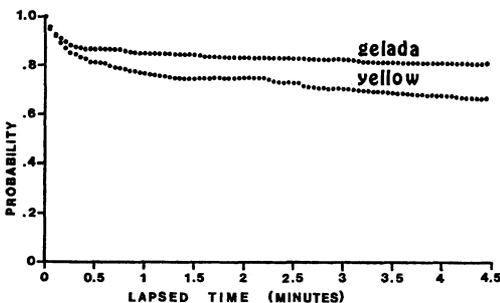


FIG. 9. Time correlation functions for feeding in adult male gelada monkeys and yellow baboons. For explanation, see text.

than for the geladas (1 min vs. 3 min) even though the average feeding bout for the yellow baboons was shorter," probably because "the food resources that are actually utilized are much more patchily distributed for the yellow baboons than for the geladas" (Slatkin, personal communication).

If food items can only be processed one at a time, the amount of food obtained per minute of foraging time will be limited by processing time. One of the advantages of cheek pouches is that they avoid this limiting effect of processing time (especially for mastication) on harvest rate. It is surely no coincidence that cheek pouches occur in all cercopithecine primates (baboons, macaques, mangabeys, vervets, etc.) but not in the colobines (langurs, colobus, etc.). Cercopithecines tend to feed on relatively small quantities of concentrated foods that have a more patchy distribution than the food of the leaf-eating colobine monkeys. It is also noteworthy that among cercopithecines, cheek pouches are smallest, relative to body size, in geladas (Murray, 1973): Over much of their range these animals live in habitats in which food is more uniformly distributed than is the food of baboons in *their* habitats. Where the two occur in the same region, as at Debra Libanos, Ethiopia, the geladas spend much more time feeding (Crook and Aldrich-Blake, 1968).

Now let us try to include the various temporal characteristics of an animal's state time course in a single, testable model. Consider the following two characteristics of these time courses. (i) The transitions from one state to another are not rigidly fixed sequences. However, for each two-state sequence i, j we can estimate the conditional probability p_{ij} that, given the animal is in state i , the next state he enters will be state j . As a first approximation, it seems reasonable to suppose that within any one habitat type, the distribution of these probabilities is stationary. By a habitat type, we refer here to a (plant) community in which each species that affects the animal's foraging can be represented by a single spatial distribution. (ii) The duration of stays ("bouts") in each state is a random variable, not a constant. It seems

reasonable to suppose, again as a first approximation, that within any one habitat type, the conditional probability that an animal will go from state i to state j by time t given that he was in state i at time 0 depends only on the pair of states i, j and the amount of time t that has been spent in i . For each pair of states i, j the distribution of times between transitions can be described by the function $F_{ij}(t)$ specifying the probability that the animal will go from state i to state j at or before time t , given that he entered state i at time 0 and that state j is the next one he will occupy.

A system that can be described by the properties assumed in (i) and (ii) above is called a semi-Markov process.⁶ Such a process contains two sets of parameters, the set p_{ij} of conditional transition probabilities and the parameters of the distribution F_{ij} .⁷ Once these two parameters are known, many other characteristics of the time process can be derived.

Focal-animal state samples, which we described at the beginning of this section, contain the data necessary to estimate these parameters. The transition probabilities p_{ij} are estimated from the number of i -to- j moves, in the usual manner: $p_{ij} = n_{ij} / \sum_k n_{ik}$. The observed times between i -to- j moves are used to estimate the distributions $F_{ij}(t)$.⁸

In summary, we give:

Principle Eight. The time course of an animal's activities within any habitat that can be represented by a single spatial distribution can be approximated by semi-Markov processes, the parameters of which are related to characteristics of the spatial distribution of resources.

⁶ For a lucid exposition of many fundamental theorems of semi-Markov processes, as well as a guide to the literature, see Ginsberg (1971, 1972).

⁷ When the F_{ij} are all exponential and independent of j , the semi-Markov process reduces to a Markov process. According to Slatkin (personal communication), the distributions are not exponential for either cynocephalus baboons or geladas, but are close to it.

⁸ In practice, beginning and terminating sample periods produces end effects. The method for treating these truncated intervals is given by Moore and Pyke (1968).

9) *Foraging strategies.* We assume that natural selection will favor those individuals that utilize their forage time in such a manner that they obtain the largest yield of energy (or other nutritional component) per unit of time.⁹

For a variety of reasons, a baboon's movement from one food item to the next will usually take place at a rate that can only vary within fairly narrow bounds. Energy expenditure probably is a step function of gait, with running consuming far more energy per unit distance or unit time, thus reducing feeding efficiency as well as making it more difficult for the animal to maintain a stable body temperature. Consequently, an animal that ran from plant to plant would lose more than he gained: feeding efficiency is not synonymous with feeding rate. As a result of this progression-rate restriction a baboon cannot make any appreciable improvement in his yield rate by going more rapidly from one food item to the next. On the other hand, a slower pace would reduce the rate of food intake and increase the amount of time necessary to obtain a sustaining amount of food. For baboons in hot and arid regions, it would keep them on the feeding ground and away from shade and water for longer periods of time.

