

Are great apes aggressive? A cross-species comparison

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Abstract This paper aims to characterise the aggressive behaviour of great apes: the orang-utan, the gorilla, the chimpanzee and the bonobo. We start by discussing the lack of consensual definitions for terms such as violence, aggression and agonistic behaviour. Secondly, we describe the evidence of aggression in each species. Finally we describe several referential models developed to explain the way of life and aggressive behaviour of the first hominins through insights provided from the behaviour of non-human primates.

Key words Aggression; great apes; models.

Resumo O presente artigo tem como objectivo caracterizar o comportamento agressivo dos grandes símios: orangotango, gorila, chimpanzé e bonobo. Começamos por discutir a falta de definições consensuais para termos como violência, agressão e comportamento agonístico. Posteriormente são descritas as evidências de agressão para cada espécie. Por fim, são descritos vários modelos referenciais desenvolvidos para explicar a forma de vida e o comportamento agressivo dos primeiros hominínios, através de evidências vindas do comportamento dos primatas não-humanos.

Palavras-chave Agressão; grandes símios; modelos.

“When I asked Samoan informants about the feeling of alofa ‘love’ which exists between parents and children, I was surprised to learn that many of them believed a father’s beating was an appropriate sign of his love” (Gerber, 1985:131).

Conceptual framework: aggression, violence and dominance

In the past, aggression was seen by psychologists as “a socially negative tendency that poses serious problems to society” (de Waal, 1996b:159), i.e., an anti-social behaviour resulting from both internal and external factors on the individual.

The term ‘aggression’ has proven remarkably difficult to define in a manner pleasing or useful to all disciplines. Between primatologists and ethologists in general, there is little or no agreement regarding the definition of aggression (Fedigan, 1992; Silverberg and Gray, 1992; Casanova, 2003).

According to Hinde and Groebel (1989), behaviour directed towards causing physical injury to another individual is labelled as aggressive. Silverberg and Gray (1992) note that aggression is used in the behavioural domain as a synonym for an intense assault against some object(s) or some other being(s). Thus, aggression could be defined as “any behaviour directed toward the goal of harming or injuring another living being who is motivated to avoid such treatment” (Baron, 1977: 7), or as “one of the means (of a party) to test and to provoke the other, and to make each party’s interest clear” (de Waal, 1996b: 162). To Wilson (1975: 577), aggression is a “physical act or threat of action by one individual that reduces the freedom or genetic fitness of another”. Siann (1985: 12), on the other hand, distinguishes aggression from violence by stating that while aggression “involves the intention to hurt or emerge superiors to others, but does not necessarily involve physical injury, violence involves the use of great physical force or intensity and, while it is often impelled by aggressive motivation, may occasionally be used by individuals in a mutual interaction which is regarded by both parties as intrinsically rewarding”.

The difficulty in defining the term aggression lies in the heterogeneous nature of a collection of terms that bear a family resemblance to the concept (e.g. forcefulness, ferocity, conflict, force, violence, combativeness, etc.). Hinde and Groebel (1989) distinguish between conflict, conflict resolution, aggression, attack, violence, competition, and even war. To these authors, violence implies inflicting of physical harm to another individual (or object). The harm inflicted is usually intended to be severe, although it may not be. As for the term conflict, Hinde and Groebel (1989) refer to it, in a broad sense, as a disagreement over status or the allocation of feeding or social resources. A conflict may occur between individuals or groups, and usually

implies that the individuals involved perceive the situation as one that can be won or lost. Thus, when a resource is limited, there is competition over it. While competing, participants may not be aware of the conflict since both parts may, for example, search for food independently. Finally, war is defined as a special type of aggression: it involves aggressive groups in which the individuals are in some degree organized towards achieving a common goal. It is usually institutionalized (although not always), with individuals occupying distinct roles (Hinde and Groebel, 1989). According to Silverberg and Gray (1992), aggression is used in different domains: the social domain (an intersocietal situation that is characterized by such violence); in the communicative domain (for a suggestion or equivalent of violence); and in the psychic domain (for an emotional discharge). Thus, the term is used to characterize the acts of individuals and social groups and is applied both to acts and to the readiness to initiate an act.

While for many purposes it is convenient to group together as aggressive behaviour all instances in which individuals or groups direct their behaviour so as to harm others, this category conceals considerable internal heterogeneity (Hinde and Groebel, 1989). This is reflected in the numerous attempts that have been made to classify aggressive acts into distinct sub-categories. When referring to childhood aggression, both Feshbach (1964) and Manning and colleagues (1978) define aggression by relating the term to its underlying motivations:

- 1) instrumental or specific aggression (concerned with obtaining or retaining particular objects or positions or access to desirable activities);
- 2) hostile or teasing aggression (directed primarily towards annoying or injuring another individual);
- 3) defensive or reactive aggression (provoked by the actions of others), and
- 4) games aggression (involving deliberate attempts to inflict injury escalating out of physical games).

Tinklenberg and Ochberg (1981) classified aggressive violence in adolescents into 5 categories: instrumental, emotional, felonious, bizarre, and dissocial. These and other attempts to categorize aggression often provide additional clarification. Still, no typological system is wholly satisfactory (Hinde and Groebel, 1989). It is difficult to find a cross-cultural valid

“etic” definition of violence such that its use can command considerable inter-observer reliability (Silverberg and Gray, 1992). The problem may not only lie in the fact that authors use different conceptual frameworks, but these same authors (and respective frameworks) are also influenced by the culture in which they live (Costa, 2004; Casanova, 2006). Thus, what can be labelled violent and aggressive in one culture may not be classified the same way by a different culture.

Aggressive behaviour involves behaviour by *individuals*, and thus necessarily depends on behavioural mechanisms within individuals (Hinde and Groebel, 1989). Episodes of aggression may involve an *interaction* between 2 (or more) individuals and an interaction refers to a series of exchanges occurring within a limited span of time (Hinde and Groebel, 1989). The nature of each interaction will be affected by the features of both individuals involved. If two individuals often interact aggressively, we may say that they have an aggressive relationship. The nature of any particular relationship depends on the nature and patterning of the interactions of which it is composed. Simultaneously, the nature of a relationship affects the nature of its constituent interactions, because the individuals concerned guide their behaviour according to their experience within and expectations for that relationship. And, in the longer term, the behaviour individuals *can* show is affected by the relationships they have experienced. Relationships are a set within networks of other relationships such as family groups and work mates, among others. Each relationship is affected by the nature of the *group*, and the nature of the group depends upon the constituent relationships (Hinde and Groebel, 1989). Thus, according to Hinde and Groebel (1989) it is useful to consider a succession of levels of social complexity: individuals, interactions, relationships and groups, all with a two-way causal relationships between them.

Ethological studies have demonstrated that emotional displays of anger most commonly serve to reduce the likelihood of aggression between two organisms. This means that a connection between anger and inflicting harm is not an automatic one: the primary adaptive function of anger is expressive and is not to inflict harm. The expression of anger serves as a warning signal to others (Feshbach, 1989). As stated by Hinde (1974) aggressive behaviour is that directed to cause physical injury in other individuals. “In primatology the term (...) is frequently applied to all sorts of self-assertive behaviour – displays, supplantation (...) and yet as Barnett (1968) notes, the intent of

these signals may not be to cause physical injury, but to induce withdrawal of another animal” (Fedigan, 1992: 73). This means that individuals may behave aggressively without engaging with opponents in attacks (but by inducing withdrawal). Thus an animal may exhibit agonistic behaviour without physically attacking his/her target. Sometimes, agonistic behaviour may have the purpose of avoiding violence between individuals, which may have high costs (Casanova, 2003). Agonism does not equate with violence since violence is its most extreme form, but not the most common (de Waal, 1989b). In order to constitute agonism, the action must be composed of several specific behaviour patterns [like chasing and biting (de Waal, 1989b)]. Aggression can be seen as non-vocal threats (attacks and displays), and aggressive and submissive behaviour (Chapais, 1991). Aggressive behaviour develops during infancy, when infants join their mothers and siblings in their acts (Chism, 1991). Thus, there are scaling acts along a continuum of violence ranging from anti-violent, through non-violent and to violent. Hinde and Groebel (1989) also point out the fact that there is a mosaic of elements of attack and threat. An attack on another individual usually involves risk of injury for the attacker. The attack is associated with self-protective and withdrawal responses. Because of the close association between the elements that constitute the mosaic, many authors lump together attack, threat, submissive and withdrawal behaviour as agonistic behaviour, even though some types of behaviour in this category are clearly aggressive and others are not (de Waal, 1989b; Hinde and Groebel, 1989). To Fedigan (1992) a working definition/operational term such as ‘agonistic behaviour’ is suitable.

