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A RECONSIDERATION OF THE ROLE OF PREDATION ON LARGE MAMMALS IN TROPICAL HUNTER-GATHERER ADAPTATION

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Current models of hunter-gatherer adaptive strategy indicate variability with latitude (gathering predominant in the tropics, fishing in the mid-latitudes and hunting only in the high latitudes). This article questions the adequacy of the ethnographic data on which predictions about hunter-gatherer subsistence behaviour in some tropical environments are based. As an alternative, the pattern of covariability between plant community structure, large mammal biomass, and rainfall in equatorial regions is employed to predict high levels of hunting in certain low latitude environments. The present distribution of animal protein-dependent pastoralists in tropical Africa supports this model. It is suggested that large mammal hunting may have been of greater significance in the adaptive strategies of prehistoric savanna hunter-gatherers than in those of ethnographically-observed tropical hunter-gatherers.

A relationship between hunter-gatherer diet and latitude was first proposed by Lee (1968), who suggested that the dietary proportion of animal meat, fish and vegetables is directly related to their availability, and that this availability is in turn related to latitude. Lee predicted that tropical hunter-gatherers would subsist primarily on gathered plant foods, as these were the most abundant and easily obtainable resources, while hunting would only become an important element in high latitude regions where plants were not readily available. This proposal has been widely accepted, and extended to expectations about prehistoric hunter-gatherer adaptation (e.g. Clarke 1976). However, the analysis presented here suggests, first, that ethnographic data from the tropics are not drawn from a sufficiently wide set of environments to be used to generalise to tropical environments as a whole; and, second, that plant foods are not uniformly abundant in tropical environments. Ecological principles predict that some hunter-gatherer populations in tropical environments were probably far more dependent for their subsistence upon hunting large mammals than Lee's model suggests.

Lee's model was derived from two lines of evidence: (1) direct observation of the !Kung San of the Kalahari in Botswana; (2) cross-cultural comparisons of hunter-gatherer subsistence activities using data drawn from Murdock's Human Relations Area Files (Murdock 1967; Lee 1968).

The first showed that the !Kung, living in an extremely arid environment, depended primarily upon gathered plant foods for their subsistence, and that hunting of large mammals was of only minor importance to their survival. Lee

(1968) showed that plant foods were abundant, predictable, reliable and available throughout the year. They were also highly nutritious, and offered better returns than animal resources, which were unpredictable and patchily distributed through time and space. This picture has since been substantiated by Tanaka (1976) for the Central Kalahari San, and detailed by Silberbauer (1972; 1981) for the G/wi. The second line of evidence placed the San studies in a broader context. Amongst extant hunter-gatherer populations the proportional dependence upon hunted resources varied with latitude (fig. 1). A correlation derived from these data ($r = 0.45277$, $p < 0.001$) showed that the limited dependence of hunting among Kalahari San would be expected for a population living at this latitude.

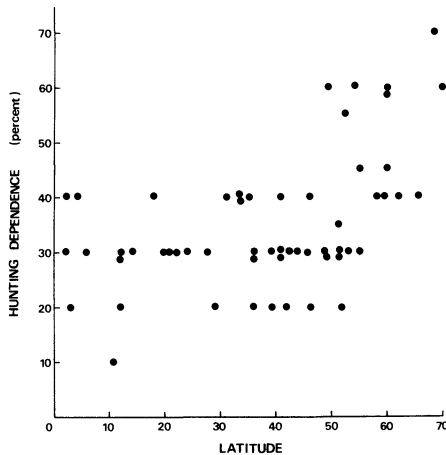


FIGURE 1. Relationship between percentage dependence on hunting and latitude in ethnographically documented societies.
(Data: Lee 1968)

It may be concluded that contemporary hunter-gatherers in tropical latitudes do not rely substantially on hunting large mammals. Lee's significant contribution led directly to the abandonment of earlier characterisations of Palaeolithic and Mesolithic populations as 'hunters', and recent work stresses the importance of plant foods, recognising a greater continuity with the hominid's primate ancestry (Isaac 1978; Tanner 1981; Harding & Teleki 1981). Hunting of large mammals is now seen as an occasional and opportunistic part of the hunter-gatherer subsistence strategy, not the key element in human adaptation.