These relations can be summarized as follows:

Principle Nine. For animals that forage on slowly renewing, stationary food items and that move from one food item to the next at an essentially fixed rate, the foraging pathway with the shortest average distance per usable food calorie will be optimal in the sense of yielding the most energy per unit time.

Consider a species that feeds on a slowly renewing, stationary resource that occurs as a set of point sources. Suppose we know the mean gross caloric value of a food type, the maximum rate of movement from

item to item, the caloric cost of moving a unit distance, the spatial array of the food items (assumed to be stationary point sources and to be slowly renewing), and the place in the habitat where foraging begins. What is the optimal foraging pathway for the animal to follow?

Consider first a "one-step evaluator," that is, an animal that can see and estimate the distance to each of the various food items within its perceptual range, but cannot take into account their spatial relationships to each other. Assume for the moment that the animal cannot estimate the caloric yield of the food items, but can only treat them as of equal value. Such an animal can do no better than go to the nearest food item at each move. If he is lucky, he will never have to go so far that he depletes his energy reserves. If, in addition, the animal can, at a distance, estimate the gross caloric content of each food item (i.e., can act on the basis of a perceived correlate of caloric content) as well as the caloric "cost" (energy required in moving that far, then harvesting and processing food), his optimal strategy is to deduct from the gross caloric value of each food item the cost (in calories) of using that food item, then go to the food item with the highest net yield—of course eating any other food that he passes en route.

Now suppose we have a somewhat more skillful animal, one that can, like the last one, estimate the distance from its present position to any food item in its perceptual range, but one that can also estimate the distance from that point to the food item nearest to that point. Such an animal is able to detect a minimal "clump," consisting of but two food items, and will be called a "two-step evaluator." Suppose also that the animal cannot at a distance estimate the value of a food item (or that the items are essentially identical). For such an animal, there exists an optimal strategy: (i) choose among the pairs of points (food items) on the basis of which pair has the shortest total distance from animal to nearer point and from there to the farther point; (ii) begin with the closer member of the pair, then go to the other one. If on

⁹ Schoener (1971) distinguishes between those animals ("time minimizers") that accomplish this by minimizing time required to obtain a subsistence amount of food and those that do it by maximizing food input for a set amount of foraging time ("energy maximizers").

the other hand the animal can evaluate the caloric content of each food item and the caloric cost of each point-to-point pathway, he should find that ordered pair of points for which the total net caloric yield is highest.

A two-step evaluator may be able to increase his yield (and cannot decrease it) if he re-evaluates his strategy in the same manner at each point (i.e., at the first point of each selected pair).

This type of analysis can be continued through a series: three-step evaluators, four-step evaluators, etc. For all such animals the goal is the same: minimize the total distance traveled¹⁰ or, for an animal that can evaluate calories, maximize the total net caloric yield. But the expected value is not: the advantages of an n -step evaluator over an $(n-1)$ -step evaluator are the ability to detect larger clumps, thereby reducing costly clump-to-clump movements, and the ability to reduce the risk of following a chain of points out to the tip of a "peninsula" of points that would require excessive walking in order to get back to a foraging area.

We do not know, for baboons or any other animal, whether the fine-grain geometry of their nutrient distribution is a major determinant of their movements nor whether individual differences in foraging movements are related to the chance of survival. It seems extremely likely that both effects exist and are of sufficient magnitude that they are measurable.

Denham (1971) writes: "I assume that a specific primate population will occur only where food of a kind usable by that species is present. Thus we can control for, or disregard, the 'food supply composition' variable." But the nutritional value of food

items can be disregarded only if the nutrient compositions of all food items are identical. It is precisely the varied distribution of nutrients that presents a challenge to the selective feeding ability of animals. If animals can select nutritious foods and can thereby "balance their diets," any adequate model of foraging strategies must treat food items as something other than indistinguishable points in space. Just how good the foraging strategies of baboons are remains to be seen. Certainly the available evidence suggests a very considerable ability:

"In reviewing our records of baboon's food plants . . . we have been impressed by the apparent capacity of these animals to feed selectively on the most nutritious parts of the plants available in their habitat at each time of the year" (Altmann and Altmann, 1970, p. 169).

