

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/227672447>

# Human Territoriality: An Ecological Assessment

Article in *American Anthropologist* · October 1978

DOI: 10.1525/aa.1978.80.1.02a00020

---

CITATIONS

438

---

READS

606

2 authors, including:



**Eric Alden Smith**

University of Washington Seattle

94 PUBLICATIONS 6,558 CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:



Project

Political ecology of institutionalized inequality in small-scale societies [View project](#)

# Human Territoriality: An Ecological Reassessment

RADA DYSON-HUDSON

ERIC ALDEN SMITH

Cornell University

*The question of human territoriality has frequently been debated, but most previous discussions have not sufficiently emphasized ecological variables as major factors determining territoriality. We argue that current theories in sociobiology, especially the model focusing on economic defendability of resources, need to be considered in analyzing human territoriality. According to this model, territoriality is expected to occur when critical resources are sufficiently abundant and predictable in space and time, so that costs of exclusive use and defense of an area are outweighed by the benefits gained from resource control. This model is developed, and then applied to several locally adapted human populations (Northern Ojibwa, Basin-Plateau Indians, and Karimojong). Variations in territorial responses for these groups seem to accord with the predictions of the economic defendability model. [territoriality, resource defense, human ecology, sociobiology, spatial organization]*

THE QUESTION OF HUMAN TERRITORIALITY has been the focus of much discussion and controversy (e.g., Crook 1973, Esser 1971). Discussions of human spatial organization have tended to polarize into an either-or situation: either humans are territorial by nature or they are not. At one extreme, Ardrey (1966:1) believes that territoriality is a genetically fixed form of behavior which has evolved in most species, including our own. Cohen (1976:55) believes in the existence of a fundamental "human tendency to achieve territorial control (whether instinctively or culturally derived)." On the other hand, evidence indicating a lack of rigid territoriality in many contemporary hunting and gathering groups has been viewed as supporting the argument that humans are not by nature territorial (Reynolds 1966:449).

The territoriality controversy in anthropology has primarily focused on hunter-gatherers. King (1975, 1976) and Peterson (1975) are recent examples of a long line of anthropologists (e.g., Radcliffe-Brown 1930, Service 1962, Williams 1974) who argue that some form of territorial band is the optimum pattern of spatial organization for hunter-gatherers under all or most ecological conditions. Various authors (e.g., Lee and DeVore 1968, Damas 1969) have argued that a more flexible pattern of spatial organization and resource utilization is typical of hunter-gatherers. However, both of these approaches overlook the diversity of

RADA DYSON-HUDSON is associate professor of anthropology at Cornell University. After completing a D.Phil. in biology at Oxford University, with a thesis on *Drosophila* ecology, she became interested in the relevance of biological theory to an understanding of human behavior. She carried out a three-year ecological field study of East African pastoralists, the Karimojong of Uganda (jointly with Neville Dyson-Hudson). Rada Dyson-Hudson has written on the ecology of the Karimojong livestock system in numerous articles and book chapters. Recently, her interests have extended to sociobiological theory and its relevance to understanding human social behavior.

ERIC ALDEN SMITH is a doctoral candidate at Cornell University, currently conducting fieldwork on energetics and hunting strategies among the Inuit in the eastern Arctic. His principle interest is the application of evolutionary and ecological theory in the analysis of human behavior.

hunter-gatherer social and territorial organization (Martin 1974) and fail to consider adequately the effects of different patterns of resource distribution on patterns of spatial organization. Even when variations in human spatial organization are noted, they are often presented as deviations from some natural norm or optimum.

Current research in sociobiology indicates an enormous complexity in animal territoriality which parallels the complexity of spatial organization found in human groups. Sociobiologists and ecologists have developed a general theory of economic defendability of resources in order to analyze the diversity of animal spatial organization, which allows us to ask more interesting and sophisticated questions than those that have dominated discussions of human territoriality in the past.

We believe that the issue of human territoriality can be approached by analyzing anthropological data from a theoretically sound perspective, using the models developed by various biologists, and that this approach will be useful in explaining the diversity of human spatial organization. (These in fact parallel some of the ideas, implicit or explicit, in Steward's 1938 study of human ecology.) In particular, attention needs to be paid to the ecological contexts and consequences of human behavior in a much more extensive and rigorous fashion than has been typical of studies in either ecological anthropology or popular ethology. Rather than devoting our energies to such questions as "Is *Homo sapiens* an innately territorial species?" we suggest examining human resource defense and utilization within an adaptive framework.

The goal of this paper is to advance our understanding of the behavioral ecology of the human species with regard to resource defense and spatial organization, by analyzing some of the cross-cultural (multipopulation) data of anthropology in the theoretical framework of sociobiology (Wilson 1975) and evolutionary ecology (Crook 1970, Pianka 1974). First, some recent developments in the study of animal territoriality and resource utilization are briefly summarized, and a general model relating resource distribution to spatial organization is presented. Then we examine the relevance of these concepts for the human case by examining the predictions of the model in light of the evidence from several locally adapted populations, where relationships between the social organization and environmental parameters are more amenable to ecological analysis.

We do not intend to offer a general review of human territoriality here. Rather we wish to apply the ecological model presented in the following section to three selected examples as a preliminary test of its explanatory usefulness with respect to humans. The examples we have chosen are the Basin-Plateau Indians, consisting of several different groups in geographical proximity and sharing certain linguistic and cultural features but exploiting different micro-environments; the Northern Ojibwa Indians, showing significant changes over time in spatial organization and subsistence strategies; and the Karimojong of East Africa, illustrating the degree of complexity in spatial organization that can exist in a single human population at one point in time.

We define a territory as an area occupied more or less exclusively by an individual or group by means of repulsion through overt defense or some form of communication (see below). Personal space and territoriality are often lumped together, but in this paper we are concerned with the latter. The question of whether humans are innately aggressive is also often implicit or explicit in arguments about human territoriality. We will not deal with this aspect of the controversy (see Wilson 1971 and Durham 1976 for a discussion of this point).

#### ECOLOGICAL THEORY

While human territoriality has been a major issue for little over a decade, the study of animal territoriality in general (and of avian cases in particular) has a significantly longer history. Several general reviews are available (Burt 1943, Carpenter 1958, Hinde 1956,

Klopfer 1969, Tinbergen 1957, Wilson 1975), so neither a history of the concept nor a listing of alternative definitions will be attempted here. Rather, we will attempt to demonstrate how current ecological approaches to the study of spatial organization shift attention away from older questions about territoriality (Is there a defended area or only mutual exclusivity? Is the tendency innate or learned?) to a focus on the critical parameters of resource distribution and economic defendability.

In the definition of what constitutes territoriality, much dispute has revolved around whether to emphasize *defense* of a particular area, or *exclusive use* of an area regardless of how it is maintained. In order to distinguish territoriality from cases where exclusive use is due solely to factors such as widely dispersed resources or very low density of individuals, we choose to adopt the definition used by E. O. Wilson (1975:256): a territory is "an area occupied more or less exclusively by an animal or group of animals by means of repulsion through overt defense or advertisement." This definition emphasizes the behavioral basis of territoriality without overemphasizing one possible mechanism of spacing (aggressive defense) at the expense of other possibilities (e.g., mutual avoidance based on olfactory or visual markings).

Before proceeding further, some prevalent misconceptions must be dealt with. First, it must be realized that the great amount of variability exhibited by animals in aspects of their territorial organization makes many generalizations misleading or invalid. This variability has been the source of much argument and confusion in the literature. Variability can be noted in *structural* (or definitional) categories, such as whether territories are exclusive or overlapping, defended or nondefended, geographically stable or somewhat mobile, or seasonal or permanent. Variability is equally apparent in *functional* characteristics of territories, in that many different patterns of resource utilization are involved (thus, biologists speak of feeding territories, mating territories, all-purpose territories, etc.).

A second major source of error is the conception of territoriality as an innate or species-specific trait. While this may be a valid view for some species (given an adequately sophisticated notion of "innate"), it is clearly mistaken for a wide range of species. Not only can territorial behavior come and go seasonally in many species (something which has long been recognized), but a local population may shift to or from a territorial system rapidly in direct response to nonseasonal alterations in resource distribution. Such variability has been documented in a number of populations recently. For example, artificial introduction of resource concentrations was followed by a shift from nomadic flock-foraging to strict territoriality in White Wagtails (Zahavi 1971). While studies of cynocephalus baboons in various habitats have generally disclosed a nonterritorial (home range) system, recent fieldwork on a population inhabiting a resource-rich swamp habitat revealed a case of exclusive and mutually defended territories (Hamilton et al. 1976). Ongoing studies of various species of nectar-feeding birds have elegantly demonstrated that individuals will shift to and from territorial defense of nectar sources as part of a strategy of maximizing energetic efficiency (Wolf and Hainsworth 1971, Gill and Wolf 1975). The lesson of these and other studies is that territoriality cannot profitably be viewed as an innately fixed and homologous drive found in a multitude of species.

