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FOOD AVAILABILITY AND SOCIAL STRESS IN CAPTIVE BABOONS: REFERENTIAL DATA FOR EARLY HOMINID FOOD TRANSPORT AT SITES

ABSTRACT: Social stress due to food availability has been studied in captive baboons, as a common behavioral pattern exhibited by several primate species. The aim of the study is to draw information about food transport and availability, and the effects of these factors on social behavior and residue accumulations. This information can be applied to early African archaeological sites if hominids still behaved as the rest of primates. The conclusion is that redundant carcass transport to sites is better understood if food extracted from them was high yielding rather than the low yielding resources from carcasses scavenged from other carnivores' kills.

INTRODUCTION

After more than two decades of controversy with respect to the behavioral meaning of East-African Plio-Pleistocene sites, a consistent taphonomic approach has been the basis for inferring that some of those sites were mainly the result of hominids carrying stones and carcasses to determined spots (Bunn 1982, 1991, Bunn, Kroll 1986, Bunn, Ezzo 1993, Potts 1982, 1988, Blumenschine 1988, 1991, 1995, Blumenschine, Marean 1993, Selvaggio 1994, Capaldo 1995, Domínguez-Rodrigo 1997). These spots provided hominids with shelter, shade, and early access to some sources of raw material, water and food (Potts 1988, Dominguez-Rodrigo 1994a). After the abandonment of those sites, the intervention of other carnivores, mainly hyenas, further deleted and modified the bone accumulations originally made by hominids, turning sites into palimpsests (Blumenschine 1988, 1991, 1995, Capaldo 1995, 1997).

Although Binford (1981) and Potts (1982, 1988) suggested that such places were created in highly competitive settings and, therefore, that the interaction between hominids and carnivores was frequent, the paleoecological analysis of sites suggests otherwise, when interpreted under the light of current trophic dynamics in similar habitat types (Blumenschine 1986, 1989, Dominguez-Rodrigo 1996, in print). The riverine and lacustrine riparian environments that sites appear associated to are the least competitive areas in savanna ecosystems, showing a reduced interaction between carnivores and other mammals. Thus, instead of minimizing their stay in those spots, hominids could have safely prolonged their time of occupation and the range of activities carried out in them. -

This ecological situation has been taken into account in the "Central-place foraging" model (Isaac 1983) and in the "Refuge" model (Blumenschine 1991, Blumenschine et al. 1994). That is, hominids were transporting carcasses from open areas, in which competition is usually high, to closed-vegetation riparian zones, where they processed them with the aid of stone tools. The difference of these two models lies on the type of product consumed by hominids: in the "central-place foraging" model, hominids were assumed to have carried fleshed carcasses to sites, which yielded enough food to be shared by several individuals, whereas in the "refuge" model, hominids are

thought to have transported mainly defleshed bones with high marrow yields. Despite these differences, both models converge on the idea that Plio-Pleistocene sites were relatively safe spots where carcass transportation, processing and consumption took place. Some authors (e.g., Binford 1981, Blumenschine 1991, Potts 1988) believe that hominid behavior at these early sites can be accounted for in ethological terms, with a hominid behavioral pattern within the behavioral patterns of extant apes. From an archaeological perspective the problem is: could hominids have generated the bone and artifact concentrations that appear at sites maintaining a similar socio-economic structure to that observed in other primates?

One of the main features of primates is that most of them live and forage in groups (Clutton-Brock, Harvey 1977, Wrangham 1983, Dunbar 1988, Dominguez-Rodrigo 1994). Group foraging enhances the adaptation of individuals by improving their foraging efficiency, their resource defense, and as a means of protection against predators (Dunbar 1988). Kummer (1971) pointed out that primate societies are essentially "group solutions" to ecological problems. Therefore, it is not surprising to observe that grouping patterns among primates show a relation with the selective criteria of the different environments, as attempts to respond to the demands of trophic pressure (Clutton-Brock, Harvey 1977, Dunbar 1988, Dominguez-Rodrigo 1994a).