Dominance has typically been associated with aggression and competition, although primates often compete without being aggressive towards each other (Walters and Seyfarth, 1987). Although hierarchies of dominance are constructed mainly on rank interactions (formal or ritualised), which may be peaceful, disruptive or aggressive (de Waal, 1989a,b), dominance rank may not be synonymous with aggression and violence (or agonism). According to Lee and Johnson (1992: 392), dominance “is defined either by the ability of one animal to take a resource from another, or by its ability to make another avoid or submit during an approach or aggression. These responses define the outcome of dyadic interactions, which are then placed into a hierarchical system ranking all relevant individuals, and reflects basic or intrinsic rank.”

“Dominance relationships are commonly characterised by three structural properties: stability, transitivity and linearity (...). Under such conditions individuals can be assigned unambiguous ordinal dominance ranks that correspond to the number of individuals in the group that they dominate” (Boyd and Silk, 1983: 45). Dominant individuals are generally able to use their status to gain priority of access to resources (food, water, sexual and social partners). Dominant relationships are generally established by repeated interactions where outcomes can be predicted and learned. High status confers many advantages in allowing unchallenged access to limited resources (McFarland, 1992). In groups of relatively stable composition that travel as a unit, dominance relationships tend to be independent of the location of the group, and to take the form of a stable linear hierarchy (McFarland, 1992). Although social dominance has become almost synonymous with resource-holding power (Casanova, 2003), social life is far more complex and “being a dominant according to one criterion does not automatically implies dominance according to other criteria” (Noë *et al.*, 1980: 91). For example, female chimpanzees can take food away from males, but they lose fights with them (de Waal, 1982; 1989b). Dominance can thus be seen as an emergent property of a relationship, but it may also be an attribute of an individual (Casanova, 2003). Dominance is not an attribute or trait possessed by an individual apart from a social context: it is rather an inference about relationships between individuals in a social group. Since dominance resides not in individuals but in asymmetric relationships between individuals that vary with social context and time, it cannot, in a narrow sense, be genetically transmitted (Fedigan, 1992). Dominance alone does not determine that a male will mate more successfully because females have a role in mating and partner selection. There is no reason why female choice should not affect the nature and outcome of a male-male competition (reviewed in Casanova, 2003).

Dominance is a major organising factor among females of many primate groups (Barton and Whiten, 1993) but it is not the only factor. Furthermore, the claim that dominance, rank, and aggression determine mating and reproductive success in polygamous primate societies is not true for all species (Bernstein, 1976; Bygott, 1979; de Waal, 1987; Walters and Seyfarth, 1987; Cowlshaw and Dunbar, 1991; Fedigan, 1992). According to Hinde (1974), dominance has the nature of an intervening variable, providing a

useful explanation only to the extent that the different ways in which it can be assessed are compatible.

Hierarchy may function as a mechanism to control agonistic behaviour because individuals can predict the responses of other members in the group. In the presence of a strong and well-established hierarchy, there is less violence among individuals (de Waal, 1989b; McFarland, 1992). However, for females the costs that must be included in the formation of an achieved dominance hierarchy are rarely outweighed by payoffs, because of the price of injury to the female and to her current or yet-to-be conceived infants (Smuts, 1987). The organisation of a group is based on a hierarchy that makes it easier for individuals to “know” their role, their actions, and mutual or respective responses. Each individual responds to expectations of him/her (and this may allow greater security and calm). Hierarchy is a principle of organisation that occurs at many levels in the control of behaviour. In a hierarchy, elements are ordered in such a way that higher control lower-ranking individuals (McFarland, 1992).

In summary, primates are highly social animals whose societies are characterized by permanent associations and high levels of co-operation between individuals. These associations are frequently furnished with conflict of interests, given that the individuals continue to compete for resources such as food and water (de Waal, 1996b). Thus, presently, aggression is seen by some authors as a product of conflicting individual interest and a product of social decision-making as it is described in the *Relational Model* proposed by de Waal (1996b). The main causes of aggression are personal defence, protection of certain conspecifics and competition. Aggressive behaviour in primates usually occurs during intra- and inter-group competition for limited resources, dominance status and social partners. But this does not mean that aggression occurs every time those situations arise (Chapais, 1991). Taking this into consideration, behavioural mechanisms to control aggression must be at work so that relationships can prevail (de Waal, 1996b). Primates have behavioural strategies to decrease the frequency of aggression, and submission is one of them (Chapais, 1991).

In conclusion, aggression is a flexible behavioural response, finely tuned to past experience, present conditions, and expected future events (Huntingford, 1989). As such, it is amenable to control. Humans have probably inherited from their primate ancestors certain simple behavioural

predispositions that may be used in aggressive interactions both within and between groups (Huntingford, 1989).

After this summarized review regarding some of the problems surrounding the conceptual definition of aggression, the present work will focus on the 4 extant great apes: orang-utans (*Pongo pygmaeus* and *Pongo abelii*), gorillas (*Gorilla gorilla*), chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*).

Agonistic behaviour in great apes

Orang-utans: Bornean (*Pongo pygmaeus*), Sumatran (*Pongo abelii*)

Orang-utans are unusual among great apes in that they appear to lack distinct social units or groups (McConkey, 2005b). They are typically described as solitary although their social organization is yet to be clarified (Singleton and van Schaik, 2001).

Orang-utans are wide-ranging animals (Rijksen and Meijaard, 1999), having very large, stable and overlapping home ranges (Singleton and van Schaik, 2001). Some individuals, the *residents* (Rijksen and Meijaard, 1999), occupy a defined area for several years, but, to seasonally exploit abundant foods, they may go beyond it (Galdikas, 1988; Knott, 1998; MacKinnon, 1974 *in* Caldecott and McConkey, 2005). Others, the *commuters*, use regularly a particular area for several weeks, disappearing and returning each year (Rijksen and Meijaard, 1999). The *wanderers* are only seen rarely and may never return to an area (Rijksen and Meijaard, 1999). The study of Singleton and van Schaik (2001) does not support the existence of this last category.

There are inter-species differences regarding social organization and ranging patterns. Sumatran orang-utans live in communities composed of one or more clusters of females that are genetically related, and one adult male (Singleton and van Schaik 2001; 2002). Occasionally, these clusters may join as a single group (Rijksen and Meijaard, 1999). On the other hand, Bornean orang-utans typically live in very loose, dispersed communities (McConkey, 2005a). They spend most of their time alone or in mother-offspring nuclear units (MacKinnon, 1974 *in* McConkey, 2005a). The reduced degree of social interactions observed (McConkey, 2005a) may be explained by scarcity of large and reliable food sources across most of Borneo (Yeager,

1999 *in* McConkey, 2005a). Nevertheless, females are much more likely to form parties than males (Mitani, 1989; Galdikas, 1985 *in* McConkey, 2005a), given that they tend to settle near their mothers (Galdikas, 1988 *in* McConkey, 2005a). Fully adult Borneo males spend the majority of their time alone, being the least social of all orang-utans (Galdikas, 1985 *in* McConkey, 2005a).

Although orang-utans may be considered as non-territorial apes (Caldecott and McConkey, 2005), adult males exhibit some degree of context competition. These contexts range from mutual intolerance to spatial avoidance (van Schaik and van Hooff, 1996). Avoidance, mutual or one-sided, occurs when individuals are in each other's vicinity (Rijken, 1978 *in* van Schaik and van Hooff, 1996). If fully adult males come into contact with one another, violent battles may occur (van Schaik and van Hooff, 1996; Knott, 1998), explaining why adult male orang-utans have the highest incidence of disfigurements (McKinnon, 1974 *in* van Schaik and van Hooff, 1996; Galdikas, 1985a *in* van Schaik and van Hooff, 1996). Their long calls might act as an efficient spacing mechanism (van Schaik and van Hooff, 1996).

Among males, mating contests can occur when they find themselves in the presence of a receptive female (Galdikas, 1985a *in* van Schaik and van Hooff, 1996). Mating conflicts are common, given that males generally benefit from mating with females, even if they prefer not to co-operate (van Schaik and van Hooff, 1996). According to Smuts and Smuts (1993) this context can create the right conditions for infanticide to occur. However, not a single infanticide episode was observed in orang-utans (Schaik and van Hooff, 1996).

Flanged males, the ones with prominent cheek pads (Delgado and van Schaik, 2000), have higher levels of testosterone, higher status, and so more secure access to an established home range, food resources within it, and receptive females that may be available (Caldecott and McConkey, 2005). A flanged male is also more combative, which means that he is also at a higher risk of injury in fighting (Caldecott and McConkey, 2005).

In Borneo, aggressive interactions are more regularly observed amongst the Kutai individuals than amongst Gunung Palung ones. This may be the result of higher density and more socially individuals (Mitani *et al.*, 1991). Bornean males do not actively defend territories, but resource competition exists. In areas where resources are abundant, aggregations may occur, but

males can be aggressive towards each other when in close range. These battles sometimes can have fatal results (Knott, 1998; Galdikas, 1985 *in* McConkey, 2005a; MacKinnon, 1974 *in* McConkey, 2005a), although combat is rare, as adult males tend to avoid each other.