While variability, functional diversity, and flexibility must be given due consideration in analyzing animal spatial organization, this does not mean that a general theory of territoriality is unattainable. With the discrediting of the simpler ethological conceptions of territoriality, theoretical modeling and empirical investigation are being guided by a cost-benefit model that focuses on *economic defendability* (Brown 1964).<sup>1</sup> According to this model, territorial behavior is expected when the costs of exclusive use and defense of an area are outweighed by the benefits gained from this pattern of resource utilization. Economic defendability is determined by the interaction of foraging behavior and territorial defense with the particular distributions in space and time of critical resources.

It should be noted that a number of possible measures may be employed in modeling economic defendability: time, energy, reproductive fitness, or even survival. For most purposes, in dealing with food resources, the use of energy-per-unit time to measure both costs and benefits would seem to be both valid and feasible, although with other types of resources different measures may be more suitable. For operationalizing and empirically measuring economic defendability ratios, we feel that energy is definitely superior to reproductive fitness. However, the underlying assumption of our reasoning is that adaptation (whether genetic or phenotypic) ultimately maximizes fitness and that the net rate of energy gain will tend to correlate highly with this ultimate measure (as discussed in Smith 1977). In other words, the model presented here assumes that: "The territorial strategy evolved is the one that maximizes the increment of fitness due to extraction of energy from the defended area, as compared with the loss of fitness due to the effort and perils of defense" (Wilson 1975:269).

Economic defendability has several components that interact to produce a cost-benefit ratio. The costs of territoriality include (1) the time, energy, and/or risk associated with defending an area; (2) the possible diversion of time and energy from other necessary activities; and (3) the possible negative consequences of relying on a spatially limited area for resources. The benefits of territoriality are simply those that result from exclusive access to critical resources; however, this benefit is conditioned by factor 3 (above) and is relative to alternative (nonterritorial) modes of resource utilization. For any case of territoriality, the ratio of benefits to costs should exceed 1.0 (and probably by a comfortable margin). It can also be argued that adaptive processes in the long run will tend to produce optimal results and, thus, that the benefit/cost ratio for a territorial system should have an average value greater than the nonterritorial alternatives available to the individual or group. However, this last expectation involves the assessment of a broad range of opportunity costs, and the economic defendability model is not sufficient for this purpose.

The cost-benefit ratio of a territorial strategy is highly dependent on the pattern of resource distribution, and it is this relationship which must be examined in attempting to account for the presence or absence of territorial organization in any population. For our purposes, the important parameters of resource distribution are predictability and abundance. Predictability has both a spatial component (predictability of location) and a temporal one (predictability in time). Abundance or density of a resource can be measured in several ways: in terms of average density over a broad area (the average for the territory or home range), as an average value within a particular type of microhabitat (within-patch density), and in terms of the fluctuation in density over time (the range of variability). While all these parameters of resource distribution will interact to determine the adaptive value of any foraging strategy, in the interests of clarity we will first consider each parameter separately in terms of the general model of economic defendability.

Resources that are predictable in their spatiotemporal distribution have greater economic defendability than unpredictable resources. A habitat where critical resources are predictable will be most efficiently exploited by a territorial system (holding other resource distribution parameters constant). Geometrical models of foraging indicate that it is more efficient (requires less foraging time or energy for a given amount of return) for individuals to disperse to mutually exclusive foraging areas when food resources tend toward a uniform distribution and are predictable (Horn 1968, Smith 1968). Unpredictability of resources results in lowered benefits of territorial defense (in terms of resources controlled), and, below a certain threshold, territoriality will be uneconomical or even unviable (Brown 1964).

With a sufficient degree of resource unpredictability, clumping of individuals (often termed coloniality for nonhuman species) is expected to occur. Under these situations, efficient resource utilization may depend on the pooling of information about the location

of ephemeral resource concentrations. Information may be shared either passively, as in cases of observation and following of successful foragers (Horn 1968, Ward and Zahavi 1973), or actively (as in the case of chimpanzees who advertise finds of patchily distributed and asynchronously fruiting trees by drumming [Reynolds and Reynolds 1965:423]). As an illustration of some of these principles, among primates, the arboreal folivores (such as *Alouatta*, *Colobus*, and *Presbytis*) usually exhibit strong territoriality, in contrast with most frugivorous and omnivorous species (Bates 1970). This increased frequency of territoriality has been attributed in part to the high defendability of leaf resources, which can be very predictable in the tropics and subtropics (Brown and Orians 1970, Denham 1971, Crook 1972, Eisenberg et al. 1972).

Abundance or density of resources is a more relative parameter than predictability and must be related in each particular case to foraging bioenergetics and group size. In our model, resource density really means *effective* density, not absolute abundance. (Thus, a given area may have a higher biomass of small rodents than of large game, but a human group would probably capture a greater amount of the large game and with greater efficiency; in our terms, the large game would exist at a greater effective density in this example.) In general, increased average density of critical resources makes a territorial system more economically defendable, simply by reducing the area that needs to be defended and thus reducing defense costs. However, density of resources *within a patch* combined with a high degree of unpredictability reduces the economic advantage of territoriality. That is, with sufficient within-patch density and patch unpredictability, localized and ephemeral *superabundances* result, where the temporary glut of resources is more than can be consumed and thus is best shared (either actively or passively) rather than defended. Such a situation may be characteristic of the critical resources for various populations, such as insectivorous birds (Horn 1968, Emlen and Demong 1975), colonial seabirds feeding on dense and unpredictable concentrations of fish (Lack 1968:134 ff.), and chimpanzees foraging for patchily distributed fruit trees (Eisenberg et al. 1972).

Without delving further into theoretical complexities or specific cases, the formal relationships between the parameters of resource distribution discussed above and the economic defendability of different foraging strategies can be summarized schematically (Table I; a graphic version is given in Fig. 1). Note that predictability and abundance of resources interact to determine the adaptive value of different patterns of resource utilization. In summary, a territorial system is most likely under conditions of high density and predictability of critical resources. However, it must be noted that if a resource is so abundant that its availability or rate of capture is not in any way limiting to a population, then there is no benefit to be gained by its defense and territoriality is not expected to occur. With relatively scarce but still predictable resources, large home ranges with some degree of overlap would be expected. With unpredictability of resources above a certain threshold, a territorial tie to a fixed area is not economically defendable, and the degree of movement in foraging over a large area must increase (nomadism). Depending on the average density of the resources within a patch, unpredictable resources are most efficiently exploited by communal sharing of information (high average density) or by a high amount of dispersion (low average density). While this sort of simplified correlation between resource distributions and foraging strategy cannot do justice to the complexity of specific cases, we feel it provides a general framework for explaining the occurrence (or nonoccurrence) of territoriality that is far superior to many alternative formulations.

In the next section, we test the relevance of the economic defendability model for an understanding of human territorial behavior. Ideally, we should make a systematic survey of territorial behavior in a random sample of human societies. However, the nature of the data on human territoriality makes such a systematic survey difficult. The term "territory" and "territoriality" tends to be applied to hunter-gatherers and pastoralists, while what may be

TABLE I. RELATIONSHIP BETWEEN RESOURCE DISTRIBUTION AND FORAGING STRATEGY.

	<i>Resource Distribution</i>	<i>Economic Defendability</i>	<i>Resource Utilization</i>	<i>Degree of Nomadism</i>
A.	Unpredictable and Dense	Low	Info-sharing	High
B.	Unpredictable and Scarce	Low	Dispersion	Very high
C.	Predictable and Dense	High	Territoriality	Low
D.	Predictable and Scarce	Fairly low	Home ranges	Low-medium

equivalent behavior among agriculturalists is described in terms of land tenure systems. Even when a group is described as territorial, the nature of the group, the means of territorial defense, and the distribution and abundance of resources, often are not specified. Therefore, to test the model, we selected two ethnographic studies of locally adapted populations which appeared to provide the requisite data for comparison with animal models and data from a third locally adapted population for which we have detailed firsthand information.