However, the applicability of Lee's model depends on, among other things, whether the ethnographic samples are representative of the population from which they are drawn, in this case the 'totality of hunter-gatherer populations'. If they are not, then the hunting-latitude correlation on its own is not sufficient to substantiate the model. Figure 2 is a histogram showing the distribution of ethnographically-documented hunter-gatherer societies by latitude. As can be seen, it is markedly skewed towards the high latitudes. This may be compared with an 'expected distribution' of hunter-gatherers by latitude—that is,

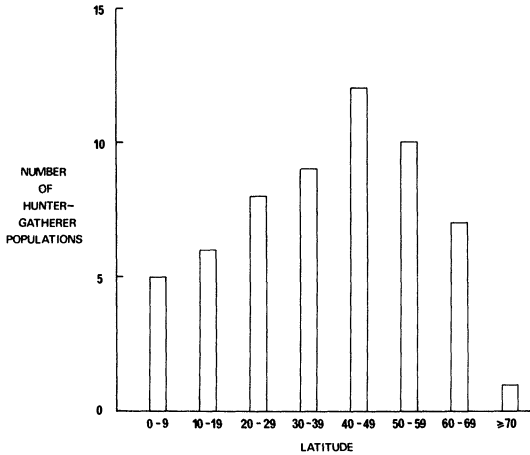


FIGURE 2. Distribution of ethnographically documented hunter-gatherer societies by latitude. (Data: Lee 1968)

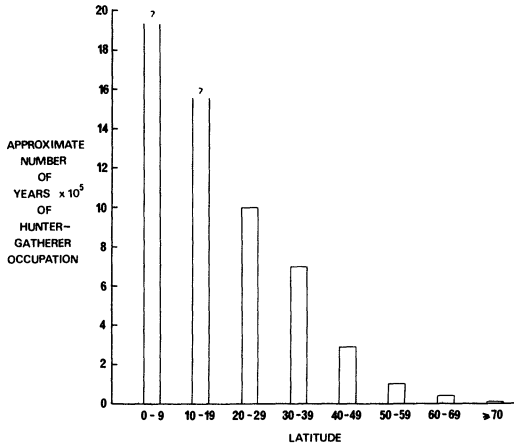


FIGURE 3. Approximate length of time hunter-gatherers have occupied various latitudes. (Data: Clark 1979; Fagan 1980)

considering the ethnographic populations as a sample of prehistoric and contemporary hunter-gatherers combined. Such an expected distribution is clearly difficult to calculate, but is grossly represented here by a histogram showing the length of time different latitudes have been occupied by hunter-gatherers during the Quaternary (fig. 3). A comparison of figures 2 and 3 reveals a poor fit between expected and observed distribution. It may therefore be argued that latitude cannot be used as a predictor of proportional dependence upon hunting, particularly in the low latitudes where the ethnographic record is exceptionally poor. This inadequacy suggests that it may be fruitful to examine ecological and environmental structure directly, as a means of modelling hunter-gatherer adaptive strategy. It will be attempted here for tropical African environments. These environments are of particular importance: not only are they exceptionally poor in terms of contemporary

populations, but they also include the environments in which the hunter-gatherer adaptive strategy evolved.

To proceed with this analysis we may begin by noting that in tropical regions environmental variation is based largely on rainfall (Lieth & Whittaker 1974; J. Phillipson 1975; Strugnell & Pigott 1978). The ethnographic samples from Africa are drawn from areas receiving either high or low rainfall (fig. 4). There is an absence of samples from areas of intermediate annual rainfall (500–1500 mm per annum). In view of this it may be useful to examine the way in which plant and animal resource availability varies with rainfall.

