FOOD AVAILABILITY AND SOCIAL STRESS IN CAPTIVE BABAONS: 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.

KEY WORDS: Meat – Stress – Aggression – Food dispersal

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, Etzo 1993, Potts 1982, 1988, Blumenschine 1988, 1991, 1995, Blumenschine, Marzke 1993, Selvaggio 1994, Capaldo 1995, Dominguez-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those sites, the intervention of other carnivores, mainly hyenas, further deleted and modified the bone accumulations originally made by hominids, turning sites into palimpsests (Blumenschine 1988, 1991, 1995, Capaldo 1995, 1997).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 fleshy 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 higher 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, Ports 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 variation 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 found 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 vanna ecosystems (Dunbar 1988). Species that always act more cohesively than forest primates, especially those whose ecological niche includes larger open-habitat areas, such as baboons (P. c. cynocephalus, P. hamadryas, P. ursinus, P. papio) and gorillas (Gorilla gorilla), which are more resistant to disturbance than Monkeys. However, individualism is not the only aspect to consider. The relationship between the density of predators and the habitat size is crucial, because it determines the quality and quantity of food resources available to the group. In this context, the study of foraging behavior in primates is essential to understand their ecological and social evolution.

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 baboons (P. anubis and P. hamadryas) that live in the zooological 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.

**METHOD AND SAMPLE**

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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, Binford 1982, Krum, 1986, Blumenschine 1993, Oliver 1994). Other defenders of the "scavenging" hypothesis, suggest that such a food-sharing attitude did not probably exist, due to fact that animal food was scavenged and, therefore, not very likely to have yielded a surplus greater than the needs of one individual (Binford 1981, Blumenschine 1996). 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, Ports 1982, 1985, Blumenschine et al. 1994).

In this work, we will try to test some of the assumption stemming from the "scavenging" hypothesis. We will combine three aspects of hominid behavior essential to this hypothesis: group foraging, primates social structure, food type and availability. We will argue that scavenging and selection of referential places in certain habitats (rare pattern woodland) may be inconsistent with 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 foods or other essential resources, and those that are due to living in close proximity to other individuals. The competition for limited food may generate a social stress that could have turned into regular intra-group aggressive behavior which in turn can also affect the group. We will suggest that food transported to such sites must have been high-yielding to avoid such a social stress situation. This hypothesis has been tested in the field, and results show that meat eating becomes one of the key factors in this context. It is also pointed out that this type of transport ceases to 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 availability was measured by the number of meals eaten, the number of food sources and the time spent feeding. The results show that the social reaction to the different situations of food availability is the same, irrespective of the previous feeding situation (normal or suppressed). A high frequency of aggression episodes resulted during 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 with abundant food, stress diminished, but it was certainly significant, nevertheless.

### TABLE 1

<table>
<thead>
<tr>
<th></th>
<th>Small Amount of Food</th>
<th>Large Amount of Food</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>NOMINAL FEEDING</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>fruit</td>
<td>0.11 (0.0)</td>
<td>0.06 (0.0)</td>
</tr>
<tr>
<td>meat</td>
<td>0.04 (0.0)</td>
<td>0.04 (0.0)</td>
</tr>
<tr>
<td>both</td>
<td>0.11 (0.8)</td>
<td>0.16 (0.8)</td>
</tr>
<tr>
<td>stress without aggression</td>
<td>0.11 (0.6)</td>
<td>0.16 (0.6)</td>
</tr>
<tr>
<td>stress with aggression</td>
<td>0.11 (0.4)</td>
<td>0.15 (0.4)</td>
</tr>
<tr>
<td>n of sectors food is moved</td>
<td>0.11 (0.8)</td>
<td>0.16 (0.8)</td>
</tr>
<tr>
<td><strong>FEEDING SUPPRESSED</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>fruit</td>
<td>0.07 (0.0)</td>
<td>0.04 (0.0)</td>
</tr>
<tr>
<td>meat</td>
<td>0.03 (0.0)</td>
<td>0.04 (0.0)</td>
</tr>
<tr>
<td>both</td>
<td>0.07 (0.6)</td>
<td>0.04 (0.6)</td>
</tr>
<tr>
<td>stress without aggression</td>
<td>0.07 (0.5)</td>
<td>0.04 (0.5)</td>
</tr>
<tr>
<td>stress with aggression</td>
<td>0.07 (0.3)</td>
<td>0.04 (0.3)</td>
</tr>
<tr>
<td>n of sectors food is moved</td>
<td>0.07 (0.1)</td>
<td>0.04 (0.1)</td>
</tr>
</tbody>
</table>

**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 during 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.
During normal feeding episodes, baboons were fed with abundance of strea 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: normal feeding period and suppressed feeding phases. In the latter, stress appeared most of the times (78%), and some physical aggressions were also observed.

Stress emerged from the competition among individuals and was strictly subjected to a rigid hierarchical system. Dominant males and then dominant females had access to resources before the remainder of the group, 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 aggression, even 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 stay 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, but the baboons in Nyoro did not do this 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 (Domínguez-Rodrigo, 1998), but in 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 demarr, baboons, with several bone splinters adhering to epiphysal fragments due to the peristium. They were exposed under controlled circumstances in different places. To minimize the risk of intervention of other scavengers, 2 of them were placed near each other 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 in observation. In one experiment, baboons did not modify the bone at all, although they stayed around the place where bones were exposed for a while and transported some of them to nearby place. However, in the other two experiments baboons moved bones from the site. Even if the resource was scarce, hierarchical pressure caused bone dispersal from the site, in distances up to 10 meters from the last 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 individual escaped. Aggressions to prey in the absence of food, limiting the movements of baboons and, thus, making individual encounters easier.

CONCLUSIONS

The "refuge" model proposed by Bluemenschine suggests that hominids might have transported carcasses to particular loci in the riparian closed habitats with the purpose of avoiding carnivore competition (Bluemenschine 1991, Bluemenschine 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 in situ or 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 intake, and 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 in the spot, because they are gregarious and their body size is the bigger in the savanna predators. Mammals such as carnivores situated in the intermediate or lower scale of that trophic chain eat their prey 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 prey to high grass patches or behind bushes. Leopards will transport their prey into trees. 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 propagate redundant transport of the peripheral "refuge" spots. Even in those cases in which more than one individual are transported to the same place (like some leopards do so due to the scarcity of appropriate tress), preys rarely exceed the number of three. Bone accumulations observed by the 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 carcass that involves a high energetic cost and a much higher risk of losing the prey to competitors 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 not the main trigger of 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 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—obtained through scavenging (Bluemenschine 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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REFERENCES


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