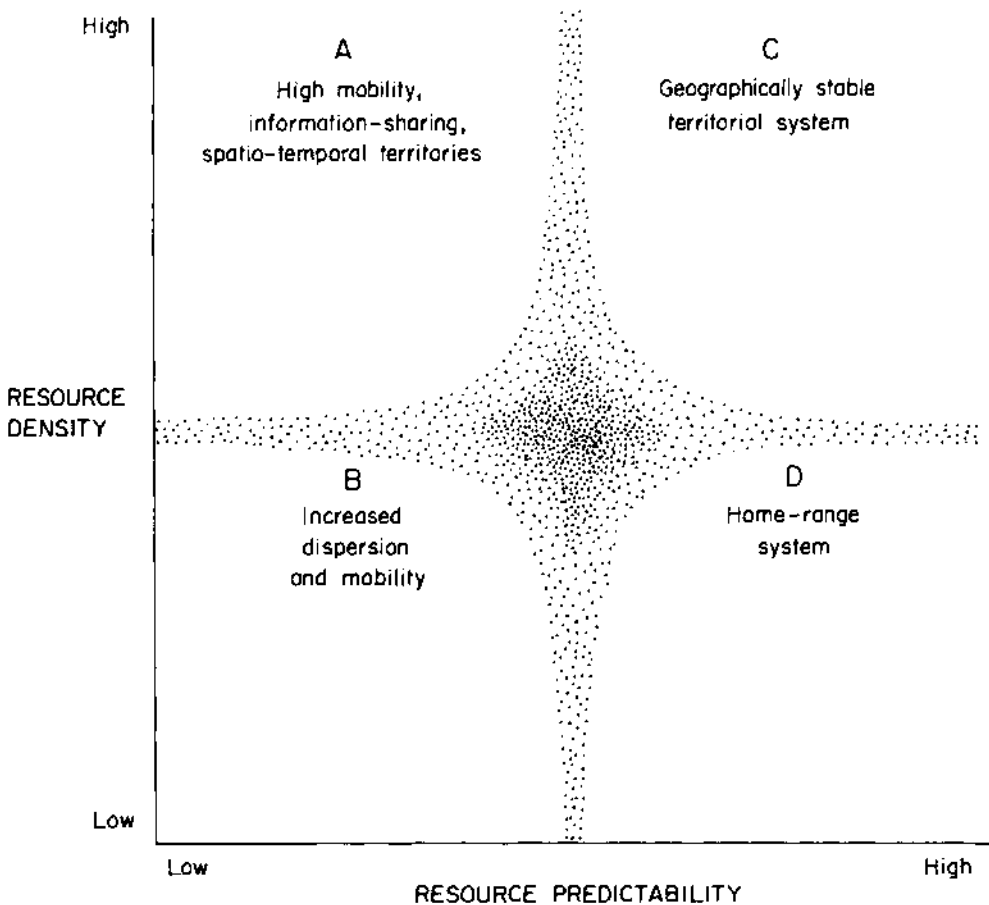


Fig. 1. General predictions of the economic defendability model for spatial organization.

## HUMAN TERRITORIALITY: THREE CASES

The variation in spatial organization in response to variations in resource distribution found in other animal species can also be seen with human populations. Our first example, the Basin-Plateau Indians, consists of several different groups in geographical proximity and sharing certain linguistic and cultural features but exploiting different microenvironments. The Northern Ojibwa Indians are more geographically, culturally, and ecologically unified, but here a detailed historical record shows significant changes over time in spatial organization and subsistence strategy. Following our examination of these hunter-gatherer cases, we present a more detailed study of the Karimojong of East Africa, illustrating the degree of complexity in spatial organization that can exist in a single human population at one point in time.

In applying the deductive argument of our general model of economic defendability, we will examine data for each particular case in a definite sequence. We will first consider the resource distribution for the area in question, delimiting as far as possible the abundance and predictability of key resources. Then we will turn to the patterns of resource utilization reported for the particular population (patterns of cooperative foraging, information sharing, competition, etc.). Finally, we will examine the spatial organization of the population, focusing on the degree of dispersal, nomadism, and territoriality. Our goal is to determine whether the resource distribution parameters are related to the patterns of resource utilization and spatial organization of each case in the manner predicted by our general model.

Our examples, then, are not a representative sample but were chosen to illustrate various aspects of human territoriality; in this way we feel we can begin to test the economic defendability model in a broad manner and yet avoid the superficiality that would be entailed by a general review of human spatial organization in a paper of this length. In summary, our three examples were chosen to demonstrate intergroup variation for a single region (Basin-Plateau Indians), variation through time (Northern Ojibwa), and intragroup variation at one point in time (Karimojong).

*Basin-Plateau Indians*

Steward (1938) in his classic study of the indigenous populations of the Great Basin region of North America described great differences between groups in the degree to which territories were delimited and defended.<sup>2</sup> Within the Great Basin and the adjoining Colorado and Columbian Plateau areas, Steward recognized four ethnolinguistic groups, of which three concern us here: Western Shoshoni, Southern Paiute, and Northern Shoshoni. In accordance with the model of economic defendability, we will analyze Steward's data by first examining the parameters of resource abundance and predictability. Then we will examine the patterns of resource distributions that maximize or optimize the efficiency of their utilization.

In the area inhabited by the Western Shoshoni (the Central Great Basin) the rainfall was low and patchy. The density of game and most plant foods was very low (Steward 1938:20,33). In terms of predictability, the usual pattern for arid regions held, in that both plant and animal resources "had in common the extremely important characteristics that the place and quantity of their occurrence from year to year were unpredictable, owing largely to variations in rainfall" (Steward 1955:105). Owing to the low primary productivity, game was exceedingly scarce, and large game did not live in herds. Small game, such as rodents, lizards, and insects, probably contributed more to the diet than large mammals (Steward 1938:33).

The Western Shoshoni lived primarily on plant foods, principally grass seeds and piñon nuts, although leaves, roots, and berries were also eaten. The grass seeds they depended on ripened sequentially from the lowlands to the highlands as the season progressed from spring



to summer to fall. Steward (1938:19-20) described particular features of seed distribution as follows. First, particular grasses with edible seeds seldom occurred in dense patches, so that Shoshonean gathering techniques, which Steward considered to be reasonably efficient, did not provide great quantities. Second, because the harvest period in any locality was short and the seeds of most species fell off the plant within a few days or weeks of ripening, many were not harvested. Third, the location of patches of seed plants was unpredictable, as the abundance of seeds bears a close relationship to the distribution of rainfall.

Piñon nuts (occurring in the Piñon-Juniper belt at 1,500 to 2,100 m.) were the major winter food of the Western Shoshoni. As this resource provided a major contribution to the diet, it is important to consider its distribution and abundance. In Steward's words:

It is the most important single food species where it occurs, but harvests are unpredictable. Each tree yields but once in 3 or 4 years. In some years there is a good crop throughout the area, in some years virtually none. In other years, some localities yield nuts but others do not. When a good crop occurs, it is far more abundant than the local population can harvest. . . . The period during which they [the pine nuts] can be harvested is . . . 2 to 3 weeks, rarely longer [Steward 1938:27].

These local and short-lived concentrations of pine nuts can be viewed as temporary super-abundances.

Western Shoshoni patterns of resource utilization and spatial organization can be analyzed as responses to characteristics of specific resources. The low average density of resources is reflected in a population density of approximately 0.13 people per square kilometer (0.05 people per square mile) (Steward 1938:49). Most hunting was carried out by solitary individuals, but any large game captured was distributed among groups of families sharing a camp. Cooperative hunting (antelope drives, rabbit net hunts) resulted in a higher per capita yield than solitary hunting. However, the effect on local prey populations was so drastic that such hunts could only be held on a very infrequent basis in any one locale (Steward 1938:33, 231).

Grass seeds were collected by individual family units. Population dispersal was marked during the period of the year when grass seeds were the major food resource, since the low density of these resources made aggregation for foraging inefficient. "Participation of many persons in seed and root gathering not only failed to increase the per capita harvest, but it generally decreased it so greatly that individual families preferred to forage alone so as not to compete with other families" (Steward 1955:107). During this period, the population was also highly nomadic in response to the highly ephemeral and unpredictable nature of the major resource.

In the fall, the individual family gathering groups who happened to be nearby would converge on a piñon grove which was yielding a crop. They would gather as many nuts as possible and cache them for winter storage. Several families would spend the winter together in small "villages" at the site of these pine nut caches. The very erratic pattern of yields brought different families together at different places each fall, and the need to spend the winter at the cache meant that at their most sedentary time of year, no consistent group of families could amalgamate and establish either band or family ownership of piñon groves (Steward 1938:233).

Cooperation between families via information sharing is referred to frequently by Steward (1938:19, 27, 254, etc.). Thus, individual families often found out about the location of good piñon crops, patches of ripe seeds, locust concentrations, or rabbit drives being organized through word of mouth. Apparently this method played a major role in distributing the population with respect to local and ephemeral resource concentrations, although Steward does not discuss this in any quantitative detail.

