



MANUEL DOMÍNGUEZ-RODRIGO

THE ORIGINS OF HUMAN BEHAVIOUR: A QUESTION OF GRADUAL SHIFT OR QUALITATIVE LEAP?

ABSTRACT: *The traditional views on the evolution of human behaviour have overemphasized some of the material aspects of culture, conceived as properly human. However, during the last years, the studies of apes have revealed the existence of these adaptive traits in other primates. This fact has seriously damaged the validity of such a materialist-biased approach (only what is left in the archaeological record is liable to be interpreted) as a clear-cut human diagnosis. Gradualist and punctuated explanations of the emergence of human behaviour are mentioned as theoretical frameworks and the need is proposed of focusing such issue from a socio-ecological consideration.*

KEY WORDS: *Social behaviour — Subsistential behaviour — Tool-use — Meat-eating — Food-sharing — Cooperation — Plio-Pleistocene sites.*

INTRODUCTION

Several authors have traditionally claimed that the most diagnostic features of human evolution were tool-use and meat eating (Ardrey 1976, Dart 1949, 1960, Isaac 1978, Lee & De Vore 1968, Washburn 1960, Washburn & Moore 1974). Since Darwin's "Descent of Man" (1871), these evolutionary traits have been considered as a basic adaptation of hominids to the savanna ecosystem, as well as a subtle change in their subsistence behaviour, which meant the acquisition of meat through predation. Albeit this last issue has received several criticisms during the last two decades, the hunting-versus-scavenging debate has not minimized the importance of meat intake in the considerations of hominid evolution. Some researchers, mainly archaeologists, have emphasized its relevance and have interpreted its emergence as a sudden change in the behavioural pattern of homi-

nids, whereas others tend to consider such alteration in subsistence as a more gradual process.

The interpretation of these elements, as well as others of similar importance — Isaac (1978) stressed the key role that two other features (food-sharing and labour division) had played in human evolution — can receive a new light from Primate Ethology. The observation of the range of the ape adaptive patterns reveals that the classical distinction between hominid and non-hominid behaviour, based on the terms previously exposed, needs revision. Some of the features that were before considered as exclusively human have also been discovered among some primates. The difference established, concerning their emergence and evolution, is in some instances a question of degree and in others, a matter of contextual meaning. If we compare the way that extant apes exhibit these traits to the behaviour of the Plio-Pleistocene hominids that we can infer from the archaeological record,

we realise, on the one hand, how artificial the evolutionary thresholds thus established are, and on the other hand, the need of focusing the exegesis of "human uniqueness" more on its social dimension, which seems to be quite innovative in this regard.

THE ETHOLOGICAL EVIDENCE

Several studies about primates have documented during the last decades that most of the features previously thought of as strictly human are present in extant apes, although under a more rudimentary aspect. This discovery has helped to understand that the lack of evidence of a particular kind of behaviour in an extinct species — likely due to perishable indicators that are not conserved in the geological record — does not necessarily mean the lack thereof. Some of the elements that were traditionally considered as milestones of human evolution are succinctly exposed below, within the context of ape behaviour, where they are now known to exist.

Tool-use

If we observe the patterns of tool-use in apes, we can notice that there is an increasing trend of using different items as tools, according to the evolutionary status of the species involved. The more advanced a given taxon is — from a biological consideration — the higher the frequency of tool-use behaviour seems to become. In this sense, long-term field-studies of orangutans have mostly yielded negative results, concerning the manipulation of natural items as extra somatic means of adaptation (Galdikas 1982, Rijksen 1978), although the capability of tool-use in captive specimens has been demonstrated (Lethmate 1982, Russon & Galdikas 1992). The most striking example thereof is the proved ability of these apes in making and using flaked stones under the pressure of external stimuli (Wright 1972). The highland and lowland gorillas pose the same problem. Despite several years of observation, no sign of tool-use has been obtained in the wild (Fossey & Harcourt 1977, Watts 1984). Nonetheless, spontaneous manipulation of several items has been reported in captivity (Wood 1984).

In contrast, chimpanzees use tools in all settings. As McGrew (1992) correctly underlines, in the wild they use a variety of tools made from a variety of materials to accomplish a variety of tasks. They use stones as hammers to crack open nuts (Boesch 1978), sponges of leaves to gain access to the water contained in natural holes, within the trunk of different trees (Goodall 1968), probes of vegetation to obtain termites (Goodall 1964) and woody branches as weapons against male rivals or to deter some predators (Kortland 1965). A remarkable feature of chimps is their flexibility in making tools and the contrast of tool-kits among different populations, which is only understandable — according to several authors — from

a "cultural" viewpoint, meaning by this term distinct social traditions (McGrew 1992). For instance, a comparison — carried out by McGrew et al. (1979) — of raw materials used by chimps in different sites to accomplish the task of termite-fishing has yielded as a result the unequal incidence in each raw material according to the chimpanzee group. And even concerning the same raw material there exists a substantial difference in the patterns of its modification. Whereas some groups peel the bark of their twig or vine tools, others do not. Something similar happens with stone tools. Some chimpanzee communities use lithic hammers and anvils, whereas others prefer to utilise pieces of wood as hammers and tree-roots as the fixed substrate that supports the objects to be hammered.

There is also a variation of the habitual patterns of tool-use among different groups to accomplish the same task spectrum. Some of them use certain types of tools for determined functions and others either use different tools for the same purpose or do not use any tool at all (Goodall 1973, McGrew et al. 1978, McGrew 1992). This variation may be explained by the fact that it is the result of an extra somatic mean of adaptation, achieved through a process of acquired knowledge, which is socially inherited and, therefore, transmitted from generation to generation.

However, a distinction must be established between common chimpanzees and bonobos. The latter differ from the former in tool-behaviour. So far, research has reported no evidence of habitual tool-use. This might be accounted for the particular kind of adaptation of bonobos, which are less terrestrial than chimpanzees as they spend most of their time on trees, not having the same subsistential needs nor the access to the same food products. Nevertheless, studies carried out on captive bonobos have yielded a range of spontaneous behavioural patterns indistinguishable from those of chimpanzees (Jordan 1982).

Meat-eating

A more diffuse trend — compared with tool-use — towards omnivorism is observed in apes according to their evolutionary stage. In this sense, although orangutans and gorillas are exclusively vegetarians, meat consumption has been observed with a relative frequency in chimpanzees (Goodall 1968, Teleki 1973). Meat-eating in orangutans is very occasional (Sugardjito & Nurhuda 1981). According to several studies, savanna chimpanzees hunt more often than the apes whose habitat is the dense tropical forest. This is also documented in other primates that inhabit such environments. The most predatory species, the savanna baboons, are precisely adapted to open-vegetation areas.