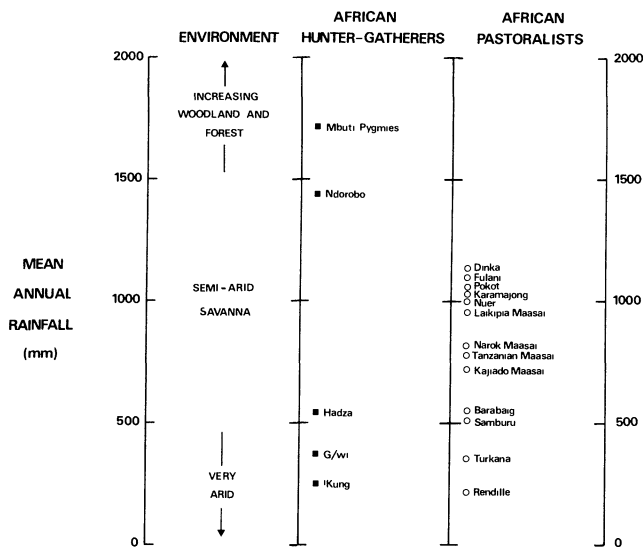


FIGURE 4. Distribution of environments, ethnographically-documented hunter-gatherers, and pastoralists in tropical Africa in relation to mean annual rainfall. (Data: Lee 1968; Coe *et al.* 1976; Stenning 1965; Evans-Pritchard 1940; Dyson-Hudson 1981; Dyson-Hudson, R. & N. 1969; Woodburn 1968)

Extensive work has been carried out on the ecology of large mammals in Africa, and certain patterns are now emerging. Figure 5 shows the relationship between mean annual precipitation and large mammal biomass in tropical Africa. A strong positive correlation exists between these variables (Coe *et al.* 1976). Large herbivore biomass increases markedly with rainfall up to approximately 1000 mm per annum, above which it increases less rapidly and eventually begins to decline. The reason is that the grassland environments most suitable for the specialised herbivores capable of achieving high biomass occur predominantly in the rainfall range 500–1500 mm per annum.

When the distribution of extant hunter-gatherers in relation to rainfall is considered (fig. 5) it may be observed that no such populations occur where large mammals are most abundant. This observation may be extended. No data on large mammal biomass are available for the Dobe region where the !Kung live, but using the regression equation derived by Coe *et al.* (1976) for predicting large mammal biomass on the basis of mean annual evapotranspiration rates, fig. 5 also shows the expected large mammal biomass for the

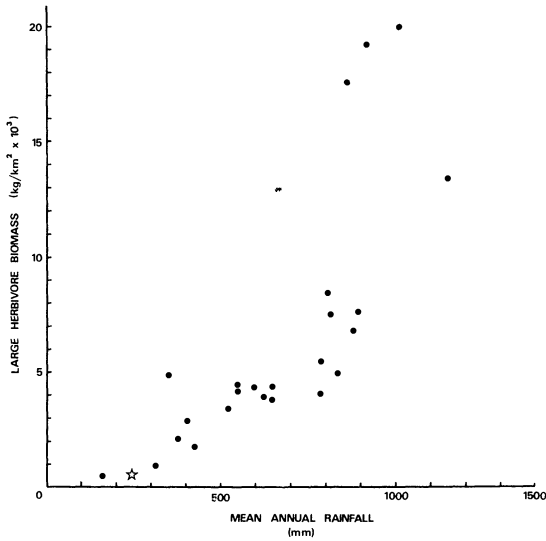


FIGURE 5. Relationship between mean annual rainfall and large herbivore biomass in tropical Africa. Estimated large herbivore biomass for the Central Kalahari is indicated by the star, calculated according to the regression derived by Coe *et al.* (1976). (Data: Coe *et al.* 1976)

Kalahari. This lies very close to the minimum for tropical Africa, and may be one reason why hunting is of little importance to the !Kung San.

Lee's model, however, was based not simply on limited availability of animal resources, but on high returns and low risks involved in plant food exploitation compared to hunting. While the low figures provided on effort for vegetable gathering may be open to question (see Hawkes & O'Connell 1981), it may be reasonably argued that primary subsistence dependence on plant foods will remain, regardless of increases in animal availability, as long as vegetable foods are in abundance.