Long calls, given when males arrive to a new location, can reduce the chance of violent interactions, as they may allow males to space themselves (Caldecott and McConkey, 2005). The frequency of long calls emission increases with individual density (Delgado and van Schaik, 2000; van Schaik, 2004 *in* McConkey, 2005b).

At Sumatra, flanged adult males generally avoid encounters with each other, but when they meet violent aggressive displays can also happen and these may result in potentially fatal fights (Singleton and van Schaik, 2001).

In the swamp forest at Suaq Balimbing, Sumatra, fruit availability is greater and more reliable, which frees orang-utans to be more social, given that the main constraint to proximity, food scarcity and competition, does not exist (Delgado and van Schaik, 2000).

Intersexual aggression is not frequently observed, although it is a common mating strategy of subordinate males (Galdikas, 1985 *in* McConkey, 2005a).

Adult female orang-utans tend to settle near the range where they were born and maintain friendly relationships with local females, which are probably relatives (Singleton and van Schaik, 2001). Further studies on female-female dyads' aggressive behaviour are needed in order to understand the nature of female-female relationships.

Gorillas (*Gorilla gorilla*)

Female gorillas live in stable, cohesive groups and associate permanently with males (Watts, 1996). While males exhibit conditional dispersal, female natal (and secondary) transfer are common [but not universal (Watts, 1996)]. In all great apes there is a tendency for female dispersal from natal groups. Although in a gorilla unit individuals are unrelated, individuals frequently develop affiliative relationships between them (Watts, 1996). Aggression exists but it is not as common as affiliative behaviour (Harcourt, 1979a; Stewart and Harcourt, 1987; Watts, 1992; 1994b; 1996).

Gorillas exhibit some degree of diversity in what is regarded as agonistic behaviour (Harcourt, 1979a; Stewart and Harcourt, 1987; Watts, 1994a; 1996; Bermejo, 2004; Stokes, 2004). Competition arises from patchy feeding resources such as fruit (Watts, 1996; Mallavarapu *et al.*, 2006) or social partners (Watts, 1996; Mallavarapu *et al.*, 2006). Tutin (1996) mentioned that near fruit trees violent interactions among gorillas can lead to serious injuries. Bermejo (2004) states that western gorillas are more frugivorous, travel longer daily distances, and have larger home ranges than mountain gorillas (Sabater Pi, 1977; Tutin, 1996; Bermejo, 1997; Doran *et al.*, 2002). Mountain gorillas eat much less fruits than lowland gorillas (Robbins and McNeilage, 2003; Ganas *et al.*, 2004; Scott and Lockard, 2006). This sub-species has the narrowest diet, mostly composed by few folivorous sub-species (Fossey and Harcourt, 1977; Watts, 1996). On the other hand, Western lowland gorillas are the most frugivorous sub-species (Sabater Pi, 1977; Tutin, 1996; Bermejo, 1997; Doran *et al.*, 2002) with the Lopé population exhibiting the broadest documented diet: much terrestrial herbaceous vegetation throughout the year, but also large amounts of fruit (Watts, 1996). Finally, eastern lowland gorillas in mountain habitat eat mostly terrestrial herbaceous vegetation and have a dietary breadth intermediate between mountain and western gorillas (from Lopé). It has been suggested that such differences may be associated with changes in sociality. Since among western (and eastern) gorillas fruit consumption is higher, there might be an increase of within-group competition relative to mountain gorillas. According to Mallavarapu and colleagues (2006), among captive western lowland gorillas the female dominance hierarchy is more clearly established than in mountain gorillas. Nevertheless, in Zaire (Mbeli Bai), Stokes (2004) found no evidence for agonistic dominance hierarchy among western lowland females only. Also, data does not support that increased frugivory in western lowland gorillas raises levels of within-group contest competition (Stokes, 2004). Stokes (2004) further reported that agonistic relationships among females were poorly developed and highly variable. Aggression was largely undecided and there was little evidence of an agonistic hierarchy of dominance among females. The same was observed regarding the formation of agonistic coalitions. The author (Stokes, 2004) stated that relationships among females were ephemeral and subject to the influence of reproductive status. There was also no clear effect of relatedness in agonistic relationships (and response to female immigration

was variable). According to Watts (1994a), in female mountain gorillas little feeding competition and egalitarian social relationships with poorly defined dominance hierarchies may be observed. Watts (1994a) could only identify non-violent linear supplant dominance hierarchies based mainly on approach-retreat interactions. Thus, female mountain gorillas do not form clear agonistic dominance hierarchies, where one member of a dyad consistently wins contests while the others loose (Watts, 1994a; 1996). Female agonistic relationships resemble those of a more egalitarian species in which females typically lack female kin as allies. According to Watts (1996) egalitarian and individualistic dominance relationships are expected for folivorous primates from whom food resources are generally low in nutrient quality, widely and evenly distributed, and accessible to all group members alike, and, therefore, from whom within-group feeding competition is low (see Koenig *et al.*, 1998). In contrast, it is expected that competition for food resources that exhibit defendable patches, such as fruiting trees may be associated with female-philopatry, strong female dominance hierarchies, and female kin-alliances and is seen as an effective strategy for monopolizing such resources (Wrangham, 1980). However, in the experiment conducted by Scott and Lockard (2006) where 3 captive western lowland gorilla groups were provisioned with clumped, defendable high-energy nutrient foods, female gorillas could not be ranked on the basis of decided agonistic interactions and thus a linear agonistic dominance hierarchy could not be seen. Nevertheless, these gorillas also did not exhibit egalitarian social relationships (Scott and Lockard, 2006).

Stokes (2004) mentions that the rates of agonistic behaviour between dyads of females and silverback western lowland gorillas were consistent between groups [milder aggression via displays instead of physical attacks – see also Harcourt (1979b) and Watts (1992)] and a little higher than between female-female dyads. Agonistic interactions between male-female dyads are not as rare as in female-female dyads. In fact, male aggression as a mating strategy has been recognized in mountain gorillas and other primates (Harcourt, 1979b; Wrangham, 1979a; Watts, 1992). In gorillas it has been called “courtship aggression”. This courtship may be considered as a short-term strategy [soliciting mating opportunity (Watts, 1992)] or a long-term strategy [to retain potential mates (Sicotte, 2001)]. The fact that in some primate species females exert a considerable choice for mate quality may explain this behaviour [hamadryas baboons: Palombit *et al.* (1997);

savannah baboons: Smuts and Smuts (1993); Mbeli gorillas: Stokes (2004)]. According to Stokes (2004), it has been suggested that male policing of female-female aggression serves to reduce competitive differentials among females, and thus retain mates [mountain gorillas: Watts (1992); spectacled langurs or *Trachypithecus obscurus*: Watts *et al.* (2000)]. Silverback interventions in conflictive female-female dyads were rare (Stokes, 2004), although Watts (1996) mentioned that among mountain gorillas males often intervene when female-female dyad conflict arises. Watts (1996) also refers that male aggression towards females is common, but intense aggression and wounding are very rare in within-group interactions (Watts, 1992). Most of the times females respond submissively by emitting signals that they rarely emit towards other females. Stokes (2004) stated that females spent more time near each other than near the silverback male. This was also observed in the study performed by Mallavarapu and co-workers (2006). However, Watts (1996) reports that among mountain gorillas most adult females spend more time close to males than to each other. Mountain gorilla males often display at females and sometimes disrupt mating by submissive males (courtship aggression). Male-female relationships in groups with two or more males vary with male age and rank, number of females per group and female resident histories (Watts, 1992; Sicotte, 1994). Females with infants also spend more time close to males than those without infants (Watts, 1996).

Grouping patterns are connected with the dyads that are involved in aggression (and other social behaviour). Western gorillas are more fluid in their grouping patterns than mountain gorillas are (Watts, 1996), and exhibit sub or super-grouping on a regular basis (Doran and McNeilage, 1998). In Western lowland gorillas, inter-group encounters are more varied and groups are more tolerant towards each other (Tutin, 1996) than the typical aggressive response of mountain gorillas whose inter-group encounters are related with the acquisition of females rather than to the defence of a group's range (Sicotte, 1993) or feeding resources. According to Bermejo (2004), encounters between western silverbacks (and their groups) with lone males result in 50% avoidance episodes and 50% vocal display episodes. The more common response was tolerance. In some occasions super-nests were formed (Bermejo, 2004). Bermejo (2004) studied several groups and noticed that the home ranges of these overlapped with the ones from lone males. High home range overlap and limited site fidelity are features of many primates

in which female transfer occurs (Isbell and van Vuren, 1996; Watts, 1996). Tutin (1996) also reports home ranges overlapping extensively in Lopé.