Chimpanzees eat most of the meat that they get from predatory actions (Teleki 1981) and only occasionally have been observed to pirate a freshly killed prey from baboons (Morris & Goodall 1977). How-

ever, new observations have further confirmed that chimpanzees do scavenge from time to time and that those groups reported to scavenge do not live in areas as dense as the tropical forest (Hasewaga et al. 1983). This subsistential behaviour is also reported among savanna baboons (Strum 1981). The range of species hunted and scavenged by chimpanzees is usually made up of light-weight animals (under 60 kg). This may be explained because larger animals are less frequent in woody areas and more difficult to process without being properly equipped. According to Goodall (1986), a chimpanzee group composed of 40 individuals, may hunt as many as twenty or more preys in less than a year. Nevertheless, this seems to vary from a region to another. The rate of meat-eating reached by the various populations of chimpanzees (measured by analysis of faecal specimens) reports that the groups living in association with the savanna ecosystem eat more meat than the groups that live in strictly dense tropical forests (Goodall 1986, McGrew 1992). This result is further supported by the observation of kills among different communities. East-African chimpanzees hunt in a higher frequency than Central or West chimpanzees not associated to savanna environments (McGrew 1992). All this together can be taken as an evidence of increasing meat-eating among the primate species that are adapted to more open-vegetation areas.

Sex differences in subsistential behaviour

This attitude has erroneously been termed "sexual labour division" by some primatologists. They interpret the ecological differences of both sexes as a division of labour, based on a slight variation in their incidence on food resources. Some products may be eaten more frequently by one sex than by the other, but labour division is one thing and sex variation in subsistence is another. The former requires a defined social group where sex differences exist in foraging and a process of reciprocity is established, by means of the exchange of food between both sexes. Therefore, one cannot argue about labour division without discussing the social organization of a group, which requires a mutual dependence between male and female to account for such a strategy. Otherwise, we are simply talking of sex differences in subsistential behaviour as is the case in extant apes.

A divergence in ranging behaviour between males and females has been reported in gorillas and chimpanzees (Wrangham 1975). In orangutans, males are more terrestrial than females (Galdikas & Teleki 1981). Sex difference in the utilisation of the feeding levels, in the time spent exploiting different resources and in the types of foods chosen for consumption has also been documented in orangutans and chimpanzees (Clutton-Brock & Harvey 1977, Galdikas & Teleki 1981). This indicates a variation between the male and the female subsistential patterns in pongids. Some authors (e.g. Galdikas & Teleki 1981) interpret it as the previous stage to the hunter-gatherer sexual division and, therefore, as the initial phase of an evolu-

tionary continuity. In this sense, the most striking case of sex difference in food procurement is hunting and meat-eating. In this action, only males have been seen on most of the occasions to initiate predation, to pursue and capture preys (Teleki 1973). Adult males also divide the carcasses obtained and get most of the meat they contain in detriment of females that eat less of this food in comparison. According to Wrangham and van Zinnicq (1990), males may kill at least 30 times more often than females. Thus, predation on mammals by chimpanzees is mostly a male activity. So if we take into account that males concentrate on capturing preys — most of the occasions, by hunting, and that females focus their preferences on getting insects — which some authors have defined as "gathering" (McGrew 1992), we can notice that there is a sex difference in food acquisition that could constitute the basis of what later, in the evolution of our genus, became the human hunter-gatherer social behaviour.

Food-sharing

Again the definition of food-sharing must be outlined, as was the case of the division of labour. If we mean by these terms the transfer of food from some individuals to others, by taking nutrients from or by requesting to one another (McGrew 1992), then food-sharing exists among apes. But if we define it as the reciprocal exchange and the distribution of food as a *post factum* action, instigated by the intention of getting energetic resources for a collective benefit — expressed through its sharing with other individuals, then it is only a human behavioural manifestation. If we assume the first definition, then we can notice that there is an increasing trend of food-sharing in apes, according to the evolutionary and adaptive position of each species. Whereas in gorillas and orangutans the transfer of food occurs occasionally — from female progenitors to their offspring, in chimpanzees it is not only restricted to this maternal relationship. Transfer of meat among males and females is observed when a prey is hunted (Teleki 1973). Vegetal foods are also items likely to be transferred to different members of a group, irrespective of the age and sex (McGrew 1979, 1992). In all instances "food-sharing" adopts the form of a distribution of nutrients that is carried out by means of individual requesting and individual allowance to let another member of the group get part of the food that is being consumed.

Social interaction

Once again there is a trend in apes to develop a social relationship that gets more complex as the species is more evolved. The least social ape species is the orangutan. It tends to live alone or in small units composed of a female and its offspring. A somewhat more advanced social organization appears in gorillas, with a reproductive male as the head of

a hierarchized nucleus made up of several females and their descendants. Chimpanzees further develop this trend and are structured in groups, where several adult males and females live together under the authority of a main male. But the degree of social interaction is not necessarily manifested in the formal aspect of the social structure exhibited. The dynamics of social interaction are much more developed in chimpanzees than in any other ape, irrespective of the habitat that the species is adapted to. Dense tropical forest bonobos are as social as savanna chimpanzees. The time that the individuals of the same group remain together and in physical contact is remarkable. Chimpanzees are keen to groom and the time they spend in this activity is long enough to suggest that it is a regular activity carried out daily, whose frequency is not observed in any other ape.

Summary

There seems to exist an evolutionary trend in apes towards increasing some adaptive traits and developing some attitudes according to their evolutionary position. The behaviour of gorillas and orangutans includes almost no tool-use — although their capability of doing so has been experimentally demonstrated, no meat-eating, episodic transfer of food from female progenitors to their offspring, a limited social interaction — which in the case of gorillas is more complex, due to their kind of society — and slight sex differences in subsistence. In contrast, chimpanzees — as human beings' closest ancestors, with which we probably shared a common link about six millions years ago, if the biomolecular data are right — make use of a varied tool-kit (they are both tool-makers and tool-users), they eat meat more frequently than any other ape, by means of a combined predatory (predominant) and scavenging (marginal) strategy, they transfer food to one another and show sex differences not only in tool-use but also in the processing of a variety of plant and animal foods. They also exhibit a complex social interaction.

As all these features become more remarkable in groups adapted to more open-vegetation areas, it seems reasonable to think, from an evolutionary viewpoint, that the first hominids might have further developed these characteristics as they were adapted to the savanna ecosystem, where the selective pressure is stronger. Thus, some sort of material culture might have pre-dated the first lithic artifacts that appear in the archaeological record. This can be further supported by the fact that in open habitats the danger of predation is more intense than in closed areas, making necessary for hominids to adopt a self-defence strategy that might have been based on tool-use. Bearing in mind that as much as a 1/4 of the tools made by chimpanzees are used as weapons (McGrew 1992), and that savanna groups use them more often than dense tropical communities, early hominids might have increased this trend of tool-use and function,

helped by a new locomotion system and an anatomic structure that made both the use and the transport of tools, more efficient.