Plant food availability can be examined in relation to rainfall, much as has been done for large mammal biomass. However, there are various reasons why the availability of plants edible by man and suitable as a staple resource do not behave in the same way as large mammal biomass. Such plants are in fact more readily available in arid regions than in the semi-arid savanna, which relates to the way in which plants adapt to environmental constraints (Grime 1977). In dry environments, particularly those with extended dry seasons and unpredictable precipitation, plants may store nutrients and water in organs with impervious skins, often underground. These adaptive features protect the plants against environmental hazards such as high temperatures and low and unpredictable rainfall. At the same time, by building reservoirs of water, protein and carbohydrates they also form ideal and easily obtainable food sources for hunter-gatherer populations. Thus it is the specific survival strategies of plants in arid environments that provides the resource base of hunter-gatherers in these environments, and enhances, or even makes possible, the existence of hunter-gatherers. Tanaka (1976) states that there are at least 67 edible species of plant in the Central Kalahari, many of which exist in sufficient abundance to form a major resource.

However, as rainfall increases in both quantity and predictability, and the dry season becomes less extensive, plants pursuing these 'storage-based' survival strategies become less viable, and are unable to compete with those species capable of responding more rapidly to an increased availability of water and nutrients—the grasses. Semi-arid, tropical environments are dominated by grass, the basis of the typical savanna community. While grass may form the ideal food base for specialised herbivores—hence the increase in large mammal biomass—they do not provide a suitable resource for hominids, who require concentrated, high quality plant foods. It follows that these environments are in fact poorer in plant foods suitable for human populations than more arid ones. For example, in Amboseli National Park in East Africa there are only estimated to be seven plant species that might form a reasonable source of food, and none of these would be comparable in either abundance or nutritional value to the Tsama melon or Mangetti nut of the Central Kalahari. Thus while the 0–500 mm per annum rainfall regimes are rich in plant foods, the 500–1500 mm regimes are comparatively impoverished. However, at the other extreme, when rainfall exceeds 1500 mm per annum, tree and herbaceous vegetation become more common, and suitable (but different) plant foods become available again for the hunter-gatherer. Thus woodland and forest hunter-gatherer populations, such as the Mbuti Pygmies, will subsist primarily on plant foods, as in the higher rainfall regimes these are again more abundant.

In summary, therefore, it may be argued that areas receiving less than 500 mm of rainfall each year are characterised by a flora in which highly nutritious storage adaptations are common, and by a low large mammal biomass; areas with between 500 and 1500 mm of rainfall per annum, on the other hand, are characterised by grass-dominated plant communities, unsuitable for direct human consumption, and a high large mammal biomass. Above 1500 mm per annum a wooded and forested environment reduces the resource base of the large herbivores, thus simultaneously increasing edible plant biomass and decreasing large mammal biomass. It may be predicted on this basis that below 500 mm and above 1500 mm rainfall per annum gathering-based economies will be the more viable, but in between these limits hunting is likely to be of greater importance. The ethnographic samples shown in fig. 4 fall close to, or outside, these limits, thus occurring only in those environments that combine high plant food availability and reduced animal food availability. Figure 6 summarises this pattern of environmental and resource variability with rainfall in tropical Africa, and, on the assumption of a congruence between resource availability and human subsistence strategy, expected hunter-gatherer adaptation.

Further evidence to support this hypothesis for the greater importance of hunting in tropical semi-arid regions is provided by the current distribution of pastoralism in relation to mean annual rainfall in sub-Saharan Africa. Pastoralism is a subsistence strategy almost entirely dependent upon large mammals—exploited for milk, blood and meat (Dahl & Hjort 1976). Pastoralists thus differ significantly from ethnographically observed hunter-gatherers, such as the !Kung, in having large mammals, not plant foods, as their primary resource. Figure 4 shows that pastoralism occurs principally within the 500–1500 mm