Although Parnell (2002) reported that 60% of the encounters at Mbeli Bai between western gorillas were neutral and 30% agonistic, Bermejo (2004) noted that encounters were peaceful. Nevertheless, Bermejo (2004) recorded many vocal displays but contact aggression was notably less frequent than previously reported for mountain gorillas (Harcourt, 1978; Sicotte, 1993). Magliocca and Gautier-Hion (2004) observed 238 encounters between 243 units. Of these, 62% were neutral, 29% agonistic, and 9% pacific. Agonistic interactions were mainly observed between silverback and black-back dyads. The unit that arrived last initiated 66% of the encounters (Magliocca and Gautier-Hion, 2004). Tutin (1996) mentions that in 11 years of research at Lopé, observers only saw 40 encounters between two groups or a group and a lone male. Of these, 22 involved 2 groups, 16 a group and a lone male, and in 2 episodes the participants involved could not be determined. The encounters took an average of 54 minutes. Tutin (1996) never witnessed a fight although a male with 16 deep puncture wounds died after an encounter and in 2 cases there were signs of blood. Most interactions occurred close to concentrations of ripe fruit. Nevertheless, Tutin (1996) also mentioned that there were indications of tolerance between certain groups. Aggressive interactions among group members were rarely seen: only 3 cases of displacement or aggression were seen in feeding contexts. In contrast, gorillas were often heard running towards fruiting trees giving excited vocalizations (Tutin, 1996).

According to Watts (1996), encounters between groups, or groups and lone males are contests in which males try to attract or retain females, to protect their own infants and, very rarely, to kill infants or other males (Watts, 1989; Sicotte, 1993). Data summarized by Sicotte (1993) supports two predictions based on consideration of potential gains from escalated aggression (Watts, 1994a). Male aggression is more intense, and the risk of fighting higher when more potential female emigrants are present. Also, encounters between 2 established groups are usually shorter than those that either have solitary males or that are smaller, recently formed groups (Watts, 1994a). Amongst co-resident adult males, adult-adolescent dyads and adolescent peer aggression are more common than affiliation. Maturing natal males spend progressively less time near older males and receive progressively more aggression from them, but older males are usually more

tolerant towards sons and full brothers than towards distant relatives and younger males than of those closer in age (Harcourt and Stewart, 1981; Sicotte, 1994). Males have clear dominance relationships and subordinates sometimes reverse ranks with older males. They compete aggressively over oestrous females and those showing post-conception oestrous-like behaviour. Dominant males often interrupt mating attempts by subordinate males and may guard females although subordinates may “steal” some fertilizations, even while still immature and not yet maximally effective as allies in competition with outside males. Older males tolerate matings between daughters and young males (Watts, 1996). More data has to be collected in order to totally fill the above predictions (Watts, 1996).

There is a high behavioural flexibility among the three gorilla sub-species and caution must be exercised while trying to characterize the 3 different sub-species. Within sub-species, individuals exhibit features that are a result of phenotypical plasticity.

Common chimpanzees (*Pan troglodytes*)

“Violence is a tactic in social interaction, one that is used rarely because its potentially high costs can serve to make it less efficient than other tactics in most circumstances.” (Silverberg and Gray, 1992).

Chimpanzees live in complex communities organised around male kin and relatively solitary females (Wrangham and Smuts, 1980). In chimpanzee communities, social relationships exhibit a high symmetry degree. Social symmetry increases with tolerance by dominants and alliances among subordinates (de Waal, 1996b). Females interact both with each other and with males. Studies on captive chimpanzees (e.g. de Waal, 1982; 1989b) have demonstrated the vital role of females in maintaining group dynamics.

Transfers between communities usually occur well after menarche. Newly immigrated cycling females (usually younger and nuliparous or primiparous) receive more aggressive interactions from older, multiparous and resident females than the opposite (Nishida, 1989; Casanova, 2003). Immigrant females make use of their reproductive state by establishing “bonds” with the males of that community in order to have protection from resident and older females (Goodall, 1986; Nishida, 1989). Thus, when cycling, females spend more time in association with adult males

(Pusey, 1979; Goodall, 1986). While males range widely and evenly over the community range, the core area of females is smaller and scattered (Wrangham, 1979a,b; Hasegawa, 1990). Spatial organisation within foraging parties may be a consequence of dominance relationships between females. Females may respond to each other's presence by dispersing or by aggregating as a function of the degree of feeding competition. Ecological pressures appear to shape the context, frequency and structure of such conflicts. In Kibale, no differences have been observed between sexes in the general pattern of home range use. However, males were seen in the boundary areas four times as often as females (Wrangham, 1997a). In Kibale, male chimpanzees used an area that is 1.5 to 2 times greater than that of females. Females have smaller core areas within the defended home range of the males (Chapman and Wrangham, 1993). At Gombe females are more solitary, with individual core areas overlapping less than at Mahale, where females tend to be more gregarious (Hasegawa and Hirawa-Hasegawa, 1990). Females in cycle travel more widely within the community range than non-cycling females. Females do not defend the community range in the same way as males do. Ranging behaviour reveals differences in the strategies of males and females (Chapman and Wrangham, 1993), in home range size (different foraging strategies and association patterns of the sexes), territoriality and community membership.

Male chimpanzees compete much more aggressively for status than do females (Nishida and Hosaka, 1996; Wrangham, 1997a,b). It is common to observe the development of political strategies by males in order to achieve a dominant rank (de Waal, 1982; 1989b; 1996a; Goodall, 1986; Nishida, 1989; Nishida and Hosaka, 1996; Boesch and Boesch-Achermann, 2000). These political interactions take the form of coalitions, alliances and reconciliations. An adult male organises his whole life around issues of dominance (de Waal, 1982; 1989b; 1996a; Goodall, 1986; Nishida, 1989; Nishida and Hosaka, 1996; Wrangham, 1997a; Boesch and Boesch-Achermann, 2000). Wrangham (1997a) argues that although females are certainly capable of aggression towards each other and being highly political during coalition and alliances episodes just like males, they act as if they do not care about their status as much as males do. While male chimpanzees are ambitious in political affairs, females are far less involved with status rivalry and dominance (reviewed in Casanova, 2003). While males exhibit agonistic and bluff dominance, females show competitive dominance (Noë *et al.*, 1980).

Male aggression represents a major potential cost to females (Manson and Wrangham, 1991). Males can engage more easily in a physical contest over a resource because they have only to inseminate a female and this may be achieved in a short time. Male aggression has been described as a “higher risk” enterprise (Daly and Wilson, 1983). Due to reproductive costs, it may be better for females not to be involved in direct confrontation (Silk, 1993; Campbell, 1999), especially if they live in societies where other females relatives are not available to help (Casanova, 2003), contrary to the case of primates species where females can count on their mothers and sisters, among other female relatives (e.g. *Macaca mulatta*). Female chimpanzees live in male phylopatric societies and hence with the lack of matrilineal support. Thus, the greater need for females to avoid physical injury has implications for the initiation and maintenance of dominance hierarchies. Males do not show a strong or systematic preference for high-ranking females (Packer, 1979; Small and Smith, 1985). The relationship between dominance and reproductive success is weaker and less consistent for females than for males (Bernstein, 1976; 1980; Wrangham, 1980; de Waal, 1982; Silk, 1987). Female survival directly enhances reproductive success (Campbell, 1999) and thus underlies the minimal risk strategy (Chapais, 1992) exhibited by female chimpanzees. This strategy takes the form of indirect aggression or low-level direct contests. Since fighting is “risky”, escalation may not be the best option. In fact, the benefits of winning a fight can be severely diminished by the cost of even trivial injury (Paul *et al.*, 2000). Thus among chimpanzees there are striking sex differences, particularly in the frequency of agonistic behaviour (Bygott, 1979).

While females use dominance in order to gain long-term benefits, the same can not be said for males. Males, after inseminating females, can afford to pursue “risky” behaviour like striving for status and dominance and involving themselves in physical confrontation (Casanova, 2003). Competition among males is high because the associated payoffs in terms of reproductive success are also potentially high. Among males, dominance and resource holding are linked (Campbell, 1999). The variable *time* may be crucial for females, while for males contest *outcomes* are crucial. Among females that belong to a non-kin bonded species, disputes for status do not carry the same implications as they do for males (or females living in female-bonded societies). For female chimpanzees, the risks and costs connected with hierarchy formation, if this involves direct contest or

escalated aggression, might not be offset by increased reproductive success. In sum, there is a major difference between the sexes regarding parental investment, which has direct implications for strategies of dominance and status (Casanova, 2003). This does not mean that female chimpanzees are passive, destined to be subjected to male decisions and biological advantages. The outcome of reproductive strategies may also be influenced by female choice (Casanova, 2003).