10) *Resource distribution and foraging formation.* For animals that live in groups, sparse resources present a special spacing problem: How can the members of a group remain together and still avoid excessive competition? One part of the answer is to be found in the deployment of the members relative to each other while foraging for such a resource. Consider a group of animals on a plane surface, e.g., a group of baboons foraging on flat, open grassland. Under those conditions a parallel, in-line formation of individuals, moving in a rank, is the unique foraging pattern that enables each animal to maintain a continuous, exclusive forage-swath, thereby maximizing the harvest per unit distance traveled, while simultaneously minimizing each animal's mean distance to his neighbors. Thus, we have:

Principle Ten. A rank foraging formation will be favored whenever there is an advantage to remaining in a group and the group is foraging on slowly renewing resources that are of low overall density in the home range and that are not locally abundant.

When yellow baboons move away from their sleeping grove toward a distant foraging area, they move in a long file; if they then forage in an area of dry, open grass-

¹⁰ For an animal that cannot re-evaluate as it goes along and that cannot evaluate caloric content of the food items, the problem is closely related to a well-known problem in graph theory, often worded in terms of a traveling salesman who leaves the office, visits each of a specified set of factories, then returns to the office (or in an alternate version, then goes home). His problem is to minimize the amount of traveling that he does. In our case, however, the terminal point is not fixed and the set of points to be visited is not specified in advance.

land, the file formation is transformed into a long rank (Altmann and Altmann, 1970). In a sparse habitat this tendency to forage in a rank formation may be partially counteracted by several local factors: (i) a long resource processing time, so that an individual must remain in one place for an appreciable time (e.g., a baboon digging a grass rhizome out of the ground); combined with (ii) a dispersed food distribution, so that neighboring individuals may have to move ahead of stationary ones before encountering another food item. In addition, the forage-swaths may not be completely private: displacement of one yellow baboon by another at food sources sometimes occurs (Altmann and Altmann, 1970).

But wouldn't the animals be better off foraging separately? Aren't they competing for food? The answer that would usually be given is, yes, except that the group is a predator-protection mechanism (see Principle Seven): a solitary baboon is a dead baboon (DeVore, 1962). Another source of sociality under these conditions is this: the animals may not, in fact, be better off foraging independently. In a sparse habitat, foraging efficiency is probably limited by the distance between plants. To the extent that animals encounter used forage-swaths of other individuals, their foraging efficiency will be reduced. By feeding together in foraging parties that are as large as is compatible with the local food supply, the animals may be better off, because an individual will not encounter the foraging path of a member of his group until the whole group returns to the same spot. This advantage would be of particular significance in sparse habitats. ". . . When food becomes scarce, . . . participation in . . . social groups apparently results in a maximally efficient apportionment of available resources with a minimal level of hostile interactions" (Morse, 1971).

This characteristic of a rank—that it enables an individual to minimize the mean distance to neighbors while maintaining an exclusive and continuous forage-swath—is not provided by any other configuration, though under some conditions, alternative configurations may have other, overriding

advantages. In particular, a cluster or herd formation offers central individuals greater protection from predators that attack the periphery of the group. Where food is sufficiently abundant, foraging clusters may prevail. When feeding in the acacia woodland of Amboseli, yellow baboons tended to be closer to their nearest neighbors and to be more clustered than when feeding in the open grassland. Such areas were, in general, areas in which predator attacks were more probable (Altmann and Altmann, 1970). They also were areas in which food tended to be locally concentrated and in which visibility was reduced by foliage. All of these factors would contribute to the increased cohesiveness of the group.

At this point, one might ask, why can't a very large group forage in a "thin" habitat? Why couldn't the several hundred hamadryas of one sleeping rock forage as a unit, moving in one enormous rank? There are at least three factors that militate against this: (i) Those at the far ends of such an enormous phalanx would have to walk an inordinate distance whenever the group turned; (ii) hamadryas food has a patchy distribution and no patch is large enough for several hundred baboons to feed simultaneously; (iii) the irregular hamadryas habitat would repeatedly sever visual contact, thereby effectively subdividing the herd.

Geladas forage on the rich alpine meadows of the Simien Mountains, Ethiopia, in herds of several hundred individuals. If food were sparse and not locally abundant, those at the back of such a herd would find little to eat. Crook and Aldrich-Blake (1968) note that the geladas in the vicinity of Debra Libanos, Ethiopia, did not occur in large herds of the sort that had been observed in the Simien, "namely because areas of unbroken grassland were few. In fact herds of any size only congregated at the one large area of grazing near Chagal." Unfortunately, little information is available on gelada foraging formations under these conditions.

11) *Macro-strategy: area occupation density.* Suppose one records where an animal goes as it moves about in its home range.