We have also seen that meat-eating is a part of the subsistential behaviour of chimpanzees. Taking into account that in apes it is an adaptive trait that becomes more relevant according to the species involved — gorillas and orangutans are vegetarians whereas chimpanzees eat meat with relative frequency — and its habitat — chimpanzees adapted to savanna forest consume more meat than in other habitats (Wranham & van Zinnicq 1990) — it can be assumed that early hominids were also "usual" meat-eaters due to their biological status and because of being adapted to more open areas than the extant savanna chimpanzees. This might imply further developing both tactics, hunting and scavenging, which can be observed in our nearest biological relatives, due to the impoverishment of food in savanna woodland — in comparison to the tropical forest — and to the possible increasing rate of meat intake itself, though still being a minor component of diet.

This particular adaptation might have also maintained sex differences in subsistence. Males could have had more access to some products and females to others, in a co-ordinated social system that might have implied the transfer of food among individuals as often as or even more than chimpanzees do. Therefore, from a retrospective consideration, early hominids could have followed the evolutionary path initiated by apes, by further developing some traits that are common to some of the superior primates, being the difference among them all a matter of degree. Thus, our traditional interpretation, as archaeologists, of the landmarks of human evolution — based on inferences about the emergence of these features in a determined moment of the paleoanthropological record — are misleading. Tool-use, meat-eating, sex differences in subsistential behaviour and transfer of food among individuals of a social group are not new elements that emerge with the split of hominids from hominoids or later on, with the appearance of the archaeological record. They are factors of a general behaviour that are present in apes, especially in chimpanzees, and that may have evolved first with early hominids and then with the emergence of our genus. The particular kind of hominid adaptation might have impelled the development of such factors to a larger extent as is required by the selective criteria in open habitats.

Then, if we do not consider any of these adaptive traits as a key aspect in human evolution, does it mean that the differences between ape and human behaviour are a question of quantitative variation? If the answer were affirmative, then the Plio-Pleistocene archaeological record would probably not be as it is. Apes exhibit a subsistential behaviour based on a feed-as-you-go strategy (Isaac 1978, 1983). They do not transport food or postpone its consumption, nor do they create referential places where they eat. As soon as they get any nutrient they consume it. This

may be better understood from the social behaviour that rules this kind of strategy. Chimpanzees and gorillas form societies that can be described as "co-ordinated and semi-cooperative". The term is applied with the next meaning: a particular kind of rules that steer the internal relationship of a group whose adult members perform selfish acts and maintain their subsistential independence from one another, but that make them cooperate against external menaces. Thus, coordination is mainly expressed as the ensemble of social norms — usually hierarchized — that allow different individuals to live together in the same group with no subsistential interdependence. Coordination may lead to semi-cooperation not only in the self-defence of the group but also, as is the case of chimpanzees, in the obtainment of a prey.

If hominids had further increased some of the aspects that I have mentioned before, it seems likely that they could have become more cooperative. But this does not necessarily imply an alteration of the social system of coordination. If they had reacted as chimpanzees, their subsistential behaviour would not have propitiated the formation of an archaeological record. They could have used the "feed-as-you-go" strategy and would have left, therefore, no trace of their adaptation. This seems to be what happened to early hominids. But in a certain moment, and presumably related to the emergence of our genus, some artefact-plus-bone concentrations appear as a clear manifestation of a new behaviour that differs from that of apes in its subsistential aspect and — it seems very likely — in the social structure that conditions it.

THE ARCHAEOLOGICAL EVIDENCE

The best Plio-Pleistocene archaeological evidence is made up of archaeological sites. This simplistic statement is not meant to be tautological but to stress the relevance of a holistic approach to the archaeological record. Elements extracted from their context — for instance, lithic artefacts — do not have the same interpretive value as if they are considered together with the other items that configure the archaeological accumulations. These dense clusters of bone and lithic debris are the result of a new behaviour that might have something to do with the readjustment of the main subsistential and social parameters undergone by some late Pliocene hominids.

Although the mere association of stones and bones might also be thought of as the consequence of natural processes, the main authorship attributed to the hominids still retains the greatest heuristic value (Blumenschine 1988, Blumenschine & Marean 1993, Bunn 1982, Bunn & Kroll 1986, Potts 1982, 1988, Toth & Schick 1986). Natural bone concentrations, such as the sporadic remains that some large felids — and more regularly, hyaenids — may accumulate under determined circumstances cannot completely mimic anthropic sites. Skeletal bone frequency, types of bone alterations, range of taxa represented, density of

bones, spatial patterns of the different elements within the clusters, and ecological comparisons are some of the criteria used to differentiate the agents involved in bone concentrations (Blumenschine 1988, Bunn 1982, Domínguez-Rodrigo, in press(a), Potts 1982, 1988). Furthermore, cut-marks and hammer stone damage prove that hominids were actively involved in the processing of, at least, some of the remains, in order to consume their meat and marrow (Blumenschine & Bunn 1987, Blumenschine & Selvaggio 1988, Blumenschine & Madrigal 1993, Bunn 1981, Bunn & Kroll 1986, Bunn & Ezzo 1993, Potts & Shipman 1981). The controversy raised at the beginning of the last decade about the behavioural meaning of the East African Plio-Pleistocene archaeological sites — whose integrity and resolution were questioned (Binford 1981) — has actually reached a stage where scientists can assess, by means of taphonomic analysis, that hominids have been the primary agents and, therefore, the main — but not only — responsible for most of the bone-and-artefact accumulations of the period referred to (Domínguez-Rodrigo, in press (b)).

After several years of discussion, if asked now to make a statement about the essential characteristics of the formation of the Plio-Pleistocene archaeological record, most of the archaeologists would agree that there are few substantial things to add to what we thought more than a decade ago about the hominid involvement therein. Thus, it is commonly assumed that early archaeological sites were formed because of the next reasons:

1. Referential places were created in strategic points of the landscape, where lithic raw materials were brought from their original sources previously to the complete use of these sites.
2. Hominids repeatedly carried carcasses to these referential spots to process, by means of stone tools, the products they contained.