While in female-bonded primate groups, a linear dominance hierarchy among females can often be found (Lee and Johnson, 1992; Loy, 1971; Silk *et al.*, 1981; Silk, 1993), in some species – like the female chimpanzee – strict hierarchies have not been generally demonstrated (de Waal, 1982; Silk, 1993). Status rituals are very rare between females (de Waal, 1989b). Males may act as mediators in female-female aggression contexts (de Waal, 1996a). de Waal (1996a) argues that the female chimpanzee hierarchy is inconsistent and vague. In six years of data collection at Arnhem Zoo (with an estimated 6000 hours of observation) there were several female-female pairs where status rituals were never observed. de Waal (1996a) suggests that female chimpanzees lost or did not evolve mechanisms of social dominance comparable with those of their male conspecifics. However, at Tai female-female competition (especially regarding food resources) can result in a linear dominance hierarchy (Wittig and Boesch, 2003) although researchers needed more observation time in order to detect these hierarchies than when observing males.

Chimpanzees exhibit inter-group hostility with stalking attacks by males (Goodall, 1986). Males, and in some cases females without offspring (Goodall, 1986; Boesch and Boesch-Achermann, 2000; Watts *et al.*, 2006) patrol their home range. Home range patrolling episodes have distinct results. Some (although few) resulted in violent attacks to members of neighbouring communities (Nishida, 1979; Goodall, 1986; Watts and Mitani, 2001).

In Gombe, over a period of several years, Goodall and her colleagues observed the best example of what we could call *chimpanzee wars* (Schusterman *et al.*, 2003: 204; Casanova, 2006): a gradual increase in aggressive interactions between the two existent groups (Kasakela and Kahama) resulting in violent behaviour being directed by the Kasakela community towards the Kahama community, which was weaker. The violent attacks were directed not only to males, but also towards females, their offspring and even their abandoned nests. The end result was the disappearance of the Kahama community, given that all the males were

apparently killed (Goodall, 1986). According to Schusterman and colleagues (2003), these killings continued beyond the point of any reasonable retaliation because an *equivalence model* was in action, that is, the Kasakela males were searching for Kahama groups as a category and not for individual males or females.

In summary, the chimpanzee social system is based on sharp status rivalry and depends on specific dispositions for dominance and submission (Boehm, 1999), but mainly in what concerns males (Casanova, 2003). Among female-female dyads, there is evidence of considerable behavioural diversity in captive and wild groups, and social stability may help to explain why female chimpanzees exhibit so much behavioural diversity in their relationships (Baker and Smuts, 1994). Female behavioural plasticity will be better understood when further captive and wild long-term studies take place.

Bonobos (*Pan paniscus*)

“Like chimpanzees, bonobos have a fission-fusion social organization in which individuals within a community associate in groups of variable size and composition” (White, 1996: 30). Nevertheless, the composition of these parties changes less frequently than in chimpanzees (White, 1996). Solitary individuals, which in the case of bonobos are the males, are rare (White, 1988).

Bonobo relationships are more relaxed than chimpanzee ones, with community members, especially adult females, being linked by a more persistent web of alliances or friendships (Wrangham *et al.*, 1996). Unrelated females can and do bond with one another on a routine basis (Parish, 1996). Inter-sexual bonds have also been observed, but they have been considered to be the result of relatedness (Stevens *et al.*, 2006). Stevens and colleagues (2006) found that although some female-female bonds were strong, others were as strong as inter-sexual bonds between unrelated individuals. In general, male-male relations are weak (Kuroda, 1980; White, 1992; Ihobe, 1992; Kano, 1992; Furuichi and Ihobe, 1994; Stevens *et al.*, 2006). Bonobo’s relaxed socio-sexual system has been attributed to their diverse diet and resource-rich environment (Lacambra *et al.*, 2005). Compared with chimpanzee communities, amongst bonobos, grooming is more consistently dispersed between individuals, being more frequent and being performed for longer periods of time between individuals of

the opposite sex (Muroyama and Sugiyama, 1994). This feature reinforces social bonds and also contributes to a relaxed social system (Lacambra *et al.*, 2005). Males treat females in a friendly manner (Gerloff *et al.*, 1999). Genital contact is common among individuals, but it is more frequent after aggression episodes (which are rare) or when food is monopolized by an individual (Hohmann and Fruth, 2000). Sexual activity among females may serve to restore and maintain coalition relationships, by promoting reconciliation and relieving social tension (Hohmann and Fruth, 2000).

In bonobos, intrasexual aggression occurs in the context of mating, with more aggressive males mating more often than their male rivals (Hohmann and Fruth, 2003). The number of competitors can also explain the rate of bonobo male-male aggression, given that it also increases with the number of competitors present (Hohmann and Fruth, 2003). However, male-male sexual competition is much lower than in chimpanzees. The approximately 1:1 adult sex ratio in bonobos and the skewed chimpanzee sex ration in favour of adult females may explain this difference. Additionally, there is the fact that female bonobos exhibit more frequent and prolonged sexual swellings, resulting in more available females (to males) than in the case of chimpanzees (Kano, 1996). At Wamba (Zaire) all matings occur opportunistically and so neither possessive behaviour nor consortship has been observed (Kano, 1992). Adult females seem to have developed *continual receptivity and attractivity* (Kano, 1996: 153), that is, prolonged sexual swelling through their reproductive cycle, which might decrease male-male competition within group and infanticide, and maintain male-female social relationships (Furuichi, 1987; 1992; Kano, 1992). Infanticide episodes were never observed in bonobo communities (Hohmann and Fruth, 2003).

Aggressive behaviour between females can also occur in the context of mating, as they seem to compete for access to certain males (Hohmann and Fruth, 2003). Females may harass other females and so disturb matings (or mating attempts) of the target females (Hohmann and Fruth, 2003). Aggression between female-female dyads increases with the number of sexually receptive females in the party (Hohmann and Fruth, 2003). Nevertheless, and since already referred above, the 1:1 adult sex ration in this species makes sexual competition much lower than in chimpanzees.

There is weak evidence for inter-sexual aggression among bonobos (Hohmann and Fruth, 2003). Aggressive behaviour from males toward females is rare and never conducted to a successful mating encounter

(Hohmann and Fruth, 2003), although they might increase the mating success of the aggressive male in future (Smuts and Smuts, 1993). Aggression by females, on the other hand, is more common, but is never motivated by male aggression (Hohmann and Fruth, 2003). In captivity, males are frequently wounded by one or more females (Parish, 1996). In the wild, alliances between females to attack males are also observed (e.g. Furuichi, 1989; Kano, 1992), although female support of other female aggressors is rare (Hohmann and Fruth, 2003).

Inter-group interactions are frequent, resulting, in the majority of episodes, in high-pitched excitement rather than conflict (Kano, 1992), which is very rare (Idani, 1990). Occasionally, immigrating adult males, without female allies, are the target of coalitionary charges with high levels of aggression by resident males (Marshall and Hohmann, 2005). Bonobo males do not participate in patrols or raids on neighbouring communities (de Waal, 1995; Gerloff *et al.*, 1999; Parish *et al.*, 2000). Sometimes different groups come together to feed and rest in a peaceful atmosphere. During such encounters, males can become excited, but tend to stay behind the line of contact between groups. Females, on the other end, may enter the other group and copulate with unfamiliar males (Idani, 1990).

At Wamba inter-group encounters range from group fights to peaceful intermingling (Idani, 1990; 1991; Kano, 1991 *in* Kano, 1996), resulting in the absence of fatal aggression between groups, as a few times happened with chimpanzees (Kano, 1996). Within peaceful intermingling, even inter-group heterosexual copulations are observed between sexually mature individuals (Kano, 1996). Some dyads of males were observed showing little aggression to each other (Kano, 1996), although this is not comparable to the inter-group aggression that can occur in chimpanzee communities.

Travelling to the past: what can extant primates tell us about the life of the first hominins?

“If we, in our travels in space, should encounter a creature that shares 98% of our genetic makeup, think of the money we would spend to study this species. Such creatures exist on earth and we are allowing them to become extinct” (McGrew, 1992: 215).

To understand what humans are and how they got to the present evolutionary stage, anthropologists use specific methodological tools. Travelling in time is one of the many tasks performed by anthropologists. To reconstruct the behaviour of the first hominins, anthropologists use anthropological and archaeological fossil remains, just as detectives use certain procedures to reconstruct crime scenes. Although it may be possible to observe fossil remains and understand certain behaviours of a specific species (e.g. locomotion behaviour), there is much behaviour that does not fossilize (especially social behaviour). Based on extant species, anthropologists draw inferences about the life and behaviour of extinct species. Thus, anthropologists use evidence coming from different sources: anthropological and archaeological fossil remains, primatology and behavioural ecology, ethnography, and ethno-archaeology. Anthropologists use different model types (e.g. referential models, strategic models among others) and different species (human and non-human primates or social carnivores) to reconstruct what might have been the life of the first hominins. By models we mean the process of constructing a scenario (Moore, 1996). “A referential model may be based on homology (similarity due to common descent, e.g. related chimpanzee), or analogy (similarity due to common adaptation; e.g., terrestrial baboon)” (Moore, 1996: 278) or social carnivores (Casanova, 2006).