For animals like baboons that forage in a group, one can keep track of the mean position or center of mass of the group (Altmann and Altmann, 1970). If such records are accumulated over many days, it becomes apparent that the animals do not move about at random. The areas in which members of a baboon group spend much of their time tend to be areas in which several resources co-occur (Table 1). Conversely, areas that the animals seldom enter and in which they remain only briefly tend to be areas in which resources are sparse and hazards are high.

None of this is surprising. If the animals are to survive in an area, they must go where the resources are, and they must avoid hazardous areas as best they can:

Principle Eleven. *The survival of an animal depends on its ability so to allocate the distribution of its activities among the parts of its home range that it gains access to the essential resources therein, while avoiding excessive exposure to hazards.*

This statement is not meant to be taken as a truism, asserting only that animals move about in such a way that they manage to survive. Rather, it is meant to be testable. An animal that spent a large part of its time in areas in which predators were abundant and resources were sparse probably would not fare as well as one that spent more time utilizing abundant, safe resources. But how large are the actual individual differences in strategies for exploiting localized resources and avoiding localized hazards? And how much difference do they make, in terms of survival and reproduction? Unfortunately, we do not yet know, but I believe that these questions can be answered and in what follows I shall discuss one approach to this problem.

Suppose that we evaluated the resources and hazards that occur in the various parts of an animal's home range. We could then see how accurately we could predict the animal's occupancy density distribution and localized activities from such data about the habitat, and whether differences in rates of survival or reproduction could, in turn, be related to different patterns of land use and to differences in the net value of home

TABLE 1. Resources, other than food, in the 14 most-used quadrats of one group of yellow baboons in Amboseli. These 14 quadrats, each 0.4 x 0.4 mile, included about one-quarter of the home range area of the group, but accounted for about three-quarters of its time. (After Altmann and Altmann, 1970, Table XX.)

Rank of quadrat	Per cent of time	Number of sleeping groves	Per cent of nights	Number of waterholes	Per cent of drinks	Number of rainpools	Per cent of drinks	Major passes
1	20.67	3	36.0	1	0	1	1.7	to 5 sleeping groves
2	9.39	1	0	2	16.7	4	6.7	to 5 sleeping groves and 2 waterholes
3	6.33	2	13.6	1	5.8	1	2.5	to 3 sleeping groves
4	5.97	1	0	3	10.8	1	0.8	to all waterholes in eastern woods
5	5.96	2	26.4	1	0	1	0	to 4 sleeping groves
6	5.61	1	0	1	0	9	10.0	to eastern woods
7	3.57	2	12.8	2	4.2	0	0	to 2 sleeping groves, 2 waterholes
8	3.52	1	0	1	8.3	2	4.2	to 3 sleeping groves, 1 waterhole
9	2.65	2	4.0	1	0	1	0	to 3 sleeping groves, 1 waterhole
10	2.45	1	2.4	2	0	1	1.7	to 1 sleeping grove, 2 waterholes
11	2.33	1	0	1	0	1	0.8	between eastern and western woods
12	2.23	1	0	1	0	1	1.7	to 2 waterholes, 2 sleeping groves
13	2.13	1	0	1	0	0	0	to 1 waterhole, 2 sleeping groves
14	1.84	2	4.8	2	0	0	0	to 1 sleeping grove
15-87	25.35	1	0	1	1.7	25	22.5	

ranges.

No attempt will be made here to describe, even in principle, what a "real estate assessment" for a baboon should look like. Indeed, I suspect that it would be different, depending on the question at hand—for example, on whether one was attempting to predict the occupancy density of a particular area, was trying to find out how the requirements for a particular nutrient were being met, or was trying to relate resource utilization to survival and reproduction. But some common components of such evaluations can be described.

The choice of a time scale for the evaluation is important. In the short run, the value of an area to an animal is not constant. It depends on variations in the environment and on the past behavior of the animal.

But in the long run, each area will have a net utility to the animals, namely, the difference between what they gain from the area, in terms of access to those resources that will enhance growth, survival, and reproduction, and what they lose, as a result of hazards to life therein. For example, the value of water sources to a group of baboons is very different, depending on whether it has been a cool or a hot day, and on whether the baboons have recently drunk. The value of a forage area depends on how much it has been used since the last crop matured. Over an extended period of time, however, the baboons of an area have a total water loss that must be restored if they are to survive, and this in turn establishes an overall value to water resources of the area. The value of any particular waterhole will depend on whether it lies between, say, mid-day foraging areas and evening sleeping groves. The predation risk of any area on any particular day depends on whether a predator is nearby at the time. In the long run, however, the predation risk of an area will depend on the frequency with which predators attack animals in that area.

