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More on Predatory Behaviour in Nonhuman Primates

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To students of hominid evolution, the predatory behaviour of chimpanzees is highly significant. Basic to the model of emerging hominid behaviour is the widespread assumption that meat-eating and predatory behaviour were intrinsic potentialities and may have formed the basis of economic subsistence and sociality.

Years ago, Kortlandt and Kooij (1963) suggested that predatory behaviour among chimpanzees represented the expression of an "emergency potentiality," but relegated the exercise of that potentiality to supplementation of protein when other sources were diminished. Hladik and Viroben's (1974) recent chemical analysis of samples of chimpanzee diet in Gabon, which they feel is equivalent to that in Gombe (Tanzania), indicates that vertebrate protein is as minor a fraction of the diet as is fruit protein. Vegetable and invertebrate protein comprise the bulk of protein ingested. The significance of predation on vertebrates may lie elsewhere.

Since Teleki's (1973) documentation of predatory behaviour amongst the chimpanzees at Gombe, perspectives on predatory behaviour have shifted. The situational contexts, rather than the prey species, have become the focus: e.g., Wrangham (1974) suggests that the artificial feeding itself created high tension which broke out in killing episodes. Teleki and, more recently, Reynolds (1975) point out, however, that provisioning alone cannot account for the predatory behaviour.

Teleki notes that the majority of predatory episodes occurred around or after banana feedings. It is significant that Goodall's (1963) first reports of vertebrate meat-eating noted only three episodes in two years. The behaviour existed, but the frequency was low. Provisioning with bananas began in 1961-62. In 1968-69, 30 episodes of predatory behaviour were observed (Teleki 1973); all of these took place within 150 yards of the banana-feeding area. Baboons constituted 83% of prey taken in 1968-69, when both species were regularly together at the feeding area. When supplementary feeding was drastically reduced in 1969-70, baboon consumption dropped to 22% of prey. Although there is a substantial increase in predatory episodes in December 1968, after reduction in banana feeding had reached a plateau over the prior five months, that increase is considerably smaller than the maximum frequency apparent before the reduction in provisioning. Since the majority of predatory episodes occurred in the context of banana feeding, an examination of this food rather than of artificial feeding warrants analysis.

Bananas are primarily carbohydrate, 96.6-99.5% utilizable. About 20% of the ripe fruit consists of sugar, and slightly more than 1% is starch; it is a fair source of calcium and iron and contains copper, iodine, manganese, zinc, and cobalt; it is rich in magnesium, sodium, and phosphorus. By far the most abundant of its mineral constituents is potassium, constituting 1.21-1.68% of dry weight (Von Loesecke 1949:20). In a series of experiments with rats, Lat (1967) confirmed that certain food components inhibited or excited the sensitivity of the organism to external stimuli. Ingestion of potassium chloride clearly counteracted the inhibitory effect of a protein diet. In addition, the spontaneous intake of casein correlated positively with the intake of potassium chloride, as if the animals were seeking a substance which would restore equilibrium. Lat concluded that rats are "aware" of the importance of potassium in protein utilization. Given choices of food

substances, rats spontaneously sought potassium-rich food in the context of high protein intake.

Alternatively, or in addition, bananas are high in amylacetate (which, indeed, is responsible for their aroma). Amylacetate, which is highly soluble in lipids, may in high concentration alter the properties of the cell membranes. Mitochondria are largely comprised of lipids, and the ultimate effect of high intake of a food rich in amylacetate would be energy depletion. Lipoproteins are found in vertebrate meat; and while the bonding of lipo fraction to protein is not fully understood, that molecule represents a resource of lipid to the system (I. Campbell, personal communication).