However, during the last years recent considerations are trying to make us conceive hominid behaviour not as human-like as the models proposed to account for site formation maintain (see below). More remarkable than the hunting-versus-scavenging debate is the issue of what hominids really consumed from carcasses. Accepting that they selected some parts from several carcasses and that they transported them to referential places, Blumenschine (1991) has suggested that hominids mainly scavenged defleshed bones from felid kills — anticipating themselves to hyaenas — with the only aim of extracting the marrow that they contained. This would mean that their behaviour at sites would not have been as human as previously thought, because marrow fat constitutes a limited food yield that would not have encouraged its sharing with other members of the same group. Thus, sites are not conceived as spots where food is shared, but as refuges where hominids individually introduced and consumed low food yields. Blumenschine's assertions are mainly based on the analysis of skeletal representation and bone modification at sites (Blu-

Blumenschine & Selvaggio 1988, Blumenschine 1991, Blumenschine & Marean 1993). Nonetheless, the studies made on bone destruction processes and skeletal representation demonstrate that early sites may have undergone a severe process of destruction and alteration by ravaging carnivores such as hyaenas and, therefore, the elements represented are not indicative of what hominids really carried to these spots (Marean et al. 1992, Blumenschine & Marean 1993). They might have transported a whole carcass — with high energetic yield, or a few defleshed bones — with low yield. However, a recent study on long bone marrow yields of African ungulates by Blumenschine & Madrigal (1993) shows that the abundance of long appendicular bones at Olduvai sites is indicative of the selectivity by hominids in exploiting the energy from them. As they say:

"Hominids were preferentially breaking those larger mammal bones that provided the greatest gross energy gain. In neglecting many lower-yielding bones, hominids were not maximizing energy gain from marrow exploitation, nor were they operating in an extremely-limited mode. (...) Rather the amount of food energy available to the hominids who broke marrow bones at the sites seems to have been adequate." (Blumenschine & Madrigal 1993: p. 580).

This evidence that hominids selected high-yielding bones, according to the authors, is consistent with passive scavenging from abandoned felid kills, confrontational scavenging and hunting. Blumenschine also argues that the evidence for hammerstone breakage and frequency of percussion-marks specimens at some sites suggest that hominids broke most of — if not all — the marrow bones (Blumenschine & Madrigal 1993). But this only indicates that hominids extracted marrow from bones. It does not exclude that they could have eaten the meat that these bones might have contained. As a matter of fact, there are several arguments that could be used to prove it:

1. Concerning surface bone alterations, besides percussion-marks, a significant amount of bones at sites exhibit several cut-marks (Bunn 1981, Potts & Shipman 1981). Both the quantity and presence of these marks on determined sections of the bones cannot be satisfactorily accounted for *as the removal of scraps of flesh that commonly survive carnivore consumption* (Blumenschine 1991). Firstly, they appear regularly on meat-bearing bones (Bunn & Kroll 1986) and secondly, upper-limb bones from carcasses at felid kills usually are utterly defleshed. Furthermore, to remove the occasional scraps of flesh of these bones stone tools become unnecessary, but even when they are applied to them, no mark is left on their surface (Domínguez-Rodrigo, under study).
2. Every reconstruction of a behavioural model must be based on a multiple-variable approach. By focussing on bones, Blumenschine does not take into account that sites contain lithic artifacts and stones that suggest their use in meat consumption. Most of the stone tools at early sites are simple or modelled

flakes and, therefore, they express a cutting-function. Microwear analysis on the edges of some of these tools shows that they were used for processing meat (Keeley & Toth 1981). The presence of alloctonous raw materials — whose original sources were fairly distant — suggests that lithic tools were essential for the survival of hominids. If they had only obtained defleshed bones, stones would become less important — bones could be broken by using tree branches as passive percussion platforms — and the type of raw material would not have been taken into consideration.

3. Blumenschine interprets sites as refuges and not central places. In my field study about carnivore involvement in carcass transport I have not reported bone accumulations by reincident transport to safe places. The points of carcass obtainment, the physical conditions of the environment, the social characteristics of the different carnivores and carcass size are some of the features that account for the lack thereof (Domínguez-Rodrigo, in press (a)). If hominids had reacted like other carnivores, they would not have generated any significant bone concentrations, as the nearest safe spot would always have depended upon a wide range of variables. However, they seem to have been regularly carrying animal resources to determined spots. Blumenschine explains this by interpreting these places not only as refuges but also as points where hominids could always find lithic tools from previous carcass-processing acts. This interpretation could be considered as Potts's "stone-cache model" revisited (see below the critical comment to it).
4. If hominids were only obtaining marrow from long bones, they could have processed them either on the spot or in another place where refuge was available. If riparian woodland was this place, they could have chosen a different spot every time they carried bones to this area, as they would have had a wide access to stones — especially in gallery forests — in case they were really needed. This could have eliminated the troubles that might have emerged at sites if such a scarce food had been transported to them. Studies on apes show that when such a thing happens, disputes, confrontations and aggressions are common among the members of the same group (de Waal 1989). That explains why, when an individual gets some food, he/she tries to eat it alone and get away from the main social focus. The social stress originated by hominids transporting low food yield to the places where other individuals might have stayed, could only have been avoided by carrying that food to other spots apart from the main areas. But this goes against the main conclusions reached through the taphonomic analysis undertaken (see above).

If hominids repeatedly carried carcasses to determined spots, it must have been because they could afford — it may even have been intentionally — food dispersal in favour of other individuals. Therefore,

this should have required that the bones carried to these sites were not marrow-limited, but that they also included meat. This is shown by the skeletal representation, the bone surface alterations and the bone modification patterns from early sites and by a social and trophic consideration of hominid behaviour (Bunn & Ezzo 1993).

This subsistential reaction is currently best explained by two different behavioural models: the "stone cache" and the "central-place foraging". The "stone cache" model, proposed by Potts (1982, 1984, 1988), based on the assumption that hominids minimised the time spent in those places — due to the threat posed by other carnivores, explains the site formation process as the creation by hominids of referential places in different strategic spots, to process the animal food they could get nearby. These "stone caches" were not home bases mainly by the next reasons:

1. A home base must be a safe place, where the members of a community can develop their social life and exchange food and information. In Plio-Pleistocene sites there are a lot of bones with tooth-marks that indicate the presence of carnivores that might have constituted a potential danger to hominids. So, as the overlap between hominids and carnivores is documented, sites cannot have been safe places.
2. The temporal lapse of bone accumulations in those sites might have lasted several years, which means a reiterated use of the spots that exceeds the period of occupation observed in modern hunter-gatherer home bases.