The evaluations can be carried out on the basis of density of resources and hazards in areas (e.g., quadrats) or of proximity

to sample points. The former procedure has the disadvantage that the results depend in part on the initial choice of quadrat size (cf. Greig-Smith, 1964). Another difficulty with quadrats for this purpose is that they cannot be evaluated independently: the value of a quadrat would depend on resources (e.g., the nearest sleeping grove or waterhole) that might be in another quadrat. Beyond that, it may be that proximities to resources and hazards are more important than their densities, and thus that an evaluation on the basis of proximities to sample points comes closer to evaluating environmental factors that are significant to the animals. One is asking, if the animal found himself at this point in his home range, how far would he have to go to the nearest edible plant? To the nearest source of water or shade? How close is he to places where leopards hide? Of course, this evaluation cannot be carried out without a knowledge of the animal's capabilities for exploiting various resources. A food that the animal cannot reach, or cannot digest, is of no value, whatever a biochemical analysis might show to be present. In hilly or mountainous areas, allowance would have to be made for the fact that walking up and down slopes represents a different cost than moving horizontally along a slope or across an alpine meadow.

The risk at a point can be estimated from frequency and proximity of predator sightings, predator attacks, alarm calls, from measurements of proportion of shade cover, local mosquito or tick density, and so forth. For baboons, there are several localized hazards, including: (i) intense insolation, lack of shade, and remoteness from water with attendant dangers of dehydration and thermal imbalance; (ii) intergroup competition; (iii) mosquitoes, schistosomiasis, and coxsackie B₂ (endemic to Amboseli baboons), all of which are probably most abundant or most readily transmitted in or near permanent water holes; and (iv) carnivores, which for Amboseli baboons include leopard, lion, and silverback jackal, and probably also cheetah, spotted hyena, striped hyena,

hunting dog, marshal eagle, and hawk eagle. Of these the leopard is probably the baboon's major predator.

Predators are the hazards that are the most spectacular and have received the most attention, although they may not represent the greatest risk in a baboon's life. Alternatively, others have argued that attacks by predators on baboons have seldom been seen, despite many man-hours devoted to watching them in the wild, and thus that predation cannot be a very important selective factor acting on baboon societies. But the birth of infants is also seldom seen. In neither case does the frequency with which these events are observed—or actually occur—provide an adequate measure of their biological importance. The relationship between these two classes of rare events is this: In a species in which the reproductive rate is low, the survival of each individual is of particular significance in maintaining the population, and the selective impact of a predator killing a single individual is much greater than it is in a species in which the number of offspring per individual is high.

The space-specific risk of predation for baboons results from the fact that the baboon's predators tend to concentrate their hunting to particular habitats within the baboon's home range. For example, leopards stalk from cover and are seldom seen in areas of low, open grassland.

The baboon's problem, then, is to avoid areas of high risk, and yet still get at areas with concentrated resources. However, the predators face exactly the same problem, and to the extent that baboons are a resource for the predators, the latter will go where the baboons go. Fortunately for baboons, they are not a major food source of any predator (cf. Schaller, 1972, Tables 33, 36, 37, 63, and Kruuk, 1972, Tables 11, 12, 22).

Because the value of an area within the home range depends on both resources and hazards, a particular net value of a point or area can result from various combinations of risks and resources. For example, an area might be avoided either because it contained few resources, or because the

risk of entering the area was not sufficient to compensate for the resources that were present. Another possibility, and one of importance in trying to evaluate differences in adaptation is that the utility value of an area within the home range is high, but the animals are not taking full advantage of it. In any case, we should not completely ignore areas that the animals do not enter frequently, nor remain in long, but should try to find out why that is so.

"Thus, in analyzing the utilization of home range, we must consider not only those parts of the home range that the animals enter frequently or remain in for long periods of time, but also those that are seldom and briefly entered. More precisely, we must consider the spatial distribution of home range utilization and its relationships to the distribution of both hazards and natural resources among the parts of the home range" (Altmann and Altmann, 1970, p. 200).

At the other extreme, if all the resources were in one area of the home range, and all the hazards in another, the best strategy in terms of area occupancy would be to stay in the former and avoid the latter.

Hazards and resources will affect differential occupancy of areas within the home range only if neither is uniformly distributed in time and space. Because resources and hazards often co-occur in time and space, and because the animals must sometimes go through a hazardous area to get from one resource area to another, the problem of finding a viable distribution of activities is not trivial.

SUMMARY

For the convenience of the reader, we list here the eleven principles that we have developed in this paper.

1. *Resource distribution and group size.* If a slowly renewing resource is both sparse and patchy, it can be exploited more effectively by small groups. Conversely, large groups that are simultaneously using a single resource will occur only if the supply is adequate, either because of local abundance, or because of rapid renewal of

the resource. Large groups will be more effective if a resource has a high density but a very patchy distribution and the patches themselves occur with low density, so that the resources tend to be concentrated in a few places.