The use of social carnivores may seem odd for those who are not anthropologists since those species are less similar to modern humans than are extant non-human primates are. But the use of this group of organisms is interesting from an *analogical* point of view: in fact, social carnivores live in open spaces (e.g. savannahs and open woodlands), the mosaic of environments occupied by our ancestors when they left the safety of the trees and adventured into a more terrestrial way of life. Social carnivores [e.g., spotted hyenas (*Crocuta crocuta*), wolves (*Canis lupus*), lions (*Panthera leo*) or wild African dogs (*Lycaon pictus*)] may provide us hints about the human evolutionary process and how hominin bands structured and organized themselves while facing the demands and dangers of a new territory and a new life. Although social carnivores are not homologous species in relation to humans, behind the habitat type they occupy, there are selective forces at work that give rise to specific adaptive strategies (Casanova, 1996; 2006). And these strategies provide important clues to infer the adaptive strategies possibly adopted by our first ancestors since they also occupied the same

habitat mosaic type. Similar selective pressures (in the same mosaic habitat) may give rise to similar adaptive strategies (Casanova, 2006).

The use of primate [humans such as hunter-gatherers (!Kung, Mbuti, Efe, Hadza among others) and non-humans] species as models is supported by the fact that today, contemporary non-human primates are the taxonomical groups most closely related (genetically and behaviourally) to modern humans. Due to this obvious relatedness (since in the fact we, primates, all share a common ancestor) these “cousin” species typically provide insights about the behaviour of our ancestors and sometimes even about our contemporary behaviour, although in the present work we intend only to provide models to reconstruct and explain the behaviour of the first hominins and in, specific situations, of the last common ancestor between humans and chimpanzee. The use of hunter-gatherers is supported by the fact that these, although modern humans, experience many selective forces that shaped our ancestors.

Referential models can, among other things, suggest important new ideas to paleoanthropology: for example, the dietary differences among chimpanzee sex – females construct and use more artifacts to extract and process food, being more insectivorous (termites and other insects) and extracting more varied food resources than males do, while males do more hunting. This observed pattern may provide insights into the origins of the sexual division of labour in hominins. In fact, like most female mammals, female chimpanzees are directly responsible for the survival of their offspring. Although males may patrol the home range and may protect females and infants from danger, the female gender is directly responsible for gestation, lactation, and infant rearing. Due to this fact, female chimpanzees, especially because they live in a male-bonded society, can not afford to risk themselves in hunting and patrolling (Zihlman, 1997; Casanova, 2003). Nevertheless, this does not mean that females can not hunt or patrol. In fact, females without babies (or not pregnant) do patrol and hunt, and sometimes are even more successful than males (see Goodall, 1986; Boesch and Boesch-Achermann, 2000). In humans, mammal reproductive physiology may have been the first factor that led to the sexual division of labour (Casanova, 2003; 2006).

In this paper we propose to look only at primates, both human (e.g., contemporary hunter-gatherers such as the !Kung) and non-human [e.g., baboons (Strum and Mitchell, 1987); chimpanzees (Moore, 1996; Casanova *et al.*, 2000; Casanova, 2006) and bonobos (de Waal, 2001)], as they provide more information about non-human hominoids which are our closest relatives.

Savannah baboons (genus *Papio*), a homologous species, are a good example of terrestrial non-human primates that live in multi-male, multi-female groups that include hundreds of individuals. A troop (the top organizing level of a community) is organized around a few bands, several harems, and clans. Baboon society is highly organized with complex groups, connected through a male hierarchy, where the leader of any specific clan, harem, or band is always ranked socially above or below other males belong to the same type of group. Each group is also connected hierarchically via different matriline, some dominant and others subordinate. Baboons occupy a wide range of habitats [e.g., desert, savannahs, rocky-mountains, and forests (Casanova, 2006)], and live in home ranges where all resources (food and water) are available (Smuts, 1985). If resources are scarce, home ranges become bigger (Strum and Mitchell, 1987). There is some home range overlapping and one or more core areas are more frequently used. Diet varies according to the occupied home range and is subject to seasonality. Baboons feed on food items such as roots, seeds, leaves, shoots, insects, birds, eggs, lizards, and even small mammals (Casanova, 2006). Baboons hunt other animals co-operatively and meat sharing is observed. Females constitute the nuclear core of the communities (female-bonded and matrilineal society) and form linear, stable, and highly predictable dominance hierarchies (within and between matriline), with daughters occupying the rank immediately above their mothers. Males also have dominance hierarchies although these are more volatile. Males create special bonds with infants via the establishment of strong affiliative relationships or friendships (Casanova, 2006). Allomothering is common. There are also special relationships between male-female dyads that do not necessarily involve sexual behaviour (see Smuts, 1985). Males may be aggressive towards females, although severe aggression is not as common as are mild threats.

As for the genus *Pan*, individuals also live in multi-male, multi-female communities (specifically, polygenic societies) under a fission-fusion system where parties are formed to travel and to feed, among other activities. If food resources are abundant, parties are larger and dozens of individuals may be together. If resources are scarce, communities tend to divide themselves in many parties (or sub-units), as do some human hunter-gatherer groups. Males form the nuclear group of all communities since they all share some kin relationship (male-bonded society), and because females transfer from their natal community. Male co-operate while hunting, patrolling, and

forming alliances and coalitions. They form linear dominance hierarchies while females spend much of their time alone or with their offspring. Chimpanzees hunt co-operatively and meat is commonly shared. These apes are considered frugivorous, eating fruits, flowers, roots, shoots, bulbs, honey, seeds, eggs, and small mammals such as other primates (baboons, or colobus monkeys), bush pigs, among other mammals. There is an incipient sexual labour division with males mainly patrolling and hunting and females mainly investing in their offspring. Conflicts between individuals may be solved via reconciliation where other group members may act as mediators or peacemakers. Chimpanzee communities are xenophobic and intolerant towards “others” (Casanova, 2006).

Hunting can be a dangerous activity when females are gestating or rearing offspring, a situation true for both chimpanzees and for extinct hominins since their young offspring are highly dependent. Female chimpanzees are more insectivorous than males are, and in this process they construct and use more artefacts than males and use more extractive techniques. As a result, the role of females regarding artefact building and using is far more crucial than the role of males. Just as in human communities, the strong mother-infant relationship is responsible for the transmission of knowledge and traditions, at least in the first years of the child’s life.

To some degree, contemporary hunter-gatherers (!Kung, Mbuti or Efe among many others) operate under selective forces similar to those that anthropologists believe affected some ancestral *Homo* species (Casanova, 2006). However, caution must be used in drawing analogies since modern *Homo sapiens* hunter-gatherers differ in significant ways from human ancestors such as *Homo ergaster*, *Homo neanderthalensis* or the newly discovered *Homo floresiensis*. Nevertheless, contemporary hunter-gatherers must employ adaptive strategies very different from those affecting modern humans who live in industrial societies (Lee, 1984; 2003; Lee and Daly, 1999; Parker-Brick *et al.*, 2001) and much more similar to those used by extinct hominins. Among other things, anthropologists are interested in the hunter-gatherer living patterns. These groups live in territories such as tropical rain forests, deserts, or arctic (or sub-arctic) areas and form partially nomadic bands (Casanova, 2006). In South Africa, the development of agriculture by neighbouring non-!Kung groups and, later on, the arrival of the Europeans forced the expulsion of the !Kung from their original home ranges and their numbers began to decrease (see Lee and Daly, 1999; Lee,

2003). Modern hunter-gatherers do not live exactly as australopithecines or other hominins did, of course, but their problems (and selective pressures) are similar (Casanova, 2006), and similar problems may give rise to similar answers (adaptive strategies). Mankind spent the majority of its existence following a hunter-gatherer living and subsistence pattern (Klein, 1999; Lee and Daly, 1999; Stringer and Andrews, 2005). In this work we use the !Kung as a reference only due to the amount of information available about them. The !Kung, also known as Bushman, are composed of different groups who live in the Kalahari desert of South Africa. Village types and localization varies throughout the seasons (Lee, 1984; Lee and Daly, 1999; Parker-Brick *et al.*, 2001). Ethno-archaeological remains (dated from five centuries ago) revealed that the !Kung typically constructed as many as 6 different settlements each year (Kent, 2002). The !Kung and other hunter-gatherer groups live in societies characterized by a very flexible organization (such as the fission-fusion system among chimpanzees) where individuals join (or disperse) in response to food abundance (or scarcity). Hunting is a co-operative task (mainly performed by males) and meat is commonly shared. Water holes are also shared (Lee, 1984). Communities are highly dependent on climate conditions and seasonality. Non-related and related individuals live in the same group. There is a strong social net between all villages. All individuals who live in a specific village are entitled to use all the available resources, although there are complex systems of reciprocity among residents and non-residents. While women collect plant foods which requires extraction and transformation processes [and also may hunt small mammals (Lee, 1984; 2003; Lee and Daly, 1999; Parker-Brick *et al.*, 2001)], men hunt bigger game. The majority of the !Kung diet is composed by collected plant food. The plasticity of their diet enables these hunter-gatherers to live in difficult terrain, a feature also seen in baboons, which shapes the bio-geographical range of the species. The !Kung (and other hunter-gatherers) societies are egalitarian. Fair sharing is encouraged among related and non-related individuals while selfish behaviour is strongly discouraged. Reciprocity and co-operation are very common, and leadership is rarely evident or very diffuse. There may be “leaders” or individuals who show more fitness in a specific task. Summarizing, the !Kung exhibit an assemble of important features: hunter-gatherer economy, sexual division of labour, use of simple technology, collective territory (and resources) possession, co-operations and reciprocity.