Thus, archaeological sites should be considered as the result of a different behaviour from the one inferred in the "Home base" model proposed by Isaac in the late seventies. It must respond to a positive investment of energy, that is to say, that the energetic expenditure should be optimised by the increase of the energy obtained. By elaborating energetic models, Potts concludes that if the amount of available carcasses in a given area increases, it becomes more useful to create several referential spots instead of only one. As the energy spent in the desarticulation and transport of a carcass results greater according to the augmentation of the length that separates it from the hypothetical "home base", it seems much more effective — in energetic terms — to transport it in a shorter distance. For this reason Potts considers that the formation of several referential points — or processing places — by the same group, in different habitats, would have been more beneficial in the investment and obtainment of energy. Therefore, according to this interpretation, the Plio-Pleistocene archaeological sites could have been the result of the production of several strategic points or "stone caches", which would have been provided with lithic raw material. Hominids would have used them when they had obtained a carcass near each of them and would have minimized the time spent at these sites to avoid the presence of other carnivores. It could have

been a strategy similar to that used by leopards, which transport their preys into trees to keep them away from other predators. According to Potts, this model is innovative due to the next reasons:

1. It is a behaviour that can be compared to that of extant apes.
2. It requires neither a social reorganization nor a food-sharing attitude.
3. It represents an intermediate adaptation as, although it is not exactly like any of the behaviours exhibited by apes, it does not seem as human as the proposal defended in the "home base" model.

However, such a set of assertions is somewhat exaggerated. Concerning the first issue, Potts arguments that the ethological observations stress that chimpanzees use stones as tools, transport them and are able to re-use them. Nevertheless, chimpanzees use stones sporadically and spontaneously if they find them where they require their function. For this action they can transport stones along some meters and re-use them if they were left, for instance, under a tree whose fruits are seasonally consumed (Sugiyama 1981). The "stone cache" model has further implications. It means the choice of several strategic places previously to their utilisation or after having been used once, in prevision of future utility (first planning trait). It also means that hominids should have provided them constantly with lithic raw material, which contrasts with the way that chimpanzees re-use stone tools, as they never bring new stones to a place where they have already some. Thus, one of the factors that would differentiate hominids from chimpanzees would be the *reincidence in the transport of stone*, which is what really propitiates the formation of an accumulation (second planning trait). Another element to be born in mind is the variation in the magnitude of the transport. Whereas chimpanzees move stones along some meters, hominids were able to transport them along several kilometres from their original source to the site where they appear, within an archaeological context (Hay 1976, Potts 1988, Toth 1982). From an energetic consideration, this means that, as the investment of energy for this task was more important in the case of hominids, this behaviour could only be justified if there had existed a greater necessity of tool-use than in apes. But the key difference is that, whereas the ape attitude towards stone tools is opportunistic — they use them if they are found nearby, in the moment they are needed — the hominid behaviour proposed by Potts implies a lot of foresight, as hominids would have selected some places in different areas of the landscape where they would have transported and accumulated stones, previously to their use and in prevision of their future utilisation. By anticipating to events that are to come, such behaviour is a new response to the adaptive requirements as it is not a form of reaction that accomplishes instantaneous and present biological exigencies, but foresees future needs. In this sense, Potts is wrong when he states that his model does not

differ from a normal ape attitude, as it is something unobservable among primates.

Concerning Potts's second statement about the maintenance of the same subsistential and social patterns as in apes, a deeper interpretation of his model, as he indirectly acknowledges, results revealing because it contradicts such a conclusion. The transport of stones is in theory more logical if the whole group, or at least part of it, would have participated together. Individual transport does not seem to have been very effective, as the danger of predation in the open savanna can be better coped with in group. It also does not appear to be an individual act, because if the "stone caches" had not been created for a collective purpose then there is no way they could have existed. Some hominids could have transported the stones from the strategic points created by other hominids, making the production of such sites almost impossible due to the high competition. Thus the only way a "stone cache" could have been generated is that the members of a group had participated collectively in this task. This type of inference might receive further support from the fact that in some sites the amount of distant alloctonous raw material suggests a collective transport. One of the most evident examples is the FLK "Zinj" site in Olduvai, where more than 20 kg of quartzite debris have been recovered, its original source being several kilometres away. Therefore, as Potts (1988, p. 290) himself recognizes: *At the very least, the collective, cooperative transport of stone material to particular spots on the landscape would have been necessary. Stone transport would simply imply an expectative of shared use* as a logical consequence. This means that *the process of bringing food to places where stones were available would seem to imply a communal use of stones and, possibly, animal tissues* (Potts 1988, p. 290). Without this cooperation and the collective procurement and use of lithic items to exploit carcasses — which could have been at the same time communally transported — this behaviour would not have been feasible in energetic terms and the "stone caches" could not have been produced. Communal transport of carcasses could have improved deambulation in open-vegetation areas, decreasing the risk of predation. This should have been a collective behaviour, as if a group of hominids had participated together in the generation of several "stone caches", they would have expected to get any benefit from their use. Thus, Potts's model implies similar consequences to those he pretends to criticize. The difference with the "central-place foraging" model would be that the "stone caches" would have been subsistential *foci* and not social ones.

The "central-place foraging" model, proposed by Isaac (1983a) explains the formation of the archaeological sites conceiving them as referential places that not only served as subsistential spots but also as social areas, which acted as points of cyclical dispersal and congregation of individuals, who would bring food to these spots and would probably stay there some time when no other subsistential activity

was performed. The innovative features that account for the behaviour manifested in Isaac's model are the next:

1. The incorporation to the ecological dynamics of a capability of anticipation to future needs, translated into a planning behaviour. These characteristics are best expressed in the procurement of lithic raw materials and the formation of reference places, as these are established — like in Potts's model — previously to their use.

2. The postponement of food intake and its probable shared consumption.

Although I think that Isaac's model explains better the hominid behaviour here discussed, both models share some common important features. First, the production of referential places requires the capability of anticipating events that are to come; that is to say, to behave not to satisfy an immediate necessity, but to react towards a possible future situation. Referential places are produced because their utility is foreseen in a short term (Isaac's model) or in the long run (Potts's model), but in any case, previously to their use. The establishment of these special spots requires the procurement of lithic raw material to keep them in the adequate conditions so as to accomplish their function. In this sense, the "central places" might act as a sort of "stone caches" created in safer environments, with a social and subsistential aim, where the previous disposal of stones should have been one of their main features.

Secondly, once created a referential point in the landscape, both models imply a postponement of food consumption. Carcasses are not processed on the spot where they are found, but collectively transported to these referential places where they are consumed. The communal labour of producing this kind of points and providing them with stones, as well as the search and transport of carcasses might have had as a result the shared use of stones and carcasses. All this means the emergence of a new kind of behaviour, which has no equivalent in the rest of primates. Behaviour is planned beforehand — emergence of referential places and obtainment of alloctonous lithic raw material, food — at least meat and marrow — is collectively obtained and transported to those spots — in contrast to the feed-as-you-go attitude exhibited by most primates, where it is presumably shared.