It has been observed that group cohesion is remarkably strong in species adapted to environments in which the risk of predation is high (Dunbar 1988). This characteristic becomes particularly marked among the primates adapted to savanna ecosystems (Dunbar 1988). Savanna primates always act more cohesively than forest primates, especially those whose ecological niche includes larger open-habitat areas, such as baboons (*P. cynocephalus*, *P. hamadryas*, *P. ursinus*, *P. papio*) and geladas (*T. gelada*). The trend towards a greater cohesion in primates seems, thus, to be related more to ecological criteria than to phylogenetic factors. Dunbar (1988) acknowledges that predation risks promote the formation of large groups and that the optimum group size is habitat-specific. He points out that "the value of grouping as an anti-predator strategy will depend closely on both the local density of predators and the availability of safe refuges" (p. 132).

Therefore, according to the common pattern observed in extant primates, the adaptation of hominids to East African Plio-Pleistocene savannas should have further promoted social behaviors in which group foraging must have been a key adaptive feature (Clutton-Brock, Harvey 1977, Dominguez-Rodrigo 1994a). The behavioral models proposed to account for the East African Plio-Pleistocene archaeological sites – except Isaac's (1978) "home base" model – have not explicitly stated the social repercussion of the subsistential behaviors they try to reconstruct. However, all of them defend the idea that hominids responsible for the early archaeological record were

foraging and moving along the landscape in groups.

Some researchers, close to the "early access to carcasses" or "hunting" hypothesis, suggest that hominids were already showing a "human" behavioral pattern, in which food was transported to particular places where it was collectively consumed (Isaac 1978, 1983, Bunn 1982, Bunn, Kroll 1986, Bunn, Ezzo 1993, Oliver 1994). Others, defenders of the "scavenging" hypothesis, suggest that such a food-sharing attitude did not probably exist, due to the fact that the animal food was scavenged and, therefore, not very likely to have yielded a surplus greater than the needs of one individual (Binford 1981, Blumenschine 1986, 1991). Some of them indicate that the social organization of hominids would have been more ape-like and that food transport must have been influenced by ecological pressures (e.g., competition) rather than by social stimuli (Binford 1981, Potts 1982, 1988, Blumenschine *et al.* 1994).

In this work, we will try to test some of the assumptions stemming from the "scavenging" hypothesis. We will combine three aspects of hominid behavior essential to this hypothesis: group foraging, primate social structure, food type and availability. We will argue that marrow scavenging and selection of referential places in certain habitats (riparian woodland) may be inconsistent with a group-foraging strategy, because it can be the cause of social stress situations. Ethological studies indicate that group adaptive patterns in living primates have important costs. As Dunbar (1988, p. 132) remarks, "there are two kinds (of costs): those that are due to competition for access to limited food or other essential resources, and those that are due to living in close proximity to other individuals". We believe that the scarcity of scavenged food and its transport by hominids to places of communal use (archaeological sites) might have generated a social stress, that could have turned into regular intra-group aggressive behaviors, had hominid behaved as extant apes. We will suggest that food transported to such sites must have been high-yielding to avoid such a social stress situation (Dominguez-Rodrigo 1997). Therefore, it could have been processed and consumed by more than one individual. Meat-eating becomes one of the key factors in this consideration. It is also pointed out that carcass transport was meant not only to avoid competition, but also as a response to certain social *stimuli*.

METHOD AND SAMPLE

The aim of this study was to test social stress in some primates according to food availability. For the purpose of the research, it was carried out with the colony of hybrid baboons (*P. anubis* and *P. hamadryas*) that live in the zoological garden of Barcelona (Spain). The colony of baboons was composed of 30 individuals: 17 males, and 13 females. All the individuals were adults, since females have been sterilized a few years ago.

TABLE 1. Different types of stress and lack thereof in each of the experiments. Numbers in numerator show the number of times stress/lack of stress occurred in each of the variables (feeding normal or suppressed, type of food and amount of food). Denominator shows the number of experiments of each type. Numbers in brackets are for the percentages of each episode of lack of stress, stress, and aggression. Numbers for the number of sectors where food is moved are: mean and (in brackets) minimum and maximum number of sectors.