2. *Predation and group size.* Predation selects for large groups and for groups containing at least one adult male.

3. *Localized resources and home range size.* Home ranges are limited to areas that lie within cruising range of some source of every type of essential resource. More importantly, home ranges are limited to areas lying within cruising range of the essential resources with the most restricted distribution.

4. *Sparse resources and home range size.* The essential, slowly renewing resources whose distributions are sparsest relative to the needs of the animals set a lower limit on home range size and site.

5. and 6. *Resource distribution and home range overlap.*

5. Home range overlap depends primarily on those essential resources with the most restricted spatial distribution: it will be low in relatively uniform habitats and will be extensive if several essential resources have very restricted distributions.

6. The amount of time that groups with overlapping ranges will simultaneously be in the shared portion of their ranges depends primarily on those essential resources in the overlap zone that can only be utilized slowly and whose availability is most restricted in time.

7. *Time-limited resources.* Energy will place constraints on the time budget whenever it is the essential resource with the shortest exhaustion time.

8. *Resource distributions and time budgets.* The time course of an animal's activities within any habitat that can be represented by a single spatial distribution can be approximated by semi-Markov processes, the parameters of which are related to characteristics of the spatial distribution of resources.

9. *Foraging strategies.* For animals that forage on slowly renewing, stationary food items and that move from one food item

to the next at an essentially fixed rate, the foraging pathway with the shortest average distance per usable food calorie will be optimal in the sense of yielding the most energy per unit time.

10. *Resource distribution and foraging formation.* A rank foraging formation will be favored whenever there is an advantage to remaining in a group and the group is foraging on slowly renewing resources that are of low overall density in the home range and that are not locally abundant.

11. *Macro-strategy: Area occupation density.* The survival of an animal depends on its ability so to allocate the distribution of its activities among the parts of its home range that it gains access to the essential resources therein, while avoiding excessive exposure to hazards.

POSTSCRIPT

A few years ago, when I first began to think about the ways in which various activities of baboons depend on the spatial and temporal distribution of resources and hazards in their environment, I came across a posthumous paper by Milne (1947) on East African soils. Milne had a remarkable ability to predict plant communities on the basis of edaphic, climatological and topological features. The corresponding problem for animals is no doubt more complicated, but if the composition and distribution of plants in an area depend to a considerable extent on the local geology and meteorology, and if many activities of animals are adaptations to the structure of that plant community, it should ultimately be possible to combine these relationships into a single ecological theory of baboon social systems. Such a theory could be tested, in part, by making observations on the physical ecology of two or more areas and (in order to avoid a confounding problem in zoogeography) on the plants and animals of the surrounding region. The adequacy of the theory would then be judged on how well one could predict, on the basis of these observations, the behavior, social relations, group structure, and population dynamics of the animals

in these areas. We are a long way from being able to produce such a theory, but I hope that this paper will contribute to that end—to an ecological theory of social systems, literally “from the ground, up.”