From a material consideration, the formation of archaeological sites implies a further development of tool-use and meat-eating, in addition to other things, than that observed in apes. Concerning the first issue, the emergence of such lithic concentrations does not mean the beginning of tool-use among our ancestors — as we have already seen that in some primates stone tool-use is widespread, but supposes the appearance of transformed stone tools. Late Pliocene hominids did not conform themselves to utilise stones as tools, but they modified them and elaborated artefacts with cutting edges. Some authors might argue that this simply is the next stage in an evolutionary process and that it should be considered together with an increase

of stone tool-use. But if we bear in mind that these artefacts might have served to elaborate other perishable instruments — if the traceologic analysis performed on some Plio-Pleistocene stone tools is valid (Keeley & Toth 1981) — then the consideration of their relevance should be done otherwise.

Meat-eating is also empirically demonstrated by a careful analysis of the faunal remains contained in the Plio-Pleistocene archaeological sites (Bunn 1982, Bunn & Kroll 1986, Bunn & Ezzo 1993, Potts 1982, 1988). Their importance lies not only in the demonstration that meat and marrow had become important elements in diet and, therefore, more sought-after products than in the case of omnivorous chimpanzees, but in the type of carcass consumed. While chimpanzees occasionally hunt small preys, such as monkeys, bushbucks, bush pigs, squirrels, rats or bats (McGrew 1992), the spectrum of species represented in the archaeological sites differ considerably from this description. Hominids usually consumed meat and marrow from carcasses that belonged to much larger animals. Whether they were obtained by means of a predatory strategy, an opportunistic one or a mixture of both, it implies a development of this attitude already present in chimpanzees and the attainment by hominids of a substantially different evolutionary stage.

Furthermore, cut-marks found on a lot of the bones present in the archaeological sites indicate the use of stone tools in the processing of carcasses (Bunn 1981, Potts & Shipman 1981), which is a new adaptation not observed in meat-eating extant apes, as they do not use any instrument in the consumption of their preys. This "human" feature might receive further support if hominids had hunted, by using tools, part of the carcasses whose bones are found at the sites. This is a human behaviour not found in any other primate species. Although we lack the evidence thereof, the wear-polishes found on several stone implements from five early Pleistocene archaeological sites, indicate that they could have originated by the scraping and sawing of wood (Keeley & Toth 1981), which might suggest the elaboration of wooden weapons.

But, were the Plio-Pleistocene archaeological sites formed because some hominids improved their skills to adapt themselves to a more hostile environment, by increasing their tool-use and becoming more creative tool-makers, by eating more meat — thus developing hunting and scavenging strategies — and by incorporating new features due to the combination of both circumstances?

Some authors would answer positively to this question, because they do not take into account some deeper aspects of behaviour that rule its material manifestation. They would even think of the emergence of the adaptation responsible for the archaeological sites as a gradual shift from previous behavioural patterns, structured within a theoretical framework that conceive human behaviour as a regular metamorphosis that undergoes a gradual evolutionary process. However, a gradualist consideration of a particular set of new characteristics adopted by

a determined species might be misleading. An ensemble of seemingly slight changes, when manifested at the same time, can constitute a substantial leap instead of a simple step forward.

DISCUSSION:

IN PURSUIT OF THE SOCIAL EVIDENCE

If the early members of our genus had been socially structured like the extant apes, their subsistential attitude would have been quite different. Following the ape patterns, if they had found a carcass, they would have processed it on the spot (food would be consumed where it is obtained). But due to ecological reasons (risk of predation) if the transport of carcasses became necessary, then it would have been performed to the nearest safe place. This point would always depend on the spot where carcasses were obtained — unless it was previously chosen, as in Potts's model — because if it is meant to avoid the presence of other carnivores, the transport would have been made within a short-distance range as most predators do. Both previous circumstances are contradicted by what can be inferred from the archaeological record, because such behaviours would not propitiate any relevant bone concentration, as it always would depend on the place where the carcass is found (Domínguez-Rodrigo, *in press(a,b)*). The artefact-plus-bone accumulations that make up early sites were made because some hominids were engaged in a new behaviour that implied the establishment of referential places, that were either redundantly visited or continuously used for some time and where carcasses were systematically transported and therefore accumulated. This behaviour requires a higher degree of cooperation than that observed in apes.

In this sense, cooperation would not only have been limited to the communal defence of the group, but also to one of the most relevant aspects of subsistence: food procurement and its sharing. This is a new adaptation that cannot be observed in non-human primates and must be understood within a different social pattern. Apes and monkeys share the same basic subsistential reactions, because their social structures are ruled by a similar coordinated system. Groups are socially hierarchized and there exists no interdependence among adult individuals for the daily food consumption. The hominids involved in the formation of the archaeological sites, in contrast, seem to have become more interdependent, probably adopting a kind of social relationship based on cooperation and solidarity; at least to a certain extent.

This clearly means that the "visible" elements of the human adaptation in the past are not enough and cannot significantly be used on their own to make interpretations of the human evolutionary process. If what I have just exposed is taken into account, all the material aspects innovated by some late Pliocene hominids and manifested through the formation of the archaeological sites, could be the result of an alte-

ration of the internal social parameters of those hominid groups. We might further speculate about the reasons of this change — the biological modification that led to the emergence of our genus seems fairly plausible (Bermúdez de Castro & Domínguez-Rodrigo 1992) — but we must assume that such a complex web of adaptive traits as the one that early *Homo* seems to have exhibited is not easy to understand from a mere gradualist perception.

If a biological improvement of the processing of information — and therefore of adaptation — and a redefinition of the social ties occurred simultaneously, that could account, on the one hand, for the capability of elaborating modified stone tools and, being aware of their utility, for using them in several tasks (wood and food manipulation), and on the other hand, for having access to other habitats and to a new series of resources. The processing of large carcasses could have been done not only because of an improved tool-use capability, but because the internal social interaction permitted these hominids to deambulate through habitats where they could cope with the risks. This social compromise would have forced hominids not to process at least part of their food on the spot where they obtained it, nor to move it to a nearby safer point, but to take it to a previously established referential place, where the rest of the group could join them and get a share of the energetic income. Thus, the hominids involved in this behaviour would have become not only tool-users in a higher degree than apes (gradual shift), but tool-dependants, in contrast to them (qualitative leap). They could have eaten more meat than apes (gradual shift), but their menu — meat, marrow and viscerae — was utterly different, including animals of all kind and sizes (qualitative leap). There might have existed a more relevant transfer of food than in apes (gradual shift), but this was not probably limited to the unidirectional mother-infant reaction and might have included individuals of all ages and both sexes, being the postponement of food consumption and its transport a “visible” sign that could justify the assertion of food-sharing instead of simple food transfer for this behaviour (qualitative leap). Hominids might also have further developed the hunting and scavenging strategies (gradual shift), but to hunt large animals would have required the aid of material implements because of prey size and the inability of hominids to run fast. In this sense, hunting reaches a new dimension due to the characteristics of the animals that might have entered the predatory range of these hominids and to the tactics used to get them (qualitative leap).