In turning to the general model proposed earlier, we can locate the Western Shoshoni in Quadrant B (Fig. 1) for that portion of the year when they focused on collection of wild

seeds; since these resources are both unpredictable and scarce, the most economical response is dispersion and nomadism (in this case at the family level). Piñon nuts, the main resource for the winter months, are unpredictable and ephemeral yet locally dense (a temporary superabundance), and thus the predicted utilization patterns involve nomadism, reduced dispersal, and a high degree of information sharing (Quadrant A). However, the factor of storage means that once harvested, these nuts are reliably available, leading to a sedentary period in the yearly round. In summary, the Western Shoshoni exhibited changes in degrees of nomadism and dispersal in general accordance with our model. Because of the distribution of critical resources, we argue that territoriality was an economically undefendable option. Steward's summary of the data he collected clearly supports this argument:

The Shoshoni lacked any form of ownership of land or resources on it (except eagle nests). No group habitually or exclusively utilized any clearly defined territory for hunting, fishing, or seed gathering. . . . The sparse and erratic occurrence of vegetable foods required that territories exploited by different families and villages not only should vary from year to year but should greatly overlap. . . . Under such conditions, ownership of vegetable food resources would have been a disadvantage to everyone [Steward 1938:254].

In contrast to the Western Shoshoni, the Owens Valley Paiute lived in a circumscribed but much more productive area on the edge of the Great Basin. (The Owens Valley is formed by the eastern scarp of the Sierra Nevada and by the Inyo and White mountain ranges on the west.) Because of the steep topography, the local environment exhibited extreme zonation and diversity of resources, such that all necessary food could be obtained within a 32-km. radius of each settlement (Steward 1938:50). This zonation reduced the foraging area and thus increased effective density. In addition, the streams flowing from the Sierras meant a greater water supply in comparison with the area of the Western Shoshoni. A water supply derived from streams fed by snowmelt and aquifers presumably led to more abundant and predictable resources as compared to the regions where plant growth was solely dependent on patchy rainfall. The valley inhabitants increased resource predictability and density themselves by systematic irrigation of wild seed patches (Steward 1938:53). The greater resource density of the Owens Valley is attested to by the human population density (approximately 1.25 people per square kilometer, or 0.48 people per square mile) which is roughly ten times the average density of the Western Shoshoni.

Resource utilization patterns included communal hunts, meat redistribution within the local band, and the familiar pattern of family harvesting of plant foods. However, the Owens Valley Paiute, probably unique among the Indians of the Great Basin, lived year-round in permanent villages on tributaries of the Owens River. Groups of villages were organized into well defined bands which delimited and defended territories. The band territories were cross sections of the valley cutting across the valley and extending up the mountainsides. If necessary the territories were defended by small scale aggression (little bloodshed is reported), but primarily by social and supernatural sanction. Access to resources depended on band membership, although on occasion some nonmembers gained access. Piñon areas within the band territories were subdivided into family plots. According to Steward (1938:52), families defended their piñon plots against trespass but "often invited persons even of other bands, especially their relatives, to pick on their plots." The piñon-nut harvest was organized by the band chief.

Although Steward speaks of band-owned hunting territories, he makes it clear that this territorial organization was much more flexible than was the case with respect to plant resources. The two species of game which could be driven (jack rabbit and antelope) were hunted cooperatively within band territories. The hunts were under the direction of a hunting leader, and participation was usually limited to band members (Steward 1938:53). However, not all game was hunted by band members within their own territory. Some deer

hunts involved the participation of several bands. In the southern part of the Owens Valley, bands did not claim hunting territories: "Men were permitted to hunt anywhere but naturally tended to restrict hunting to the mountains near their own villages. . . . [B]and ownership of hunting territory seems to fade out gradually from northern to southern Owens Valley" (Steward 1938:54). The fact that the Owens Valley Paiute were less territorial with respect to game than to plant resources can be explained by noting that game animals are highly mobile and, therefore, a more unpredictable resource than plant foods.

In summary, the greater predictability and density of resources in the Owens Valley as compared with the Western Shoshoni made the area economically defensible for this hunter-gatherer population. While territorial exclusiveness led to a reduced efficiency of capture for some types of resources, it apparently allowed an average increase in the individual rate of return for time and energy devoted to foraging: "The disruptive effect of the erratic yield of wild seeds, especially the pine nut, was outweighed by the importance of communally irrigated and therefore comparatively reliable seed patches in the valley" (Steward 1938:256).

The Northern Shoshoni were a third group of Basin-Plateau Indians studied by Steward. We will deal here only with those groups living on the northeastern rim of the Great Basin, in an area of somewhat higher rainfall and greater primary productivity. In the northern Great Basin (where rainfall is higher) the plant resources such as grass seeds would presumably be more predictable and less patchy than in the southern Great Basin where rainfall is lower.<sup>3</sup> However, Steward does not directly discuss the question of the distribution of the plant foods. He does note that the grazing in this area was sufficient for raising horses (while any horses which strayed into the area of the Western Shoshoni were killed and eaten because they competed directly with humans for food resources [Steward 1938:235]). The Northern Shoshoni used the horses to derive a substantial portion of their subsistence from buffalo hunting. Although the buffalo herds had a relatively low spatial predictability, they were a highly concentrated resource when encountered. We argue that the amount of available resources was increased by use of horses for search, pursuit, and transport of resources, especially buffalo but also plant foods.

The Northern Shoshoni pattern of resource utilization involved a seasonal sequence of subsistence strategies: buffalo hunting in summer; foraging for roots, berries, and game in the fall; and living primarily off the surplus buffalo meat in winter. The buffalo hunts involved the formation of large bands and a migration over the low passes in the Rocky Mountains to the Great Plains. According to Steward (1938:235), cooperative hunting of buffalo was a high-yield activity basic to Northern Shoshoni subsistence:

The herds east of the Rocky Mountains were so large that several hundred persons were not only able to maintain themselves during the hunt but to cure sufficient meat to last through much of the year. The hunts were cooperative because . . . the yield of a planned, concerted drive was so much greater than what individuals could procure alone.

These large migratory groups of hunters were also effective in defense against raids from other equestrian hunters. The return from the plains hunts was followed by a dispersal of individual families or small groups in order to forage for local resources prior to the onset of winter. Families then amalgamated again to live in winter villages in groups roughly the same in size and composition as the summer hunting parties. Clearly the horse was critical in allowing food to be gathered over a wide area and transported centrally, thus supporting large local groups. The large aggregations of people did not indicate high overall resource density: population density was low (2.1 to 0.08 people per square kilometer, or 0.8 to 0.03 people per square mile), despite the fact that much of the food (i.e., buffalo) was "imported" from another habitat.

The spatial organization of the Northern Shoshoni involved high mobility with aggregation for part of the year, mobility with dispersal for another part, and a fairly sedentary

aggregation during the winter. Since the different seasonal patterns of subsistence occurred in two geographically separated regions, and focused on very different resources, we would not expect Northern Shoshoni spatial organization to be the same in the two zones. According to Steward (1938:237) the area used by Northern Shoshoni groups overlapped, and they were not territorial at any time of year.<sup>4</sup> Clearly this would be expected for the summer phase, since pursuing highly mobile herd animals on horseback is incompatible with territorial defense. During the fall dispersal, people seem to have focused on securing foods typical of the Great Basin as a whole, which were patchy in space and ephemeral in time (Steward 1938:235), and again territoriality would not be predicted. Steward indicated that other groups raided the Northern Shoshoni, but he does not specify the time of year, so it is not clear whether winter villages were defended against outsiders. It appears that the villagers were subsisting primarily on their caches and not depending on resources derived from the area adjacent to their settlements. However the food surpluses, horses, and goods, such as skins kept at the winter villages, would have been economically defensible and capturable items. We predict that large resource areas as such would not have been delimited and defended, but that the winter villages would have been. However, more evidence is needed on both resource use and spatial organization at this time of year in order adequately to test our model.

#### *Northern Ojibwa*

The analysis of territoriality in the Northern Algonkians (including the Northern Ojibwa) has a long history in anthropology, and both empirical and theoretical controversies have been frequent. There are basically two contending viewpoints on the origins of Northern Algonkian hunting territories. Some scholars, beginning with Speck (1915, 1923; Speck and Eiseley 1939; Cooper 1939; Halliwell 1949), argue that a territorial hunting system was an aboriginal adaptation to maximize the sustained yields from game, especially beaver. Others have presented evidence that territoriality was not aboriginal for the Northern Algonkians and in fact arose after fur trading had become established (Leacock 1954; Knight 1965; Bishop 1970, 1974). While this latter view is now generally accepted, disputes still arise over what factors are the major determinants of the shift to territorial systems of land use. Leacock has emphasized the role of acculturation and barter economy in encouraging the shift from cooperative group hunting to individualized trapping, suggesting that family territories were the result of competition for fur-bearing animals whose pelts were traded for food. Knight has countered this by noting that the East James Bay Cree spent over 250 years in contact with traders and participating in the trapping economy without developing territorial systems of land tenure. Contrary to Leacock, Knight (1965:36) argues that fur-bearing animal populations fluctuate drastically (as with many other subarctic animal species), and that, in addition, fluctuations of the trading economy (changes in prices, credit availability, trading post location, etc.) must also be considered in assessing the viability of a territorial system. In Knight's view:

Until some stable and significant amount of income other than that from trapping and hunting was available to the band, long-run minimum conditions did not allow subarctic hunter-trappers to compartmentalize general band areas into permanently delineated tracts given over to the exclusive use of particular families, and still survive [1965:29].