REFERENCES

- Aldrich-Blake, F. P. G., T. K. Bunn, R. I. M. Dunbar, and P. M. Headley. 1971. Observations on baboons, *Papio anubis*, in an arid region in Ethiopia. *Folia Primatol.* 15:1-35.
- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 48:1-41.
- Altmann, S., and J. Altmann. 1970. Baboon ecology: African field research. Univ. Chicago Press, Chicago, and S. Karger, Basel (*Bibliotheca Primatologica* No. 12).
- Baker, J. R. 1938. The evolution of breeding seasons, p. 161-171. *In* G. R. deBeer [ed.], *Evolution*. Oxford Univ. Press, Cambridge.
- Chalmers, N. R. 1968a. Group composition, ecology and daily activities of free living mangabeys in Uganda. *Folia Primatol.* 8:247-262.
- Chalmers, N. R. 1968b. The social behaviour of free living mangabeys in Uganda. *Folia Primatol.* 8: 263-281.
- Cody, M. L. 1968. On the methods of resource division in grassland bird communities. *Amer. Natur.* 102:107-147.
- Cohen, J. E. 1969. Natural primate troops and a stochastic population model. *Amer. Natur.* 103: 455-477.
- Cohen, J. E. 1971. Social grouping and troop size in yellow baboons, p. 58-64. *In* H. Kummer [ed.], *Proc. 3rd Int. Congr. Primatol.*, Zurich, 1970. Vol. 3. S. Karger, Basel.
- Cohen, J. E. 1972. Markov population processes as models of primate social and population dynamics. *Theoret. Populat. Biol.* 3:119-134.
- Crook, J. H. 1966. Gelada baboon herd structure and movement. A comparative report. *Symp. Zool. Soc. London* 18:237-258.
- Crook, J. H. 1967. Evolutionary change in primate societies. *Sci. J. (London)* 3:66-70.
- Crook, J. H. 1970a. The socio-ecology of primates, p. 102-166. *In* J. H. Cook [ed.], *Social behaviour in birds and mammals*. Academic Press, New York.
- Crook, J. H. 1970b. Social organization and the environment: aspects of contemporary social ethology. *Anim. Behav.* 18:197-209.
- Crook, J. H., and P. Aldrich-Blake. 1968. Ecological and behavioural contrasts between sympatric ground dwelling primates in Ethiopia. *Folia Primatol.* 8:192-227.
- Crook, J. H., and J. S. Gartlan. 1966. Evolution of primate societies. *Nature* 210:1200-1203.
- Denham, W. W. 1971. Energy relations and some basic properties of primate social organization. *Amer. Anthropol.* 73:77-95.
- DeVore, I. 1962. The social behavior and organization of baboon troops. Doctoral Diss., University of Chicago.
- DeVore, I. 1963. A comparison of the ecology and behavior of monkeys and apes, p. 301-319. *In* S. L. Washburn [ed.], *Classification and human evolution*. Aldine, Chicago.
- DeVore, I., and K. R. L. Hall. 1965. Baboon ecology, p. 20-52. *In* I. DeVore [ed.], *Primate behavior: field studies of monkeys and apes*. Holt, Rinehart & Winston, New York.
- Dyson-Hudson, R., and N. Dyson-Hudson. 1969. Subsistence herding in Uganda. *Sci. Amer.* 220: 76-89.
- Eisenberg, J. F., N. A. Muckenhirn, and R. Rudran. 1972. The relation between ecology and social structure in primates. *Science* 176:863-874.
- Fisler, G. F. 1969. Mammalian organizational systems. *Contrib. Sci. L. A. Co. Mus.* 167.
- Forde, D. 1971. Ecology and social structure: the Huxley Memorial Lecture 1970. *Proc. Roy. Anthropol. Inst.* 1970:15-29.
- Gartlan, J. S. 1968. Structure and function in primate society. *Folia Primatol.* 8:89-120.
- Ginsberg, R. B. 1971. Semi-Markov processes and mobility. *J. Math. Sociol.* 1:233-262.
- Ginsberg, R. B. 1972. Critique of probabilistic models: application of the semi-Markov model to migration. *J. Math. Sociol.* 2:63-82.
- Greig-Smith, P. 1964. *Quantitative plant ecology*. 2nd Ed. Butterworth, London.
- Hall, K. R. L. 1962a. Numerical data, maintenance activities, and locomotion in the wild Chacma baboon, *Papio ursinus*. *Proc. Zool. Soc. London* 139:181-220.
- Hall, K. R. L. 1962b. The sexual, agonistic and derived social behaviour patterns of the wild Chacma baboon, *Papio ursinus*. *Proc. Zool. Soc. London* 139:283-327.
- Hall, K. R. L. 1965a. Social organization of the old-world monkeys and apes. *Symp. Zool. Soc. London* 14:265-289.
- Hall, K. R. L. 1965b. Ecology and behavior of baboons, patas, and vervet monkeys in Uganda, p. 43-61. *In* H. Vagtborg [ed.], *The baboon in medical research*. Univ. Texas Press, Austin.
- Hall, K. R. L. 1965c. Behaviour and ecology of the wild patas monkey, *Erythrocebus patas*, in Uganda. *J. Zool.* 148:15-87.
- Hall, K. R. L. 1966. Distribution and adaptations of baboons. *Symp. Zool. Soc. London* 17:49-73.
- Hamilton, W. D. 1971. Geometry for the selfish herd. *J. Theoret. Biol.* 31:295-311.
- Hennig, W. 1966. *Phylogenetic systematics*. Univ. Illinois Press, Urbana.
- Hockett, C. F. 1964. Scheduling, p. 125-144. *In* F. S. C. Northrop and H. H. Livingston [ed.], *Cross-cultural understanding: epistemology in anthropology*. Harper & Row, New York.
- Itani, J. 1967. Postscript by the editor. *Primates*. 8:295-296.
- Jolly, A. 1972. *The evolution of primate behavior*. Macmillan, New York.
- Koford, C. 1966. Population changes in rhesus mon-