Neither wild nor domesticated bananas are listed as a food source for Gombe chimpanzees by Van Lawick-Goodall (1968). Bananas were, however, rapidly accepted and consumed in large quantities when they were offered (Teleki 1973). The coincidence, both spatially and temporally, of provisioning and predation documented by Teleki suggests that the search for protein by chimpanzees may, as with Lat's experimental rats, be a means of regaining homeostasis. The fact that predation occurred both before and after banana feeding may not be relevant, as the chemical reaction between the substances is not sequentially bound. Predatory behaviour in chimpanzees certainly pre-dates banana feeding. The fact that predation rises again after a plateau in provisioning has been reached may be attributed to habit, or to renewed sensitivity to lower thresholds of intake, although what the diet of the animals was during that period might also be instructive. The facts that bananas, ingested in large quantities, upset equilibrium because of the effect of potassium chloride and that casein has been proven to be instrumental in restoring a balance are of major consequence. We are suggesting that predation at Gombe may be in large part attributed, not to the context of artificial feeding, but to the chemical imbalance imposed by this mineral overload in the food provided. We are not suggesting that this explanation will necessarily apply to all predatory incidents or to predation in other primate species, but only that a physiological search for the effects of particular nutrients as part of the stress syndrome may place predatory episodes amongst habitually nonpredatory animals in a different perspective (Burton 1975).

Hladik and Viroben (1974) have shown that the protein needs of the chimpanzee can be met by invertebrate protein sources. Such consumption is costly from the point of view of bioenergetics, and vertebrate meat-eating can best be understood in terms of economizing on energy (Gaulin and Kurland 1976). As Strum (1976) points out, the phenomenon itself is complex, and its explanations must be multiple. The association between particular materials and high frequency of vertebrate predation may be viewed as one more factor in the syndrome and provides an analytical approach that broadens and strengthens the attack. There is "insult" to the organism from differential levels of chemical intake—from recurrence of stimuli at levels above or below the optimal (Berlyne 1969), which have physiological (biochemical) concomitants. Preferential food intake is the means by which the organism can attempt to regain homeostasis. Predatory behaviour amongst omnivorous nonhuman primates may well be such a response. "Protein" has an inhibitory effect upon the nervous system; other nutrients in meat, such as lipoproteins, are essential in establishing, maintaining, or restoring energy transport. Any given set of predatory behaviours requires detailed analysis of the precise nutrients involved, as well as of the contexts. Biochemical imbalances resulting from "stress" created by, e.g., sympatry or density may be more fundamental than group structure or dynamics to explanations of hominid meat-eating. Once acquired, the habit would be sustained by a host of traditions or culture patterns.

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On Ceramic Technology in East Asia

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In his comments on Chang's interpretation of Chinese radiocarbon dates, Bayard (CA 16:167) remarks, with reference to the "corded-ware 'culture,'" that "in view of the very wide distribution of cord-marked ware throughout East and Southeast Asia from ca. 7000 B.C. onwards, we obviously cannot ascribe it to a single culture." He further states that "it would appear instead to be a technological innovation which spread through an incredibly wide range of cultural contexts." Data from Japan, where chronometric dates indicate even earlier use of ceramic vessels, tend to support the thesis that the original center of this technological innovation is yet to be discovered and that ceramic technology was accepted by various human groups which are otherwise characterized by a variety of techno-cultural traditions. Since the chronometric dates for early ceramic assemblages of Japan appear to be little known outside that country, I shall present an updated version of my earlier summary (Ikawa 1964). I shall then offer some speculations on the adaptive advantages that ceramic technology may have afforded.

The earliest ceramics from Japan are not cord-marked. Instead, they are decorated with appliqué of strips or dots of clay, presenting a corrugated appearance.¹ Sites where such ceramics occur are shown in table 1; their locations are indicated in figure 1. Radiocarbon dates are available for Fukui Cave in Kyushu and Kamikuroiwa Rockshelter in Shikoku. They point to an age around 12,500 B.P. for this kind of pottery. Suzuki (1975), however, reports that the fission-track age for the Fukui pottery is about 9,800 B.P.