Bishop (1970, 1974) reaches conclusions regarding Northern Ojibwa spatial organization that are not in accordance with either Knight's or Leacock's views. He argues that Northern Ojibwa groups adopted territorial systems of land tenure not primarily as a response to the individualistic barter economy nor in the context of reliance on store foods, but when (among other things), the depletion of large game forced a shift to the hunting of small nonmigratory species. We will use Bishop (1970, 1974) as the basis of our discussion of

changes in Northern Ojibwa territoriality, because of the historical depth of his account and the detailed record of changes over time. However, as is generally true of ethnohistorical reconstructions, much information is lacking or incomplete in Bishop's account. For example there is little information about density of resources, the scale of large-game movements, and the cycles of fluctuations in numbers of small game. Furthermore, Bishop does not define territoriality clearly nor is he specific about the group associated with a particular piece of land and how territorial rights were defended. However, the information that Bishop does present about changes in Northern Ojibwa spatial organization with changes in resource utilization appears to fit the predictions derived from our model.

Originally the Northern Ojibwa were hunters and gatherers living in Canada east of Lake Superior. They expanded their range northward and westward over the last 400 years, changing their subsistence patterns as a result of this movement and of contact with Europeans (Bishop 1974:332). Their precontact food resources included moose, Virginia deer, woodland caribou, beaver, several species of fish, and a wide variety of vegetable produce. However, they depended primarily on two species of large game—caribou and moose. In the 1600s and 1700s, trading of furs for European manufactured goods and later for food became established, first through itinerant traders and later through established trading posts. Over a period of 300 years, the Ojibwa changed from dependence on wild foods to a primary dependence on foods obtained from trading posts in exchange for furs. Nonetheless, until recently Ojibwa subsistence primarily depended either directly or indirectly on animals which they hunted and trapped. During recent times the Northern Ojibwa increasingly have come to depend on money earned by new occupations (such as mine laborer and fishing guide) and on money provided by the Canadian government. Now almost half of the income of the group studied by Bishop is from government sources, and trapping contributes little to their subsistence.

Between 1730 and 1780, trade goods increasingly replaced aboriginal technology, and these goods were relatively cheap and easy to acquire. The trapping of fur-bearing animals, while important for trade, did not interfere with Northern Ojibwa hunting and gathering of foods, nor did the Ojibwa depend on trade for food (Bishop 1974:10). During the period from about 1780 to 1820, there was great competition between rival trading companies, resulting in many trading posts and the availability of cheap trade goods. At this time, the primary source of food for the Northern Ojibwa was large game, and trapping was opportunistic and involved great mobility. Reliance on a mobile animal like caribou favored a "more nomadic existence mitigating the formation of well defined territories since caribou migrations are not restricted by any artificially bounded regions" (Bishop 1974:209). Bishop (1974:289-292) found that among the Ojibwa of the Osnaburgh region, territorial ownership did not exist during this period. The hunting group returned to the same general area each year but possessed no exclusive rights to resources. Boundaries between the areas used by different hunting groups were not sharply demarcated. During this period, when large game was abundant, although the members of any particular band "tended to hunt in the same general region each year, resources belonged to those who came first, even when they were within the region inhabited by another band" (Bishop 1970:11).

By 1820 large game was depleted in the area studied by Bishop. As a result of the establishment of a trading monopoly by the Hudson's Bay Company in 1821, the exchange value of furs declined. Thus, at the same time that the Northern Ojibwa came to depend more on trading posts for food and other goods, the value of their furs decreased. Consequently, competition for fur-bearing animals became intense. With the decline of large game in the Northern Ojibwa area, subsistence depended primarily on small nonmigratory game, especially hare and fish (Bishop 1970:12, 1974:209). Following the disappearance of large game and the shift to hare and fish, archives for the area studied by Bishop document a decrease in the degree of mobility and the extent of area covered by the Ojibwa hunters

(Bishop 1974:209-210). By the mid-19th century, Northern Ojibwa groups who were dependent on the fur trade and on small game had developed family hunting territories throughout most of Northern Ontario (Bishop 1974:94). Social sanctions against trespass apparently were an important aspect of defense of hunting territories (Bishop 1974:218-219). In summary, Bishop concludes that it was:

... The shift to small game, working in conjunction with a growing population in an area drastically depleted of the necessary peltry, that led to the emergence of hunting territories in Northern Ontario. . . . In the case of the Northern Ojibwa, the loss of large game, caribou and moose, and the forced reliance on hare and fish constituted the crucial factor in the development of family hunting territories [Bishop 1970:13].

From 1890 to 1945, the Northern Ojibwa dependence on trading posts continued to increase. Archival evidence indicates a decline in the rigidity of the territorial system during the first decade of this century in the area studied by Bishop. At this time, "rules against trespass had grown lax," and this change was "promoted by the return of large game, caribou and moose," animals "not confined by artificially bounded territories" (Bishop 1974:94). Bishop suggests that population growth and an increase in competition over furs led to a breakdown of social sanctions against poaching and trespass, and contributed to the decline in territoriality.

Today the Osnaburgh Ojibwa live in a village, and most of their income comes from wage labor and government assistance rather than trapping and trading. Indian trappers are now able to hire airplanes to transport them to their trapping territories (Bishop 1974:15). Also most forms of wage labor have taken men away from their community and family; and government-established schools interfere with traditional modes of subsistence. The present-day pattern of Ojibwa territorial organization is not discussed by Bishop, but clearly economic defendability of a particular area would be influenced by factors such as government regulations, enforcement of laws, and increased mobility with changing technology, as well as by the distribution and abundance of resources.

The evidence Bishop presents on the development of Northern Ojibwa territoriality seems to accord with the predictions of our model. Large game, such as caribou and moose, are highly mobile and therefore relatively unpredictable in space and time. While they were dependent on these animals as a major resource, the Northern Ojibwa did not defend territories, although the degree of nomadism and dispersal of Ojibwa hunting groups at this time is not well documented. After the virtual disappearance of large game, the Northern Ojibwa were forced to rely on small game species for their subsistence. Although this probably did not provide as abundant a subsistence base as the large game, the small game was less mobile and therefore more predictable in space, and the Ojibwa began to defend hunting territories. As indicated by our model, economic defendability of a resource area can develop even when resource abundance declines, as long as this decline is more than compensated for by increased predictability of key resources.

#### *Karimojong*

In the case of the Basin-Plateau Indians and the Ojibwa, territorial behavior occurs under ecological conditions similar to those in which territoriality occurs in other species. However, characterizing the behavior of a particular group as "territorial" or "not territorial" can sometimes conceal important aspects of their social organization. A particular human group may be described as being either territorial or nonterritorial depending on the resource which is being considered. Even human groups with subsistence economies use an enormous variety of resources at any given time. They utilize various food sources, each of which can be different with respect to such characteristics as predictability, abundance, mobility, and defendability. Human groups also use nonfood resources such as clay for pots,

salt mines, iron ore for making tools, or wood for building and burning. Furthermore, people have manufactured resources such as homes, tools, irrigation works, and livestock corrals. It is not surprising, given this enormous diversity, that within the same human population some resources may not be defended, while others may be defended in various ways. For example, crops may be defended by exclusive ownership of a particular piece of land, livestock may be defended as they move through space, while deposits of clay for pots may not be defended at all. Furthermore, if a resource is defended by defense of a territory, the size of that territory and the people who are excluded from it can vary according to the resource under consideration. These points will be illustrated by a discussion of the spatial organization among the Karimojong living in northeastern Uganda. (More details of Karimojong subsistence strategies and social organization can be found in N. Dyson-Hudson 1966 and Dyson-Hudson and Dyson-Hudson 1969, 1970.)