Scavenging would also have been different between early *Homo* and apes. Whereas it is a marginal activity — almost inexistent — of some apes, it could have been for hominids the main source of obtainment of large animal nutrients (Blumenschine 1991). If this had been so, and bearing in mind that scavenging large animals means to cope with the risk of predation by other carnivores, the difference between apes and

these hominids would also have been somewhat disproportionate (qualitative leap).

Cooperation must have been more important in hominids than in apes, too. But in this case, if hominids were socially organised in solidary groups, the interdependence of their members would have meant a new type of cooperation, that does not exist in the rest of primates (qualitative leap).

Nevertheless, bearing in mind the whole bunch of factors mentioned, what can really be considered to be a substantial leap is the common evolution and/or emergence of these elements in a determined evolutionary stage, parallel to the biological appearance of our genus. A more complex behaviour, that includes all these innovations, could account for the swift spread of human beings in the early moments of their existence and the later extinction of the rest of hominids.

Actually, the research about human evolution should be more focused on the analysis of the socio-ecological patterns of adaptation (Domínguez-Rodrigo, in press (b); Foley 1987, 1991), from a consideration of the forms of social interaction, and try to elaborate conceptual models that could be applied to our evolutionary ancestors. Recognizing some typical human features in a particular hominid genus could be thought of, by many researchers, as an ethnographic-biased interpretation with no exegetic validity. This theoretical framework has forced research during the last years to construct ethologically-oriented hypothesis and interpretations. Nowadays we assume that the primigenious members of our genus were not humans as we are, but surely they were not as ape-like as some authors believe. They probably were as much separated from apes as they were from us. In this sense, it seems feasible that some human traits observed today in our species, could have first emerged with them and that some ape characteristics were still retained in their behaviour. Against Isaac's (1983b) statement, I think that if we had these hominids alive today, we would not put them in academies, but we would not put them in zoos either.

ACKNOWLEDGEMENTS

I wish to thank professors M. Angeles Querol Fernández and Gonzalo Ruiz Zapatero for their useful comments on a draft of this paper.

REFERENCES

- ARDREY R., 1976. *The hunting hypothesis: a personal conclusion concerning the evolutionary nature of man*. Atheneum, New York.
- BERMÚDEZ DE CASTRO J. M., DOMÍNGUEZ-RODRIGO M., 1992. Heterochrony and the paleoanthropological record: the origins of the genus *Homo* reconsidered. *Trabajos de Prehistoria*, 49: 51 – 68.