NORMAL FEEDING	SMALL AMOUNT OF FOOD			LARGE AMOUNT OF FOOD		
	fruit	meat	both	fruit	meat	both
lack of stress	0/11 (0)	0/6 (0)	0/4 (0)	9/11 (81.8)	4/6 (66.6)	3/4 (75)
stress without aggression	7/11 (63.6)	1/6 (16.6)	2/4 (50)	2/11 (19.2)	2/6 (33.4)	1/4 (25)
stress with aggression	4/11 (36.4)	5/6 (83.4)	2/4 (50)	0/11 (0)	0/6 (0)	0/4 (0)
n° of sectors food is moved	7 (2–11)	13 (5–19)	8 (6–11)	1 (0–3)	3 (0–5)	1 (0–2)

FEEDING SUPPRESSED	fruit	meat	both	fruit	meat	both
lack of stress	0/7 (0)	0/4 (0)	0/3 (0)	2/7 (28.5)	0/4 (0)	1/3 (33.3)
stress without aggression	4/7 (57.1)	1/4 (25)	2/3 (66.6)	4/7 (57.1)	3/4 (75)	2/3 (66.6)
stress with aggression	3/7 (42.9)	3/4 (75)	1/3 (33.3)	1/7 (14.4)	1/4 (25)	0/3 (0)
n° of sectors food is moved	7 (4–12)	15 (6–21)	7 (4–13)	1 (0–4)	3 (0–6)	2 (0–3)

Baboons live in an enclosed area of 220 m². The use of captive primates is adequate for testing social stress of groups that have to live in a same reduced area (simulated central places or referential places). The enclosed areas of these primates are far larger than those unearthed at archaeological sites, in which hominids were processing and consuming carcasses.

This study is based on a set of experiments in which the following variables have been considered (*Table 1*):
1. Normal feeding situation. Food was introduced into the enclosures in between normal feeding episodes. Individuals were, thus, in a situation of lack of hunger. Normal feeding takes place once every 10–12 hours.
2. Modified feeding situation. Feeding was suppressed 10 hours before food for experimental purposes was introduced into the enclosure.
3. Small amount of food. Small quantities of food, insufficient for feeding the whole group were introduced into the enclosure. They usually consisted of small amounts of fruit and meat. This set of experiments was meant to simulate the low food yields transported to central places by hominids. In the case of animal food, it simulates low yields of scavengeable food resources from felid kills.
4. Large amount of food. Food in greater amounts than in the case just mentioned, just enough to feed all the group, was introduced into the enclosure. It consisted of fruit and meat. These experiments were meant to simulate transport of high food yields to sites by hominids.
5. Vegetarian food. Only fruits were used in these experiments.
6. Animal food. Only meat and marrow bearing bones were used for testing whether the type of food (meat *versus* fruit) could have any effect on the behavior of the individuals under study.

The experiments combined all these variables to test what was the social reaction to the different situations of food availability. Food was usually disposed in one of the corners of the enclosures, so that its dispersal and movement could be clearly followed along the area. The reaction of individuals was carefully recorded (in written and in video tape) from beginning to end. Social rank and sex of individuals intervening in food consumption according to their order of access was also recorded.

The enclosure where the baboons were kept was round-shaped. We divided it into 4 sectors of the same size. The aim was to observe how food was moved due to competition. Most of the food movement occurred at the outer perimeter of the sectors.

Social stress was defined as the emergence of tension among some individuals of the group, in which dominance behaviors appeared, with individuals being harassed, yelled at and/or deprived of their food. In several cases, the stress ended up in physical aggression.

RESULTS

As can be seen in *Table 1*, small amounts of food introduced into the enclosure created a situation of social stress, irrespective of the previous feeding situation (normal or suppressed). A high frequency of aggression episodes resulted due to the stressful situations that emerged because of competition for food among individuals. Not a single feeding episode was documented with absence of stress. A high degree of physical aggressions were observed (over 50% of the times), especially in those cases in which baboons were fed on meat (over 75% of the times). Therefore, scarce food encourages social stress and frequent aggressive interactions.