Although the Karimojong have a great variety of resources ranging from personal ornaments to water sources, we will focus on the resources associated with the two distinct subsistence strategies which provide the major sources of food energy—cultivating plants, particularly sorghum, and husbanding livestock, particularly cattle. The growing sorghum is predictable in space, in that it grows where it is planted, in fields on the alluvial terraces along the central reaches of the major rivers. It is also predictable in time, in that the grain ripens four to five months after it is planted. Although the yield per acre varies enormously from less than 45 kilograms per hectare (250 pounds per acre) to over 185 kilograms per hectare (1,000 pounds per acre), growing sorghum clearly is a dense and predictable resource. After the harvest, sorghum is stored in granaries within stockaded settlements near the fields, and stored sorghum also is a dense resource which is predictable in time, space, and amount. If the harvested sorghum is sufficient to provide them with food, the women, young children, and old people remain in the permanent settlements year-round, and their main food is the sorghum stored in the settlements.

Both growing and stored sorghum are resources which are defended by the woman who grows the grain, with the help of her close kin. The land good for growing sorghum is limited in amount and is owned collectively by the people of the group of settlements near that land. Specific areas are allocated to individual women, and other people are excluded from cultivating that land by the woman and her husband, supported by other members of the settlement cluster should that become necessary. Growing crops are defended against livestock by fencing and by keeping herds under continuous observation. During the critical period when the grain is ripening, the cultivator and her kin take turns standing on platforms in the field from dawn to dusk, defending crops against birds and against people who might cut and steal the succulent stalks. Harvested grain is kept in individually owned granaries inside the stockade surrounding the settlement in which ten or more women and their close kin live. Each woman protects her own grain from animal pests, including rodents, termites, and weavils. Theft by other people is prevented by keeping a guard in the settlement or by ritual means. The guards often are old people who are physically infirm, and the ritual involves placing branches of a sacred tree at each entrance into the settlement to ensure that misfortune befalls any thief. A work diary of a Karimojong settlement clearly shows that defending crop resources against animal competitors—fencing fields, guarding livestock, shouting and throwing mud balls at birds trying to steal the ripening grain, and spreading the sorghum in the sun to kill insect pests—requires activities which entail large energy expenditures by people (R. Dyson-Hudson 1972). Defense of crop resources against other Karimojong involves primarily social constraints and has a very low energy cost.

In summary, density and predictability in time and space is high for growing sorghum and harvested grain and both are defended resources. Defense of agricultural crops against animal competitors requires great amounts of time and energy. Relatively little energy is devoted to defense of these resources against other Karimojong, because social controls are so effective.

Control of access to garden land is through prior social exclusion rather than overt fighting, and disputes over the use of that garden land are rare. Harvested grain is also defended primarily through the fear of social disapproval and of divine intervention. The availability of a dense and predictable resource means that people dependent on that resource are not highly mobile.

The distribution, abundance, and predictability of the cattle/grazing land resource complex are very different from that of the agricultural land/crop complex. The cattle, which convert grazing into human food, can be considered to be predictable in time and space, in that the herdsman remain associated with their cattle by moving with them. Cattle can also be considered to be an abundant resource in that herd size is adjusted so that all the herders caring for a particular herd can subsist on the food produced by that herd, by milking and drawing blood from living animals. Cattle are a defended resource, as would be predicted by our model. They are defended against enemies and predators by guarding them during the day (with spears and shields if necessary) and by corralling them at night. However, the defense of cattle does not involve delimiting and defending particular territories (except insofar as the corrals can be considered territories). The distribution and abundance of Karimojong cattle is a function of grazing land availability. The patterns of distribution and predictability of grazing lands are complex, and we will analyze in more detail their relation to Karimojong spatial organization.

Grazing land is very abundant and widespread in Karamoja. Except for perhaps 500 square kilometers occupied by mountains, the 6,437 kilometers of virtually all Karimojong tribal land can be used at some time for grazing. However, the suitability of a particular area for grazing cattle at a particular time depends both on the conditions of the vegetation and on the presence of a reliable water source within some 20 km. (since Karimojong cattle must drink at least every other day). During the rainy season there is ample water and grazing almost everywhere in the tribal area. During the dry season, areas of good grass within 20 km. of water are patchy and unpredictable in time, space, and duration. Localized and unpredictable dry season storms produce a highly nutritious flush of plant growth. The length of time that grazing is available in a particular area depends on the amount of moisture in the soil and the number of cattle grazing in that area, and cattle are moved to take advantage of areas of temporary abundance of grazing. The herdsman construct temporary camps where the cattle can be protected at night from predators and human enemies. As compared with the women and old men who live primarily in the permanent settlements and eat mainly grain, the men and herd-boys associated with the cattle have a more mobile mode of life, in response to the low predictability of dry season grazing in space, time, and amount. Furthermore, the herders are more dispersed because of the relatively low density of plant resources and the longer food chain involved in getting food from livestock rather than directly from plants.

Particular Karimojong do not defend specific grazing grounds. There is some tendency for members of a group of settlements to use the dry season waterholes nearest to their permanent settlements. Also, an individual herd-owner tends to graze his cattle in the same general area in successive dry seasons, presumably because he gains a more thorough knowledge of the environment. But there is no private ownership of grazing lands; all Karimojong have the right to graze everywhere within the tribal area.

Because of the patchy and unpredictable nature of resources and the individualized pattern of herd movements, territorial ownership of fixed grazing areas is not a viable strategy. However, at a particular point in time the number of cattle grazing in an area can be regulated by social interactions. A herd-owner moving to a new grazing area must request permission of the people already herding in the area, who are organized into an ephemeral political unit termed a "camp cluster" (N. Dyson-Hudson 1966). These social interactions allow an exchange of information and can operate to regulate the number of herds in a



particular area at a particular point in time in relation to the available resources. In times of severe shortage the people who are associated in a camp cluster may exclude other Karimojong from the area where they are grazing, or from sharing their water supply, and enforce the exclusion by fighting with sticks (N. Dyson-Hudson 1966:73, 255). However, informants emphasize that these fights occur only in times of extreme shortage, when an individual's survival would be jeopardized by sharing the grazing resources.

The economic defendability model seems to account adequately for the complex and varied spatial organization within the Karimojong tribe. The two resource complexes we have considered fall into different quadrants on the graph of our model (Fig. 1). Grazing resources are relatively unpredictable and of varying density (Quadrants B or A) and herds-men, particularly during the dry season, are highly nomadic and dispersed, living in temporary camps and forming ephemeral but nonetheless important associations with other herd-owners. Only in times of extreme scarcity do Karimojong herdsmen defend grazing areas, and the defended areas are those which have relatively abundant grazing at that particular point in time.

In contrast, agricultural resources are relatively dense and predictable in space and time (Quadrant C), and the women who practice agriculture are sedentary and live at a relatively high population density. Specific areas of agricultural land are delimited and defended, and the harvested crops are also defended both against pests and against other Karimojong. The predictability of agricultural yields from year to year is too low for a constant number of people to depend on crops, and the flexibility of Karimojong social organization, which allows people to move between permanent settlements and cattle camps, enables them to adjust to variations in the abundance of resources.

Despite the fact that (as predicted by our model) the Karimojong do not in general have territorial defense of grazing land against other Karimojong, they do defend their tribal grazing lands against non-Karimojong. Enemies who trespass into Karimojong land are killed with spears, and their cattle are taken. There is also active raiding across tribal boundaries.<sup>5</sup> This territorial defense cannot adequately be accounted for by our model, which does not take into account different responses to members of one's own group versus outsiders. Yet among human groups such differences are very common. A system of cooperative perimeter defense involving ethnic exclusion alters the costs and benefits of territoriality dramatically (Hamilton and Watt 1970:270-272), and this might help to account for Karimojong defense of territory at their tribal boundaries. An analysis of Karimojong territorial behavior taking into consideration ethnic identity, ethnic exclusion, symbolic communication, and cooperative perimeter defense is beyond the scope of this paper.

## CONCLUSIONS

In our view, territoriality is a subset of resource-defense strategies, and resource defense is in turn an aspect of subsistence strategies. Clearly under some circumstances humans are territorial, in that they occupy certain areas more or less exclusively by means of repulsion through overt defense or through social interactions. But it is equally clear that although (as with all behaviors) the capacity to demark and defend territory must have some genetic basis, human territoriality is not a genetically fixed trait, in the sense of being a "fixed-action pattern," but rather a possible strategy individuals may be expected to choose when it is to their adaptive advantage to do so. Analyses arguing that territoriality is an evolutionary imperative, or conversely a political aberration of basic human nature, do not seem to us to have explanatory validity. We have argued that territoriality in humans is at least in part an adaptive response to environmental factors and, as such, is to be expected when critical resources are distributed so that exclusive use and defense of a resource area produces a net benefit in resource capture. Our model incorporates concepts derived from the study of

spatial organization among other animal species. The notion that spatial organization is adaptively related to resource characteristics was developed independently in anthropology, although its formulation has not been as precise as that developed in sociobiology.<sup>6</sup>

Our analysis suggests that human territoriality can, as with other animal species, be fruitfully analyzed in terms of a general model of spatial organization that focuses on resource distributions and economic defendability. However, since humans use such a wide variety of resources, even a single population can exhibit a great range of responses with respect to different resources, and describing the behavior of a particular group as "territorial" or "nonterritorial" can therefore be overly simplistic. It is not enough to know if a particular group exhibits territorial behavior. Instead, it is necessary to discuss particular resources and determine if these resources are defended, how they are defended, the circumstances under which access to these resources is restricted, and which people or groups of people are allowed or denied access to resources.