Bearing in mind the fossil evidence, data coming from paleoclimatic trends, ethno-archaeology, and paleontology, human ancestors lived a difficult life (Klein, 1999; Hart and Sussman, 2005; Stringer and Andrews, 2005). The first hominins were not predators but preys (Hart and Sussman, 2005), savannah-dwelling creatures who often took refuge in the trees to escape danger (e.g. the Taung child, an *Australopithecus africanus*, was predated by an eagle of large dimensions).

Surviving in such a harsh environment would be difficult without some kind of co-operation between individuals of the same band (Hart and Sussman, 2005; Casanova, 2006). By the end of the Miocene, several hominin species wandered about in the East African savannahs and open woodlands. Human ancestors were only about a meter tall, and they had to defend themselves from predators such leopard's, lion's and hyena's ancestors. A solitary life such as the one led by orang-utans does not seem to be compatible with survival in such a harsh environment (Casanova, 2006). Hominins would have sought to protect themselves by displaying and throwing rocks, stones, wooden sticks, and other available materials; chimpanzee groups also threaten predators by using sticks, and by throwing stones at leopards. Among the first hominins, displaying was probably common. The display behaviour of primates ranges from simple threats (e.g., specific facial expressions accompanied by eye lid repeated exhibition or by the exhibition of canine teeth), drumming and throwing stones and vegetation (e.g., chimpanzees) or chest-beating (e.g., gorillas). The main goal of displaying is to intimidate the opponent while simultaneously avoiding physical contact. Extinct hominins might have used some of these displays, and living in groups would have conferred protective advantages. Without co-operation, reciprocity and solidarity, our species could have not survived in the harsh environment where it lived. Strong affiliative bonds were surely operating (Casanova, 2006). In the beginning, affiliative bonds may have been established between related individuals. These bonds, along with empathy and other features that might have survival value, were favoured by natural selection (see Dugatkin, 1997). With co-operation between individuals, survival rates would rise. Chimpanzees and bonobos also develop strong affiliative relationships, especially between related individuals (e.g., males in chimpanzees and females in bonobos). Baboons are famous for their special friendships (see Smuts, 1985): a male and a female may share a special bond

that does not involve sexual behaviour, where individuals spent time seated together, grooming and supporting each other, among other activities.

During hunting episodes, both chimpanzees and baboons co-operate and share meat. Hunter-gatherers also hunt co-operatively and meat sharing is a key feature present in egalitarian societies. It seems reasonable to think that our ancestors followed the same strategy. In baboons, chimpanzees, and human hunter-gatherers, meat is not the major part of the diet, and meat was not always a significant part of the hominin diet (Klein, 1999; Stringer and Andrews, 2005). It is expected that our ancestors would not say “NO” to a “free meat snack”. Thus, remains of dead animals may have been consumed if found and sometimes stolen from other predators. Artifacts (e.g., hammers and stones) that were used to break up nuts and hard fruits might have been used in different contexts: to break up bones. By breaking bones and consuming the marrow, hominins obtained an extra caloric resource that other primates did not. Chimpanzees seem to “celebrate” successful hunts or the finding of a large fruit tree by embracing each other and vocalizing. Hunter-gatherers such as the !Kung also celebrate after successful hunting episodes. It is probable that the first hominins might have also “celebrated” their successful hunting episodes by embracing each other and vocalizing. It is also plausible that our ancestors used probes to catch termites, as chimpanzees do. Hominin diet has been studied using a scan (electronic microscope) to analyze the marks left on the teeth. Different foods leave different patterns of scratches as pits on the enamel. Just as chimpanzees do (or baboons, or the !Kung), hominins fed on eggs, fruits, some foliage and herbaceous vegetation, roots, and bulbs among other vegetable resources. Meat probably came from a combination of hunting, scavenging, and extraction processes such as termite fishing. There were remarkable differences in the diet of robust and gracile australopithecines (Conroy, 1997; Klein, 1999; Boyd and Silk, 2003; Stringer and Andrews, 2005), with the *Paranthropus* genus being mostly “vegetarian” (Vieira, 1995; Klein, 1999; Stringer and Andrews, 2005) and the *Australopithecus* genus exhibiting a broader, flexible diet (Casanova, 2006).

Hominins (like chimpanzees) probably spent much time in the safety of the trees (Conroy, 1997; Klein, 1999; Boyd and Silk, 2003; Stringer and Andrew, 2005). They probably built nests to sleep, like the ones built by chimpanzees. Hominin offspring were protected by their mothers and other group members. The basic family unit was the mother-offspring and

children experienced a relatively long learning period when compared to other mammal offspring. In the first hominins sexual dimorphism was very high (Conroy, 1997; Klein, 1999; Boyd and Silk, 2003; Stringer and Andrew, 2005): the mating system was not monogamous but polygamous/polygenic mating (Casanova, 2006) as in chimpanzees, bonobos, and gorillas (only the latter exhibit high sexual dimorphism). There were multi-male and single-male groups, as in gorillas. Parental investment by females was considerable, through gestation, lactation, and raising offspring. The specialization at the gender level started with slightly different diets (Moore, 1996). This small difference evolved towards a well defined and established sexual division of labour (Moore, 1996). Individuals strengthened their social bonds via allogrooming, spatial proximity, support, or food sharing. Conflicts were solved with the help of peacemakers and reconciliation was common, and leadership was informal (Hart and Sussman, 2005).

Around 3.7 million years ago the bipedal pattern was established in Africa [Tanzania, Laetoli (Conroy, 1997; Klein, 1999; Boyd and Silk, 2003; Stringer and Andrew, 2005)] although both *Orrorin tugenensis* (who lived around 7 million years ago) and *Sahelanthropus tchadensis* (who lived around 6 million years ago) were bipedal primates (and therefore, hominins).

Considering body size, cranial capacity, and diet (and the above human and non-human models), modern chimpanzees are the most similar of the primates to a last common ancestor (see Moore, 1996). “These similarities suggest that the LCA (last common ancestor) and early hominids would have been subject to selective forces similar to those affecting modern chimpanzees” (Moore, 1996: 279). According to Moore (1996), the transition between a forest-like environment and a savannah-like environment that occurred in the hominin lineage may have involved both ecological and social adaptations similar to those seen in comparisons of forest vs. savannah chimpanzees. Nevertheless, in contrast to modern chimpanzees, anthropological fossil remains indicate that australopithecines (and other hominins) were highly dimorphic.

There is no such thing as the *perfect* model; only travelling – in fact – into the past would provide the perfect “model” and that is not possible. It is probable that the behaviours that are shared today by human and non-human primates, especially the genus *Pan*, might have been present in our common ancestor. Nevertheless, analogies (and homologies) are limited. From all primate species presented, none fits *perfectly* with what it is believed

to be the past of our ancestors. But by adding knowledge of behavioural ecology and fossil remains, it becomes possible to reconstruct scenarios. Reconstructing our ancestors' way of life implies looking at different species that live in the same habitat type as our ancestors. By looking at the way these species socially organize themselves to face selective pressures, we may find insights (e.g., by *analogies* with social carnivorous). By looking at species with whom modern humans share a common ancestor, we may also be able to make some inferences about our ancestors (e.g., by *homologies* with other primates, especially chimpanzees). Primates are in fact a window to the past: the different species complement each other in the sense that different aspects of different models may be incorporated to reconstruct the life of the first human ancestors. Knowing the past will help us to better understand the present and future of the human species.

According to some evolutionary psychologists, there is evidence of a long evolutionary history of violence in human evolution. Buss and Shackelford (1997) suggest that aggression is a context-specific strategy that might have evolved to solve some particular adaptive problems:

- 1) to gain access to valuable resources held by others;
- 2) to defend against attack;
- 3) to inflict costs on intra-sex rivals;
- 4) to negotiate status and power hierarchies;
- 5) to deter rivals from future aggression;
- 6) to deter long-term mates from sexual infidelity;
- 7) to reduce resources expended on unrelated children.

In spite of this scenario, aggression was rare, and probably more frequent between groups than within groups. Although patchy resource distribution might have caused occasional between-group competition (Zolikofer *et al.*, 2002), during the Pleistocene population densities were low (Berger and Trinkaus, 1995). The harsh life made individuals consider the disadvantages of becoming involved in a direct confrontation (e.g., with possible consequences ranging from light injury to death). Aggression was probably the last option after avoidance, displaying, etc. Surely there were also cases of curiosity, empathy, and affiliation between members of different groups. Males and females might have been interested in the individuals of the opposite sex that belonged to other groups. Being part of a group helped the first hominins to survive.