When baboons were fed with abundant food, stress diminished, but it was certainly significant, nevertheless.

During normal feeding episodes, baboons were fed with absence of stress in 75% of the times, approximately. Even if stress was observed on about 25% of the occasions, not a single case of physical aggression was documented. However, in this case, there is a contrast in both experimental scenarios; normal feeding period and suppressed feeding phases. In the latter, stress appeared most of the times (78%), and some physical aggressions were also observed, in spite of the abundance of food.

Stress emerged from the competition among individuals and was strictly subjected to a rigid hierarchic system. Dominant males and then dominant females had access to resources before the remainder of the group, by being aggressive to individuals situated lower in the hierarchy.

Therefore, small amounts of food and hunger seem to be determinant in the appearance of social stress and aggression. This, in turn, provokes a high frequency of food movement or transport. Small amounts of food are transported over 9–10 sectors of the enclosure before being consumed, due to stress and competition. Large amounts of food are barely transported at all (1–2 sectors), unless when regular feeding has previously been suppressed (2 sectors). In this case, the amount of food seems to be determinant rather than hunger. Once again, food transport involves a higher number of sectors when dealing with meat. Small amounts of meat are moved from 13 to 15 sectors (on average), and bigger amounts are moved three times more than fruit.

During our study in the Barcelona zoo, we observed that baboons were interested in bone fragments, even though they were defleshed. Some of them still gnawed some of the bones 3 days after they had been given to them. They were regularly fed, so that this was not due to their being hungry. The fact that baboons might leave tooth marks on bones that were still fleshed seemed as normal as it would be for carnivores. To rule out the possibility that this interest in defleshed bones was a product of boredom or stress from confinement, a second study was carried out in Tsavo National Park (Kenya). One of us made several experiments (Dominguez-Rodrigo 1998), but on most occasions baboons were not interested in the bones exposed. Only those cases in which baboons picked up bones or moved them from their original location were counted as actual experiments. After some unsuccessful attempts, in 3 experiments baboons moved and gnawed some of the bones. Each of these experiments consisted of 2 broken and demarrowed bones, with several bone splinters adhering to epiphyseal fragments due to the periostium. They were exposed under controlled circumstances in different places. To minimize the risk of intervention of other scavengers, 2 of them were placed near the river close to the point where baboons had repeatedly been observed to come early in the morning to drink. The other experimental assemblage was placed at a sleeping site used by the troop under observation. In one experiment, baboons did not modify any bone at all, although they stayed around the place where bones were

exposed for a while and transported some of them to a nearby place. However, in the other two experiments baboons moved bones from the site. Even if the resource was scarce, hierarchic pressure caused bone dispersal from the site, in distances exceeding 10 meters from the original location of bones. In this case, as well as in most feeding episodes observed by the author of the experiments in the wild, no physical aggression occurred because individuals escaped. Aggression in the zoo is due to the enclosure limiting the movements of baboons and, thus, making individual encounters easier.