Levins (1966) has noted that scientific models cannot simultaneously maximize generality, realism, and precision. If the model of ecological determinants of spatial organization presented in this paper has maximized anything, it has been generality and (to a lesser extent) realism. Of necessity, we have simplified our discussion by considering only a limited set of potential determinants. Other factors influencing spatial organization, such as group size, specific foraging strategies, competition, political organization, and nonfood resources, have not been considered in our model, which focuses exclusively on resource distribution. Our failure to achieve precision can be ascribed to two main factors: the necessity for simplification and the lack of quantitative and operational measures for critical variables.

The lack of quantitative data relevant to the parameters of our model is a serious problem, but its solution should not be conceptually difficult. Certainly, data on resource abundance, distribution in time and space, and utilization patterns can be collected in sufficient detail in the future, although they will be difficult to reconstruct from past studies. However, a more serious problem is presented by the absence of operational measures for key concepts such as predictability (but see Harpending and Davis 1977). In addition there are complexities in analyzing the energy costs of resource defense. The case of the Karimojong indicates that energy costs for resource defense can be extremely low when common values and beliefs make ritual sanctions rather than overt defense effective in preventing trespass. The low energy costs only hold true if outsiders not enculturated into the beliefs are excluded. Exclusion of outsiders can be accomplished, for example, by cooperative perimeter defense, which also has a relatively low individual energy cost. Thus the energy costs of resource defense strategies within groups and between groups can be quite different and need separate analysis.

If the model relating economic defendability to territoriality is to be more than a plausibility argument, hypotheses must be derived from this model and tested with good quantitative data. We hope that other researchers in human ecology will gather such data and begin tests of this and related models of optimal resource use. Adequate tests of the economic defendability model would utilize cases where quantitative measures of resource density and predictability vary, either within a group (through time, as with the Ojibwa, or for different resources classes, as with the Karimojong) or across groups who share similar technology and social organization (as with the Basin-Plateau Indian groups). This is the approach we have tried to take above, but because of inadequate data we have been forced to adopt a qualitative mode of argument. In addition, the model might also be tested by examining evidence for the null hypothesis. In particular, if it could be shown that clear-cut changes from nonterritorial systems of spatial organization to well defined territorial systems occur with any frequency without correlated increases in measures of resource density and/or predictability (holding technology and social organization constant and introducing no new key resources), the model as presented would have to be rejected. Until such tests are performed,

however, we argue that the economic defendability model accounts for the available evidence in greater depth and extent than the alternative explanations of variation in human spatial organization.

#### NOTES

*Acknowledgments.* We would like to thank the following people for reading and commenting on the manuscript: Ruth Buskirk, Steve Emlen, Lew Oring, and graduate students in the "Behavior Lunch Group," Section of Neurobiology and Behavior; Davydd Greenwood, Charles Hockett, Ilene Stern Wallace, and Bruce Winterhalter, of the Department of Anthropology, and Steve McRae, Department of Natural Resources, all of Cornell University; Brooke Thomas, Alan Swedlund, and graduate students in the Social Biology Seminar, Department of Anthropology, University of Massachusetts at Amherst; and William Durham, Departments of Anthropology and Human Biology, Stanford University. Marge Ciaschi efficiently and cheerfully typed the manuscript. R. Dyson-Hudson received aid from National Science Foundation grant GS 52307 during the period when this article was written. N. Dyson-Hudson, Department of Anthropology at the State University of New York, Binghamton, provided advice and comments on the section dealing with Karimojong territoriality.

A version of this paper was read at a Symposium on Sociobiology at the American Anthropological Association's annual meeting in 1976. A longer version will appear in *Sociobiology and Human Social Organization*, N. Chagnon and W. Irons, eds. (in press, Cambridge, MA: Duxbury).

<sup>1</sup>For something to be economic, a number of conditions must be present: ranked alternative values, insufficient alternative means, choice, and so on (D. G. Greenwood, personal communication). While some social scientists may feel that the use of this term in the context of animal behavior is inappropriate, we feel that the conditions listed above are, in fact, met. In any case "economic defendability" is a term that is widely used in the behavioral ecology literature and has a sufficiently clear meaning to justify its use in this context.

<sup>2</sup>We are basing this description on Steward (1938, 1955). His model of Great Basin spatial organization has been both criticized (e.g., Service 1971, 1975; Williams 1974) and defended (e.g., Thomas 1972, 1973, 1974).

<sup>3</sup>As a general meteorological rule, patchiness of rainfall is known to increase as the total average annual precipitation decreases.

<sup>4</sup>In contrast, Service (1971:86) attributes territoriality to the Northern Shoshoni, stating that the mounted groups "monopolized the more fertile areas as pastures for their horses. They were grandly dominant over the other Indians, whom they scattered widely in small units and denied access to fishing sites and good hunting and gathering areas." However, the evidence for this view is not presented.

<sup>5</sup>Despite enormous efforts by the Administration to prevent killing and cattle raiding, this was still a common pattern of behavior in the late 1950s.

<sup>6</sup>A number of anthropologists have recently presented ecological analyses of human spatial organization, focusing especially on hunter-gatherer groups (e.g., Knight 1965, Damas 1969, Heinz 1972, Lee 1972, Williams 1974). As noted earlier, we feel that many discussions have assumed too much uniformity in resource distribution and, therefore, in optimum patterns of spatial organization. For example, Wilmsen, who takes a somewhat similar position to the one we espouse, generalizes (1973:8) that "plant foods, primarily in the form of roots, seeds, and nuts, are relatively stable and evenly distributed over suitable habitats" and are most effectively exploited by dispersal, which hardly seems to fit the Great Basin evidence we have summarized above. Wilmsen (1973:6) also seems to identify spatial unpredictability of resources (such as large game) with territoriality, when actually the model he presents defines the conditions under which clumping and cooperative foraging are optimal. Dumond (1972:296) has made perhaps the closest statement to our own view, although he does not develop a general model. In our view, anthropological analyses of hunter-gatherer spatial organization have made little progress since the fundamental insights of Steward (1938). This paper is an attempt to move beyond the generalities that currently dominate the literature toward the development of a general model that explains (rather than explains away) the *diversity* of human spatial organization.