- keys, 1960-1965. *Tulane Stud. Zool.* 13:1-7.
- Kruuk, H. 1972. The spotted hyena: a study of predation and social behavior. Univ. Chicago Press, Chicago.
- Kummer, H. 1967a. Tripartite relations in hamadryas baboons, p. 63-71. *In* S. A. Altmann [ed.], *Social communication among primates*. Univ. Chicago Press, Chicago.
- Kummer, H. 1967b. Dimensions of a comparative biology of primate groups. *Amer. J. Phys. Anthropol.* 27:357-366.
- Kummer, H. 1968a. Social organization of hamadryas baboons. Univ. Chicago Press, Chicago; S. Karger, Basel (*Bibliotheca Primatologica* No. 6).
- Kummer, H. 1968b. Two variations in the social organization of baboons, p. 293-312. *In* P. C. Jay [ed.], *Primates, studies in adaptation and variability*. Holt, Rinehart and Winston, New York.
- Kummer, H. 1971a. *Primate societies*. Aldine-Atherton, Chicago.
- Kummer, H. 1971b. Immediate causes of primate social structures, p. 1-11. *In* H. Kummer [ed.], *Proc. 3rd Int. Congr. Primatol.*, Zurich, 1970. Vol. 3. S. Karger, Basel.
- Kummer, H., and F. Kurt. 1963. Social units of a free-living population of hamadryas baboons. *Folia Primatol.* 1:4-19.
- Lamprey, H. F. 1964. Estimation of the large mammal densities, biomass and energy exchange in the Tarangire Game Reserve and the Masai Steppe in Tanganyika. *E. Afr. Wildlife J.* 2:1-46.
- Milne, G. 1947. A soil reconnaissance journey through parts of Tanganyika Territory December 1935 to February 1936. *J. Ecol.* 35:192-265.
- Mizuhara, H. 1946. Social changes of Japanese monkey troops in the Takasakyama. *Primates* 5:27-52.
- Moore, E. H., and R. Pyke. 1968. Estimation of the transition distributions of a Markov renewal process. *Ann. Inst. Math. Stat.* 20:411-428.
- Morse, D. N. 1971. The insectivorous bird as an adaptive strategy. *Ann. Rev. Ecol. Syst.* 2:177-200.
- Murray, P. 1973. The anatomy and adaptive significance of cheek pouches (*bursae buccales*) in the Cercopitheciinae, Cercopithecoidea. Doctoral Diss., University of Chicago.
- Nagel, U. 1971. Social organization in a baboon hybrid zone, p. 48-57. *In* H. Kummer [ed.], *Proc. 3rd Int. Congr. Primatol.*, Zurich, 1970. Vol. 3. S. Karger, Basel.
- Roberts, R. C. 1967. Some concepts and methods in quantitative genetics, p. 214-257. *In* J. Hirsch [ed.], *Behavior-genetic analysis*. McGraw-Hill, New York.
- Rowell, T. E. 1966. Forest-living baboons in Uganda. *J. Zool. London* 149:344-364.
- Rowell, T. E. 1967. Variability in the social organization of primates, 219-235. *In* D. Morris [ed.], *Primate ethology*. Weidenfeld & Nicolson, London.
- Rowell, T. 1969. Long-term changes in a population of Ugandan baboons. *Folia Primatol.* 11:241-254.
- Schaller, G. B. 1972. *The Serengeti lion: a study of predator-prey relations*. Univ. Chicago Press, Chicago.
- Schoener, T. W. 1971. Theory of feeding strategies. *Ann. Rev. Ecol. Syst.* 2:369-404.
- Stoltz, L. P., and G. S. Saayman. 1970. Ecology and behaviour of baboons in the northern Transvaal. *Ann. Transvaal Mus.* 26:99-143.
- Struhsaker, T. T. 1969. Correlates of ecology and social organization among African cercopitheciines. *Folia Primatol.* 11:80-118.
- Struhsaker, T. T. 1973. A census of vervet monkeys in the Masai-Amboseli Game Reserve, Kenya. *Ecology* 54:930-932.
- Tinbergen, N. 1960. Comparative studies of the behaviour of gulls (*Laridae*): a progress report. *Behaviour* 15:1-70.
- Vayda, A. P. [Ed.] 1969. *Environmental and cultural behavior*. Ecological studies in cultural anthropology. Natural History Press, Garden City.
- Watson, A., and R. Moss. 1971. Spacing as affected by territorial behavior, habitat and nutrition in red grouse (*Lagopus l. scoticus*). *In* A. H. Esser [ed.], *Behavior and environment: the use of space by animals and men*. Plenum, New York.
- Western, D., and C. Van Praet. 1973. Cyclical changes in the habitat and climate of an East African ecosystem. *Nature* 241:104-106.
- Williams, G. C. 1966. *Adaptation and natural selection*. Princeton Univ. Press, Princeton, N.J.