At a specific time in the past, home bases became important, with group members transporting resources back to them. Males hunted more frequently and females collected vegetal resources and hunted small mammals within the vicinities of the home bases. Sexual division of labour was practiced and parental investment was high. Meat and other food resources were shared and there were reciprocity systems operating, with high co-operation and affiliation. Aggression was also part of the life of these hominins (Trinkaus and Zimmerman, 1982) but only as a last resource: communities were highly cooperative in order to survive. Sharing was probably celebrated and encouraged while selfishness was discouraged (Sussman, 1999; Hart and Sussman, 2005). Individuals that persisted in acting in a selfish way could be ostracized by the rest of the group members.

There are some examples of interpersonal violence among our hominin ancestors: skeletal remains showing both cranial and rib fractures that appear to be the result of the use of clubs or other weapons (Trinkaus and Zimmerman, 1982). There is direct evidence that some of these intentional injuries were inflicted with the use of implements (Zolikofer *et al.*, 2002). There is also some evidence of interpersonal violence in *Homo neanderthalensis* specimens (Zolikofer *et al.*, 2002), probably between members of the same group, given that in socially organized species the vast majority of interpersonal interactions occur at the within-group level (de Waal, 2000).

In general, with the exceptions of bonobos, the modern great apes exhibit marked male dominance hierarchies maintained by different forms of contests. Whallon (1989: 449 *in* Knauff, 1991) suggested that during the late Paleolithic “the ape-like systems of interpersonal dominance established through relatively constant display, combat, and trial and error were replaced by systems of at least relatively egalitarian, stable, and reliable relations of rights and obligations among individuals both within and between local groups”. Recently, models presenting hominins as blood thirsty killers and highly aggressive individuals have appeared (e.g. see Wrangham, 1997a). However, behind all models there are specific contextual frameworks, from historical circumstances and cultural and philosophical influences. Sometimes these different contexts – along with their underlying principles – strongly affect the way scientists see and interpret data. Good examples may be provided by the Victorian view of females or by the economic rational behind evolutionary game theory (see Casanova, 2006). Some recent models are

profoundly influenced by evolutionary psychology and even sociobiology and might strongly bias the interpretation of evidence (see Sussman, 1999; Rose, 2000). Caution must be exercised before fully adopting any specific theoretical “orientation”.

In the past decades, physical (biological) anthropology has undergone tremendous “revolutions” by questioning many past assumptions. The large volume of new excavations create a context of museums full of remains yet to be analyzed. Discoveries always outpace publications, and the vast amounts of material yet to be analyzed and studied will take decades to interpret and report.

Conclusion

“Cooperative and affiliative behaviors are considerably more common than agonistic behaviors in all primate species. The current paradigm often fails to explain the context, function, and social tactics underlying affiliative and agonistic behavior” (Sussman *et al.*, 2005: 84).

Regarding behavioural ecology, gorillas (Watts, 1988; 1990) are the species with the most similarities between the sexes, more so than in other great apes such as chimpanzees or orang-utans. Bonobos, on the other hand, are the species with the most limited use of aggression (de Waal, 1987; Wrangham, 1993).

Male chimpanzees engage in intense contest competition with extra-community males (Goodall, 1986). Within-community contest competition is not as dangerous occurring in the form of sperm competition (Watts, 1996). When involved in violent behaviour, males may attack, severely wound, and even kill their opponents (Goodall, 1986, Watts, 1996). However, according to several decades of research, these cases are not common. As for female chimpanzees’ contest competition, it is much more restrained than in males and does not have the same consequences (reviewed in Casanova, 2003).

As for female gorillas, since they are more densely concentrated, males can monopolize access to female groups, although male philopatry and co-operative male defence of female groups can be advantageous in some demographic circumstances. Like chimpanzees, male gorillas engage

in some between-group contest competition (although not as intensely as chimpanzees), but they lack the emphasis on sperm competition (Watts, 1996). Slow maturation of infants and infrequent reproduction by female great apes means that most males have few mating opportunities (Watts, 1996).

A few male chimpanzees and gorillas are infanticidal, while the same has never been observed in bonobos and orang-utans. However, in chimpanzees there is a strong possibility of fathers killing their own infants [Mahale – see Casanova (1996) for review]. From an evolutionary perspective, infanticide by males towards their own offspring has yet to be explained.

Mild sexual coercion is observed in both chimpanzees and orang-utans and can occur in multi-male gorilla groups (Watts, 1996). Sexual dimorphism in body size limits the ability of female gorillas and orang-utans to defend themselves against male aggression, although for female orang-utans it is easier to escape by moving more quickly while in trees since they are smaller – see Watts (1996). Sexual dimorphism is lower in chimpanzees and bonobos. However, chimpanzees may act together to overcome females defences, such as coalitions and alliances. Male chimpanzees have been seen to aggressively expand their home range and add females to their communities at the expense of neighbouring communities (Kahama vs. Kasakela: Goodall, 1986).

As for orang-utans, sexual coercion is not a common generalized mating strategy, although sometimes females may not co-operate in mating. Nevertheless, it is often used by subordinate males (Galdikas, 1985 *in* McConkey, 2005a).

Bonobo males treat females in a friendly manner (Gerloff *et al.*, 1999), and reports of sexual coercion from males towards females are rare (Hohmann and Fruth, 2003). On the other hand, females might form coalitions to attack males (Hohmann and Fruth, 2003).

Chimpanzees are probably the most aggressive of all great apes. However, if we add up all the research performed until now (more than a century of data collection), aggressive or agonistic behaviour represents only a very small percentage of chimpanzee social behaviour, and even a smaller percentage if real-time measures is taken into account (Sussman *et al.*, 2005). Also, within agonistic behaviour, a distinction must be made between different degrees of violence, ranging from simple avoidance, approach-retreat interactions, and simple threats (e.g. chest-beating in

gorillas) to more severe violence or approach-retreat and supplant episodes, avoidance, and mild threats. Within aggressive behaviour, the last degree (severe violence) represents a very small percentage in the extensive primate literature review performed by Sussman and co-workers (2005); affiliative behaviours are much more common than the highly intensively analyzed (and publicized) aggressive episodes. Major theoretical models such as evolutionary game theory (Maynard-Smith, 1982) or the Relational Model (de Waal, 1996b) developed around the logic of animal combat or aggression *per se* (Casanova, 2003). Additionally, the Relational Model presents individuals as resources (social resources), with costs not only in physical but also in social terms. As de Waal (1996b) pointed out, one can not win a fight without losing a friend [since relationships have values – see also Cords and Aureli (2000)].

In some aspects, the first hominins lived a life similar to that of modern chimpanzees: they produced simple artefacts, they had slightly different diets according to gender, females had an important role in teaching the construction and use of artifact techniques, males occasionally hunted, vegetable resources were the main part of the diet, and there was opportunistic meat eating since our ancestors stole food from other predators or consumed dead animals that then found. Behavioural ecology tells us that their mating system was not monogamous, as indicated by the great sexual dimorphism present in anthropologic fossil remains of the first hominins. Organization was polygamous (polygenic). Parental investment was probably similar to that seen in chimpanzees. Social evolution in human history probably also included high levels of male parental investment, apart from the significant sexual division of labour, and sharing of valuable food between related and unrelated individuals (Knauff, 1991). Meat was shared and there was empathy between group members. Co-operation and reciprocity transformed survival into a more successful enterprise. There were special affiliative bonds between related individuals but also between non-related ones. Although they might have exhibited a set of behavioural strategies that helped prevent violent outcomes, aggression was part of social life of the first hominins, when display and intimidation tactics failed.

Due to cultural influences and underlying philosophical and religious values (e.g., the Christian-Judaic paradigm), scientists may transport their “emic” visions into their scientific interpretations (Costa, 2004; Casanova, 2006). Lately, aggression and its importance has been stressed (Casanova,

1996; 2006) and aggression has long been present in the ethological study of groups. But aggression is just one form of social behaviour, among many others. Aggression represents only a small part of an individual's time-budget (Sussman *et al.*, 2005) and in fact, can be responsible for major setbacks in survival terms: if individuals are constantly involved in physical conflicts, their stress levels interfere with their reproductive success [e.g. dominant female baboons: Goodall (1986)] or even with their survival. Of course, there is competition over resources but competition under the form of aggression may bring more disadvantages than advantages (see Sussman *et al.*, 2005). We are not saying that all extinct non-human primates or human ancestors lived under egalitarian systems or under the so-called "peace and love" bonobo model. However, the picture of early hominins as "killer ape-like creatures" is not realistic, considering the hard evidence from fossil remains, primatology, and ethnography.

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