## REFERENCES CITED

- Ardrey, Robert  
1966 *The Territorial Imperative*. New York: Atheneum.
- Bates, B. C.  
1970 *Territorial Behavior in Primates: A Review of Recent Field Studies*. *Primates* 11:271-284.
- Bishop, Charles A.  
1970 *The Emergence of Hunting Territories among the Northern Ojibwa*. *Ethnology* 9:1-15.  
1974 *The Northern Ojibwa and the Fur Trade: An Historical and Ecological Study*. Toronto: Holt, Rinehart and Winston of Canada.
- Brown, Jerram L.  
1964 *The Evolution of Diversity in Avian Territorial Systems*. *Wilson Bulletin* 76:160-169.
- Brown, Jerram L., and G. H. Orians  
1970 *Spacing Patterns in Mobile Animals*. *Annual Review of Ecology and Systematics* 1:239-262.
- Burt, W. H.  
1943 *Territoriality and Home Range Concepts as Applied to Mammals*. *Journal of Mammalogy* 24:346-352.
- Carpenter, C. R.  
1958 *Territoriality: A Review of Concepts and Problems*. In *Behavior and Evolution*, A. Roe and G. G. Simpson, eds. Pp. 224-250. New Haven: Yale University Press.
- Cohen, Erik  
1976 *Environmental Orientations: A Multidimensional Approach to Social Ecology*. *Current Anthropology* 17:49-70.
- Cooper, J. M.  
1939 *Is the Algonquian Family Hunting Ground System Pre-Columbian?* *American Anthropologist* 41:66-90.
- Crook, J. H.  
1970 *Social Behavior and Ethology*. In *Social Behavior in Birds and Mammals*, J. H. Crook, ed. Pp. xxi-xl. New York: Academic Press.  
1972 *Sexual Selection, Dimorphism, and Social Organization in the Primates*. In *Sexual Selection and the Descent of Man, 1871-1971*. B. G. Campbell, ed. Pp. 231-281. Chicago: Aldine.  
1973 *The Nature and Function of Territorial Aggression*. In *Man and Aggression*, Ashley Montagu, ed. Pp. 183-220. London: Oxford University Press.
- Damas, David, ed.  
1969 *Conference on Band Societies*. National Museum of Canada, Bulletin 228.
- Denham, W. W.  
1971 *Energy Relations and Some Basic Properties of Primate Social Organization*. *American Anthropologist* 73:77-95.
- Dumond, Don E.  
1972 *Population Growth and Political Centralization*. In *Population Growth: Anthropological Implications*. Brian Spooner, ed. Pp. 286-310. Cambridge, MA: MIT Press.
- Durham, William H.  
1976 *Resource Competition and Human Aggression: A Review of Primitive War*. *Quarterly Review of Biology* 51:385-415.
- Dyson-Hudson, Neville  
1966 *Karimojong Politics*. London: Oxford University Press.
- Dyson-Hudson, Rada  
1972 *Pastoralism: Self-Image and Behavioral Reality*. *Journal of Asian and African Studies* 7 (1-2):30-47. Also in *Perspectives on Nomadism*. William Irons and Neville Dyson-Hudson, eds. Leiden: Brill.
- Dyson-Hudson, Rada, and Neville Dyson-Hudson  
1969 *Subsistence Herding in Uganda*. *Scientific American* 220 (2):76-89.  
1970 *The Food Production System of a Semi-Nomadic Society: The Karimojong, Uganda*. In *African Food Production Systems: Cases and Theory*. P. F. M. McLoughlin, ed. Pp. 91-124. Baltimore: Johns Hopkins Press.
- Eisenberg, J. F., N. A. Muckenhirn, and R. Rudran  
1972 *The Relation between Ecology and Social Structure in Primates*. *Science* 176:863-874.

- Emlen, Stephen T., and Natalie Demong  
1975 Adaptive Significance of Synchronized Breeding in a Colonial Bird: A New Hypothesis. *Science* 188:1029-1031.
- Esser, A. H., ed.  
1971 *Behavior and Environment: The Use of Space by Animals and Men*. New York: Plenum.
- Gill, F. B., and L. L. Wolf  
1975 Economics of Feeding Territoriality in the Golden-Winged Sunbird. *Ecology* 56: 333-345.
- Hallowell, A. Irving  
1949 The Size of Algonkian Hunting Territories: A Function of Ecological Adjustment. *American Anthropologist* 51:35-45.
- Hamilton, William J., III, Ruth F. Buskirk, and William H. Buskirk  
1976 Defense of Space and Resources by Chacma (*Papio ursinus*) Baboon Troops in an African Desert and Swamp. *Ecology* 57:1264-1272.
- Hamilton, William J., III, and K. E. F. Watt  
1970 Refuging. *Annual Review of Ecology and Systematics* 1:263-286.
- Harpending, Henry, and Herbert Davis  
1977 Some Implications for Hunter-Gatherer Ecology Derived from the Spatial Structure of Resources. *World Archaeology* 8:275-283.
- Heinz, H. J.  
1972 Territoriality among the Bushmen in General and the !Ko in Particular. *Anthropos* 67:405-416.
- Hinde, Robert A.  
1956 The Biological Significance of the Territories of Birds. *Ibis* 98:340-369.
- Horn, Henry S.  
1968 The Adaptive Significance of Colonial Nesting in the Brewer's Blackbird (*Euphagus cyanocephalus*). *Ecology* 49:682-694.
- King, Glenn E.  
1975 Socioterritorial Units among Carnivores and Early Hominids. *Journal of Anthropological Research* 31:69-87.  
1976 Society and Territory in Human Evolution. *Journal of Evolution* 5:323-332.
- Klopfer, P. H.  
1969 *Habitats and Territories: A Study of the Use of Space by Animals*. New York: Basic Books
- Knight, Rolf  
1965 A Re-examination of Hunting, Trapping, and Territoriality among the Northeastern Algonkian Indians. In *Man, Culture, and Animals*. Anthony Leeds and Andrew P. Vayda, eds. Pp. 27-42. American Association for the Advancement of Science Publication 78.
- Lack, David  
1968 *Ecological Adaptations for Breeding in Birds*. London: Methuen.
- Leacock, Eleanor  
1954 The Montagnais "Hunting Territory" and the Fur Trade. *American Anthropological Association, Memoir* 78.
- Lee, Richard B.  
1972 !Kung Spatial Organization: An Ecological and Historical Perspective. *Human Ecology* 1:125-147.
- Lee, Richard B., and Irven DeVore, eds.  
1968 *Man the Hunter*. Chicago: Aldine.
- Levins, Richard  
1966 The Strategy of Model Building in Population Biology. *American Scientist* 54: 421-431.
- Martin, M. K.  
1974 The Foraging Adaptation—Uniformity or Diversity? Module in Anthropology, No. 56. Reading, MA: Addison-Wesley.
- Peterson, Nicolas  
1975 Hunter-Gatherer Territoriality: The Perspective from Australia. *American Anthropologist* 77:53-68.
- Pianka, Eric R.  
1974 *Evolutionary Ecology*. New York: Harper and Row.

Radelcliff-Brown, A. R.

1930 The Social Organization of Australian Tribes. *Oceania* 1:34-63.

Reynolds, Vernon

1966 Open Groups in Hominid Evolution. *Man* 1:441-452.

Reynolds, Vernon, and Francis Reynolds

1965 Chimpanzees of the Budongo Forest. In *Primate Behavior*. Irven DeVore, ed. Pp. 368-424. New York: Holt, Rinehart and Winston.

Service, Elman R.

1962 *Primitive Social Organization*. First ed. New York: Random House.

1971 *Primitive Social Organization*. Second ed. New York: Random House.

1975 *Origins of the State and Civilization*. New York: Norton.

Smith, C. C.

1968 The Adaptive Nature of Social Organization in the Genus of Tree Squirrels *Tamiasciurus*. *Ecological Monographs* 40:349-371.

Smith, Eric Alden

1977 *Adaptation and Energetic Efficiency: A General Model*. Manuscript. Files of the author.

Speck, Frank G.

1915 The Family Hunting Band as the Basis of Algonkian Social Organization. *American Anthropologist* 17:289-305.

1923 Mistassini Hunting Territories in the Labrador Peninsula. *American Anthropologist* 25:452-471.

Speck, Frank G., and Loren C. Eiseley

1939 The Significance of the Hunting Territory System of the Algonkian in Social Theory. *American Anthropologist* 41:269-280.

Steward, Julian H.

1938 Basin-Plateau Aboriginal Sociopolitical Groups. Bureau of American Ethnology, Bull. 120.

1955 The Great Basin Shoshonean Indians: An Example of a Family Level of Sociocultural Integration. In *Theory of Culture Change*. J. H. Steward. Pp. 101-121. Urbana: University of Illinois Press.

Thomas, David H.

1972 Western Shoshone Ecology: Settlement Patterns and Beyond. In *Great Basin Cultural Ecology: A Symposium*. Don Folwer, ed. Pp. 135-154. Desert Research Institute, Reno, Publ. in Social Science, No. 8.

1973 An Empirical Test for Steward's Model of Great Basin Settlement Patterns. *American Antiquity* 38:155-176.

1974 An Archaeological Perspective on Shoshonean Bands. *American Anthropologist* 76:11-23.

Tinbergen, Niko

1957 The Functions of Bird Territory. *Bird Study* 4:14-27.

Ward, P., and A. Zahavi

1973 The Importance of Certain Assemblages of Birds as "Information-Centres" for Food-Finding. *Ibis* 115:517-534.

Williams, B. J.

1974 *A Model of Band Society*. Society for American Archaeology, Memoir 29.

Wilmsen, Edwin N.

1973 Interaction, Spacing Behavior, and the Organization of Hunting Bands. *Journal of Anthropological Research* 29:1-31.

Wilson, Edward O.

1971 Competitive and Aggressive Behavior. In *Man and Beast: Comparative Social Behavior*. J. F. Eisenberg and W. S. Dillon, eds. Pp. 181-217. Washington: Smithsonian Institution Press.

1975 *Sociobiology: The New Synthesis*. Cambridge, MA: Harvard University Press.

Wolf, L. L., and F. R. Hainsworth

1971 Time and Energy Budgets of Territorial Humming Birds. *Ecology* 52:980-988.

Zahavi, A.

1971 The Social Behavior of the White Wagtail Wintering in Israel. *Ibis* 113:203-211.

Submitted 18 June 1976

Accepted 6 May 1977

Revised version received 30 June 1977

Final revisions received 28 September 1977