Brief summaries of artifacts associated with this ware have been presented in English for some of these assemblages

¹ The Japanese term for pottery decorated with strips of clay is *ryusen-mon* or *ryukisen-mon*, which Ikawa (1964) and Chard (1974) translate as "linear-relief pottery." Aso (1973) reports that pottery decorated with raised dots (*mametsubu-mon*, or "bean-patterned" pottery) appears to be earlier than the linear-relief pottery at Senpukuji Cave in Kyushu.

TABLE 1

LINEAR-RELIEF POTTERY SITES IN JAPAN

SITE	REFERENCE	RADIOCARBON DETERMINATION
Fukui Cave, Kyushu (Stratum 3)	Kamaki and Serizawa 1976	12,700 ± 700 B.P. (GaK-950)
Senpukuji Cave, Kyushu	Aso 1973	
Iwatsuchihara, Kyushu (Stratum 5)	Serizawa 1974	
Kamikuroiwa Rockshelter, Shikoku (Stratum 9)	Esaka and Nishida 1967	12,165 ± 600 B.P. (I-944)
Yanagimata, Honshu	Higuchi, Morishima, and Kobayashi 1965	
Nitoro Cave, Honshu	Kobayashi 1963	
Tazawa, Honshu	Serizawa 1974	
Hashidate Rockshelter, Honshu	Serizawa et al. 1976	
Hinata Cave, Honshu	Kashikura and Kato 1967	
Ichinosawa Cave, Honshu	Kashikura and Kato 1967	
Hibakoiwa Cave, Honshu	Kashikura and Kato 1967	

(Ikawa 1964). Two major lithic traditions are represented: one in which microblades detached from wedge-shaped cores make up the majority of lithic specimens, as at Fukui, Senpukuji, and Iwatsuchihara, and another in which bifacially flaked points and knives and, in some cases, edge-ground axes constitute the prominent portion of the inventory of exploitative tools, as at most other sites. Ceramic vessels as utensils in maintenance activities were accepted by groups that manufactured entirely different sets of exploitative tools according to completely different manufacturing principles. I say "accepted," because no prototype of this ware has been found within Japan, and, as I remarked earlier (Ikawa 1964:104), the corrugated, linear appliqué ware of Fukui Stratum 3 seems technically too well-made to be the result of the first attempts at pottery making.

Stratigraphic evidence indicates that the next procedural mode for ceramic decoration in Japan was impression with semicircular objects (such as fingernail tips), followed by cord impression and then by rolling of an engraved or cord-wrapped stick. The ware decorated with marks made by an engraved stick is known as *oshigata-mon*; ware marked by a cord-wrapped stick is called *yorito-mon*. Radiocarbon determinations are as follows: for the *oshigata-mon* horizon at Kishama in western Honshu, 8,400 ± 350 B.P. (M-237, shell), and for the *yorito-mon* horizon at Natsushima near Tokyo, 9,240 ± 500 B.P. (M-770-771, charcoal) and 9,450 ± 400 B.P. (M-769, shell). The *yorito-mon* horizon at Nishinojo in Chiba, however, was dated to 8,150 ± 180 B.P. (N-168, shell) and 8,240 ± 190 B.P. (N-170, charcoal).

Many Japanese scholars feel that the Jomon cultural tradition, which was to last until a few centuries B.C., actually begins with the *oshigata-mon* ware of western Japan and the *yorito-mon* ware of eastern Japan. Earlier ceramic assemblages are variously called "Mesolithic" (Serizawa 1967), "Epi-Palaeolithic" (Serizawa 1974), or "Proto-ceramic" (Sugihara 1969). The difference is more marked in lithic inventory. To some authors (Serizawa 1970, Sugihara 1974), the appearance of arrowheads marked the beginning of the Jomon cultural tradition. In any case, the fine chipped-stone artifacts, such as microblades and carefully executed bifacial foliates, disappear