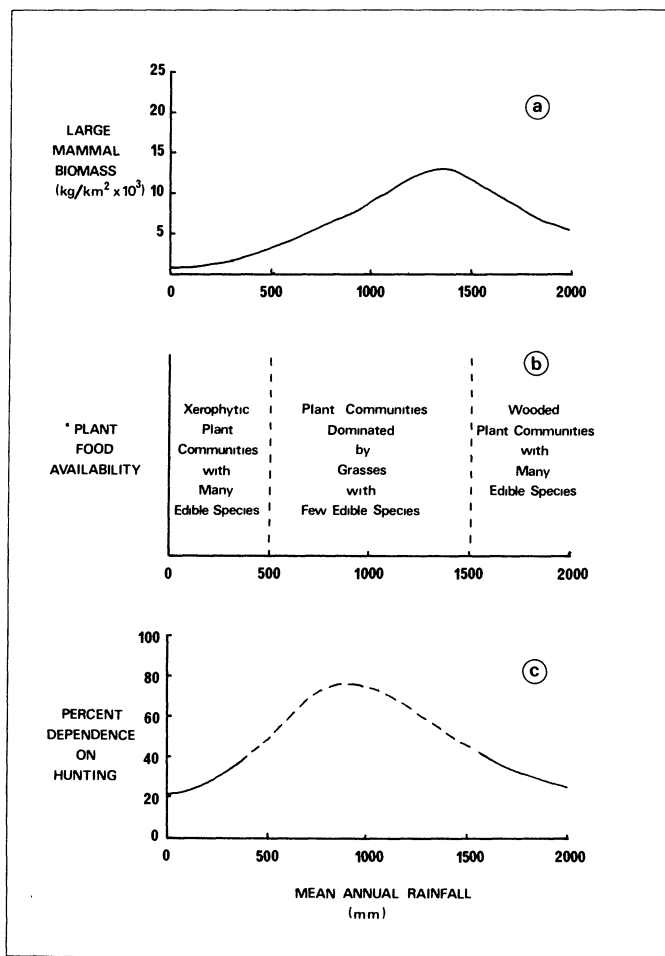


FIGURE 6. Summary of variation in (a) large mammal biomass, (b) plant food availability and (c) percentage hunting in relation to mean annual rainfall in tropical Africa.

per annum rainfall regime—that is, for which a predominantly hunting strategy was predicted. To be more precise, pastoralists currently occupy the lower half of this regime. However, since European contact, demographic increase and agricultural intensification, cereal-based agriculture has expanded into drier environments, and, due to the same factors, pastoralism has itself spread into areas of lower rainfall. Pastoralism enables human populations to sustain higher population densities in semi-arid and arid environments than hunting and gathering.

It may be proposed that pastoralism, dependent upon domestic large mammals, is a product of the same ecological factors that would have led to principal dependence upon wild large mammals among aboriginal hunter-gatherers—namely, a lack of plant foods. The origins of pastoralism and its relationship to earlier hunter-gatherer populations, have long been a problem of considerable archaeological and anthropological interest. The ecological

principles discussed here, and their implications for hunter-gatherer strategy, may also be extrapolated to this problem. Rather than stressing cultural discontinuities between hunter-gatherers and pastoralists (Murdock 1959; D. W. Phillipson 1977), the observations presented above indicate a considerable degree of ecological continuity, based on primary subsistence dependence on large mammal produce. The change from hunting and gathering to pastoralism was not a change from plant dependence to animal dependence, but a change from a predation strategy dependent upon wild, indigenous large mammals to a parasitic strategy dependent upon domestic, exogenous large mammals. Pastoralists, through harnessing the advantages of exogenous species—un-specialised feeders, low diversity—and of domestic animals—greater control, higher reproductive rates, milk and blood—were able to extend the limits of human population size in semi-arid environments, through greater control, predictability and efficiency.