- BINFORD L. R., 1981. *Bones: ancient men and modern myths*. Academic Press, New York.
- BLUMENSCHINE R. J., 1988. An experimental model of the timing of hominid and carnivore influence on archaeological bone assemblages. *Journal of Archaeological Science*, 15: 483–502.
- BLUMENSCHINE R. J., 1991. Hominid carnivory and foraging strategies, and the socio-economic function of early archaeological sites. *Phil. Trans. R. Soc. Lond.*, 334: 211–221.
- BLUMENSCHINE R. J., BUNN H. T., 1987. On theoretical framework and tests of early hominid meat and marrow acquisition. A reply to Shipman. *American Anthropologist*, 89: 444–448.
- BLUMENSCHINE R. J., SELVAGGIO M. M., 1988. Percussion marks on bone surfaces as a new diagnostic of hominid behavior. *Nature*, 333: 763–765.
- BLUMENSCHINE R. J., MADRIGAL T. C., 1993. Long bone marrow yields of some African ungulates. *Journal of Archaeological Science*, 20: 555–587.
- BLUMENSCHINE R. J., MAREAN C. W., 1993. A carnivore's view of archaeological bone assemblages. In: *From bones to behavior: Ethnoarchaeological and experimental contributions to the interpretations of faunal remains*. Ed. J. Hudson, pp.: 273–300, Southern Illinois University.
- BOESCH C., 1978. Nouvelles observations sur les chimpanzés de la forêt de Tai (Cote-d'Ivoire). *La terre et la vie*, 32: 195–201.
- BOESCH C., BOESCH H., 1981. Mental maps in wild chimpanzees: an analysis of hammer transport for nut cracking. *Primates*, 25: 160–170.
- BUNN H. T., 1981. Archaeological evidence for meat-eating by plio-pleistocene hominids from Koobi Fora, Kenya. *Nature*, 291: 574–577.
- BUNN H. T., 1982. *Meat-eating in human evolution: studies on the diet and subsistence patterns of plio-pleistocene hominids in East Africa*. Ph. D. thesis. Department of Anthropology, University of California. Berkeley.
- BUNN H. T. 1991. A taphonomic perspective on the archaeology of human origins. *Annual Review of Anthropology*, 20: 433–467.
- BUNN H. T., KROLL E. M., 1986. Systematic butchery by plio-pleistocene hominids at Olduvai Gorge, Tanzania. *Current Anthropology*, 27: 431–452.
- BUNN H. T., EZZO J. A. 1993. Hunting and scavenging by plio-pleistocene hominids: nutritional constraints, archaeological patterns, and behavioural implications. *Journal of Archaeological Science*, 20: 365–398.
- CLUTTON-BROCK T. H. (Ed.). 1977. *Primate Ecology*. Academic press, New York.
- DART R. 1949. The predatory implement technique of Australopithecus. *Journal of Physical Anthropology*, 7: 1–39.
- DART R., 1960. The bone tool-manufacturing ability of Australopithecus prometheus. *American Anthropologist*, 62: 134–143.
- DARWIN C., 1871. *The descent of man and selection in relation to sex*. John Murray. London.
- DOMINGUEZ-RODRIGO M. In press (a). Las acumulaciones óseas de macrofauna: revisión de los criterios de discernimiento de los agentes biológicos no antrópicos, desde un enfoque ecológico. *Zephyrus*.
- DOMINGUEZ-RODRIGO M. In press (b). *El origen del comportamiento humano*. Tipo, Madrid.
- FOLEY R., 1987. *Another unique species*. Harlow: Longman.
- FOLEY R. (Ed.), 1991. *The origins of human behaviour*. Unwin Hyman, London.
- FOSSEY D., HARCOURT A. H., 1977. Feeding ecology of free-ranging mountain gorilla (*Gorilla gorilla beringei*) In: *Primate Ecology*, ed. T.H. Clutton-Brock, pp.: 415–447. Academic Press, London.
- GALDIKAS B. M. F., 1982. Orangutan tool-use at Tanjung Puting Reserve, Central Indonesian Borneo (Kalimantan Tengah). *Journal of Human Evolution*, 10: 19–33.
- GALDIKAS B. M. F., TELEKI G., 1981. Variations in subsistence activities of female and male pongids: new perspectives on the origins of hominid labor division. *Current Anthropology*, 22: 241–256.
- GOODALL J., 1964. Tool-using and aimed throwing in a community of free-living chimpanzees. *Nature*, 201: 1264–1266.
- GOODALL J., 1968. The behavior of free-living chimpanzees in the Gombe Stream Reserve. *Animal behavior monographs*, 1: 161–311.
- GOODALL J., 1973. Cultural elements in a chimpanzee community. In: *Precultural primate behavior*, Ed. E. W. Menzel, pp. 144–184. Basel: S. Karger.
- GOODALL J., 1986. *The chimpanzees of Gombe*. Cambridge, mass.: Harvard University Press.
- HASEGAWA T., HIRAIWA M., NISHIDA T., TAKASAKI H., 1983. New evidence on Scavenging Behavior in Wild Chimpanzees. *Current Anthropology*, 24: 231–232.
- HAY R. L., 1976. *Geology of Olduvai Gorge*. University of California Press, Berkeley.
- ISAAC G. L., 1978. The food-sharing behavior of protohuman hominids. *Scientific American*, 238: 90–106.
- ISAAC G. L., 1983a. Bones in contention: competing explanations for the juxtaposition of Early Pleistocene artifacts and faunal remains. In: *Animal and Archaeology 1. Hunters and their prey*. Eds. J. Clutton-Brock and C. Grigson, pp.: 3–19. International Series 163, Oxford.
- ISAAC G. L., 1983b. Aspects of human evolution. In: *Evolution from molecules to men*. Ed. D.S. Bendall, pp.: 509–543. Cambridge: Cambridge University Press.
- JORDAN C., 1982. Objects manipulation and tool-use in captive pygmy chimpanzees (*Pan paniscus*). *Journal of Human Evolution*, 11: 35–39.
- KEELEY L. H., TOTTH N., 1981. Microwear polishes on early stone tools from Koobi Fora, Kenya. *Nature*, 293: 464–465.
- KORTLANDT A., 1965. How do chimpanzees use weapons when fighting leopards? *Year Book of the American Philosophical Society*, 327–332.
- LEE R. B., DE VORE I. (Eds.), 1968. *Man the hunter*. Aldine, Chicago.
- LETHMATE J., 1982. Tool-using skills of orangutans. *Journal of Human Evolution*, 11: 49–64.
- MCGREW W. C., 1979. Evolutionary implications of sex differences in chimpanzee predation and tool use. In: *The great Apes*. Ed. D.A. Hamburg and E.R. McCown, pp.: 440–463. Menlo Park: Benjamin/Cummings.
- MCGREW W. C., 1992. *Chimpanzee material culture*. Cambridge: Cambridge University Press.
- MCGREW W. C., TUTIN C. E., BALDWIN P. J., 1979. Chimpanzees, tools and termites: cross-cultural comparisons of Senegal, Tanzania and Rio Muni. *Man*, 14: 185–214.
- MCGREW W. C., TUTIN C. E., 1978. Evidence for a social custom in wild chimpanzees? *Man*, 13: 234–251.
- MORRISK., GOODALL J., 1977. Competition for meat between chimpanzees and baboons of the Gombe National Park. *Folia primatologica*, 28: 109–121.
- POTTS R., 1982. *Lower Pleistocene Site Formation and Hominid Activities at Olduvai Gorge, Tanzania*. Ph. D. thesis. Harvard University. Mass.
- POTTS R., 1988. *Early hominid activities at Olduvai*. Aldine, New York.
- POTTS R., SHIPMAN P., 1981. Cutmarks made by stone tools from Olduvai Gorge, Tanzania. *Nature*, 291: 577–580.
- QUIATT D., HUFFMAN M. A., 1993. On home bases, nesting sites, activity centers, and new analytic perspectives. *Current Anthropology*, 34: 68–70.
- RIJKSEN H. B., 1978. *A field study on sumatran orangutans (Pongo pigmeus abellii)*. Wageningen: H. Veenman and Zonen B.V.
- RUSSEN A. E., GALDIKAS B. M. F., 1992. Imitation in captive orangutans (*Pongo pigmeus*). *Journal of Comparative Psychology*, 31: 101–23.
- SUGARDJITO J., NURHUDA N., 1981. Meat-eating behaviour in wild orang utans, *Pongo pigmeus*. *Primates*, 22: 414–416.
- SUGIYAMA Y., 1981. Observations on the population dynamics and behavior of wild chimpanzees at Bossou, Guinea, in 1979–80. *Primates*, 22: 435–444.

- TELEKI G. 1973. *The predatory behavior of wild chimpanzees*. Lewisburg: Bucknell University Press.
- TOTH N., 1982. *The stone technologies of early hominids at Koobi Fora, Kenya: an experimental approach*. Ph. D. thesis. Department of Anthropology, University of California, Berkeley.
- TOTH N., SCHICK K., 1986. The first million years: The Archaeology of protohuman culture. *Advances in Archaeological Method and Theory*, 9: 1 – 96.
- WAAL F. D., 1989. *Peacemaking among primates*. Harvard University Press, Cambridge.
- WASHBURN S. L., 1960. Tools and human evolution. *Scientific American*, 203: 3
- WASHBURN S. L., MOORE R., 1974. *Ape into man: a study of human evolution*. Little Brown, New York.
- WATTS D. P., 1984. Composition and variability of mountain gorilla diets in the central Virungas. *American Journal of Primatology*, 7: 323 – 356.
- WHITEN A., BYRNE R. W., HENZI P., 1987. The behavioral ecology of mountain baboons. *International Journal of Primatology*, 8: 367 – 387.
- WRANGHAM R. W., 1975. *The behavioural ecology of chimpanzees in Gombe National Park, Tanzania*. Ph. D Thesis, University of Cambridge.
- WRANGHAM R. W., van ZINNICQ BERGMANN RISS E., 1990. Rates of predation on mammals by Gombe chimpanzees., 1972 – 1975. *Primate*, 31: 157 – 170.
- WRIGHT R. V. A., 1972. Imitative learning of a flaked stone technology – the case of an orangutan. *Mankind*, 8: 296 – 306.

Manuel Domínguez-Rodrigo
Departamento de Prehistoria
Facultad de Geografía e Historia
Universidad Complutense de
Madrid
28040 Madrid, Spain