CONCLUSIONS

The "refuge" model proposed by Blumenschine suggests that hominids might have transported carcasses to particular loci in the riparian closed habitats with the purpose of avoiding carnivore competition (Blumenschine 1991, Blumenschine et al. 1994). Hominids would have behaved as most carnivores, according to this ethological model. However, carnivores behaving that way do not generate significant bone accumulations. There are three kinds of strategies adopted by carnivores to cope with competition: consumption in situ of the prey, peripheral transport of the prey, and systematic transport of carcass remains to the same spot. The first of these strategies is optimal from an energetic point of view. It tends to maximize the energy investment. It is a strategy adopted by carnivores according to their position in the trophic chain, determined by body size and group size. Predators like the lion can afford to eat their prey on the spot, because they are gregarious and their body size is the biggest in savanna predators. Most carnivores situated in the intermediate or lower scale of that trophic chain eat their preys on the spot only if the landscape does not allow them to move the animals to a sheltered place where they can consume them. Cheetahs will preferentially move their preys to high grass patches or behind bushes. Leopards will transport their prey into tress. In those cases in which carnivores forage in groups (like hyenas or wild dogs), preys are initially disarticulated on the spot and then, some anatomical sections are dispersed around the kill site. All these behaviors do not generate bone clusters from several individuals because they usually take place around the spot where animals are killed, and transport rarely exceeds 250 meters from the kill site. This does not propitiate redundant transport on the peripheral "refuge" spots. Even in those cases in which more than one individual are transported to the same place (like some leopards do due to the scarcity of appropriate tress), preys rarely exceed the number of three. Bone accumulations observed at hyena or leopard dens only occur due to feeding purposes and not to predators seeking refuge to reduce competition. In those cases, such carnivores engage themselves temporarily in a systematic transport of carcasses that involves a high energetic cost and a much higher risk of losing the prey to competitors
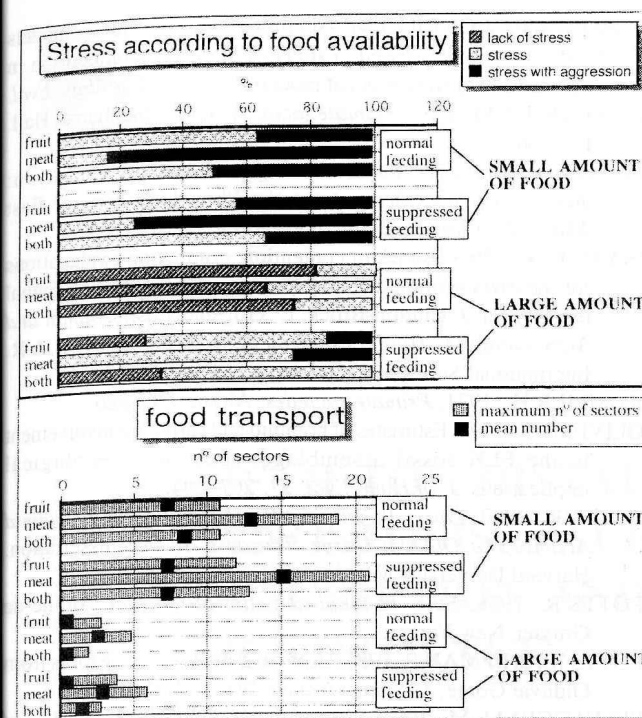

FIGURE 1. The upper section of the figure shows the percentages of the different types of stress in baboons, according to each of the variables (feeding normal or suppressed, type of food and amount of food). The lower section of the figure shows the maximum number of sectors where food was transported before its final consumption (with the mean number in brackets), also according to each of the variables.

than in the usual behavior of peripheral carcass transport (for a further analysis on carnivore behavior and refuge spots, see Dominguez-Rodrigo 1994b).

Had hominids behaved like the rest of carnivores, moving carcasses to refuge locations, they would have been expected to do so in a different place each time, depending on where carcasses were obtained. Redundant transport to the same loci can be better explained if "refuge seeking" was nor the main neither the only reason of carcass transport. From a carnivore point of view, it would be better understood if they had transported carcasses with feeding purposes too.

Food brought to or obtained at social areas tends to be dispersed instead of concentrated as it appears in archaeological sites, especially if it is scarce and if it is not shared (Figure 1). That is why some primates as well as carnivores do not generate significant material debris. In the case of carnivores, that only happens when food is transported to dens or lairs to be shared.

This study is further supported by the fact that this behavior is observed in many other primate species. Initially, we intended to carry out the same kind of research with the chimpanzee group of the Barcelona zoo. We made a few experiments and observed a high percentage of stressful situations with a lot of aggressive behaviors. For

that reason, we had to end our experiments before they provoked further physical aggressions.

As we have seen in this study, if hominids had exhibited a behavioral pattern not very different in structure from those of other primates, the redundant transport to sites of low yielding food – as obtained through passive scavenging (Blumenschine 1986, 1995) – would very likely have generated frequent social stress. Only food surplus could have enhanced hominid social behavior, if carcasses were transported to sites that were also used as gathering locations by other hominids.

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