This article has attempted to reconsider the role of predation on large mammals in the subsistence strategies of tropical hunter-gatherers. It has been shown that plant and animal foods suitable for human exploitation are both dependent on rainfall and also inversely related to each other. The conclusion is that tropical hunter-gatherers are not uniformly 'plant dependent', as would be predicted by Lee's analysis (1968). His account was based on ethnographic observations, but it has been shown that these ethnographic samples are drawn from only a part of the tropical environmental spectrum. Analysis of tropical ecological variability suggests that hunter-gatherers living in low and high rainfall regimes (<500 and >1500 mm per annum) will be predominantly gatherers, whilst those living in medium rainfall areas (between 500 and 1500 mm per annum) will be more dependent upon hunting (fig. 6).

This analysis should be qualified in three ways. Firstly, the proposed relationship is essentially between resource availability and adaptive strategy, although in the discussion presented here this relationship has been mediated through mean annual rainfall. The point should be borne in mind in respect of prehistoric situations, as the precise relationship between animals, plants and rainfall will have been subject to evolutionary and ecological changes during the Later Cenozoic. Thus the actual rainfall regimes in which high and low animal and plant biomass was predicted will not necessarily be constant but will depend upon the environmental tolerances of species through time, and the type of evolutionary community involved.

Secondly, the proposed pattern of hunter-gatherer adaptive variability has been based on covariation with mean annual rainfall. This involves an oversimplification. Strictly speaking it is not the average amount of rainfall that determines plant and animal adaptive features, but its seasonality and predictability. It is these variables that would really control tropical hunter-gatherer subsistence strategy. Nonetheless, it may be argued that mean annual rainfall and seasonality are themselves correlated (Harris 1980: 13–14) (fig. 7), and thus mean annual rainfall may be used as a surrogate variable, one for which data are more easily available.

And thirdly, this article is primarily concerned with making predictions that may be useful in examining prehistoric situations. In this context, it must be

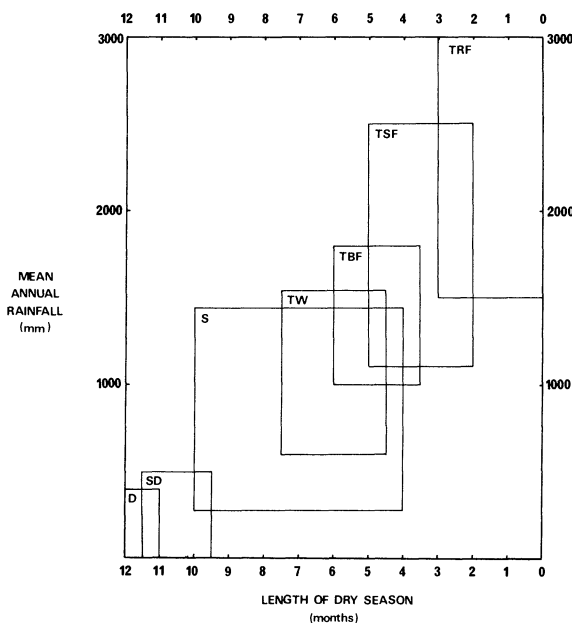


FIGURE 7. Schematic representation of the relationship between mean annual rainfall, length of season and habitat in tropical regions.

(Based on data from Eyre 1978; Harris 1980)

D = desert; SD = semi-desert; S = savanna; TW = thorn woodland; TBF = tropical broadleaf forest; TSF = tropical seasonal forest; TRF = tropical rain forest.

stressed that the proposed model does not necessarily demand that savanna hunter-gatherers did hunt on a large scale throughout prehistory. This will depend on the occurrence of the appropriate adaptive traits. What it does do is predict that the structure of resource availability would have resulted in considerable selective pressure favouring those populations able to hunt large mammals efficiently and consistently.

Lee (1968) argued that hunter-gatherer behaviour and ecology will be dependent upon resource availability. To some extent resource availability and structure may be said to covary latitudinally. Yet even within latitudes it is not possible to see either ecosystem structure or hunter-gatherer adaptation as uniform, and certainly within the tropics it is necessary to examine closely the factors governing ecological variability before attempting either to build general predictive models or to make specific reconstructions of prehistoric adaptations.

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