

Towards thirty years of ethological research on the Japanese macaque (*Macaca fuscata*) colony of the Rome Zoo: a review

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Summary – In this paper we review the major findings of almost thirty years of research conducted on the large colony of Japanese macaques (*Macaca fuscata fuscata*) housed at the Rome Zoo. The colony originated from a group of 27 monkeys that was taken as a whole in 1977 from Takasakyama, Oita prefecture, Japan. Since then, the group has been studied almost continuously. The macaque colony thus represents one of the best studied captive groups of primates in the world. In the first part of the paper, we review the research conducted on the colony, that may be grouped in three related topics: 1) mother-infant relationship; 2) allo-grooming distribution, aggression and competition; 3) demography and life histories. Research conducted in Rome contributed to clarify the causes and consequences of variation in primate mother-infant relationships, the social strategies adopted by primates in cooperative and competitive settings and their cognitive basis, and the demographic consequences of captivity. We compare the results of our research with studies conducted on other groups of Japanese macaques and/or on other primate species. This comparison highlights the consistency of results of studies conducted in captivity, in the wild or on provisioned free-ranging populations. In the second part of this paper, we discuss the benefits and fallacies of zoo research in comparison to field work and the importance of long-term data for animal behaviour studies. We also analyse the link between ethological research and the management of zoo animals. Finally, we consider the interdisciplinary implications of primate behaviour research. We emphasize how the comparative study of nonhuman primates may allow the abstraction of principles that can be profitably applied to the study of human social behaviour and evolution. We exemplify this by examining hypotheses about the relation between social behaviour, brain size and language during human evolution.

Keywords – Animal behaviour, long-term study, primates, zoo research.

A brief history of the Japanese macaque colony of the Rome Zoo

In May 1977, a group of 27 Japanese macaques (9 males and 18 females) was captured as a whole near mount Takasaky, Oita prefecture, in Southern Japan, and transferred to the Rome Zoo (Bioparco, since 1998). The group was housed in an enclosure formed by a large (i.e. 700 m²) outdoor area and by 100 m² indoor quarters with

concrete floor and walls (see Figure 1). The enclosure remained basically unchanged over the years until 2003 when the indoor quarters were expanded and redesigned. This work improved the easiness of colony management and of temporary separations of a monkey for health checks. The outdoor enclosure has two ponds with drinking water that also provide a stimulating area for play (particularly in the summer months), given that the Japanese macaques are excellent swimmers. It is also



Figure 1 - Part of the outdoor enclosure of the Japanese macaques at the Rome zoo (photograph by Raffaella Ventura).

furnished with dead trees, branches and ropes. The Japanese macaques began breeding immediately after their arrival, favoured by the relatively similar climatic conditions of Rome and the Oita Prefecture. The group thus increased in size over the years, ranging between 30 and 95 monkeys. To maintain group size under control some removals have been necessary. A few animals were removed in 1980. Others were removed in 1982, 1990, 1994 and 2004. In December 1998 most mature males were vasectomised. Birth rate has consequently dropped considerably. No new animal has ever been introduced into the group.

Socio-ecology of the Japanese macaque

Japanese macaques live in various habitats, ranging from the cold forests of Northern Japan (temperature range: -10° to 20° C) to the subtropical forests of Yakushima island, in the South (temperature range: 5° to 35° C; Fooden & Aimi, 2005). Such a distribution significantly

affects ecology, social behaviour and population dynamics, and it makes some of the following details very general and not always representative of every wild population. Japanese macaques are omnivorous and live in multimale/multifemale groups of 20-60 animals, although provisioned groups may exceed 200 monkeys (Melnick & Pearl, 1987). Breeding is seasonal and characterised by consortships, a period lasting from few hours to several days during which a male and a female are often in close proximity, groom each other and mate (Takahata, 1980). Gestation lasts around 170 days and infants are weaned after 15-20 months in the wild and after 6-12 months in captivity or in provisioned groups (Fooden & Aimi, 2005). The mating season occurs in Autumn and infants are born the following Spring (in Rome the mating season is somewhat delayed; Scucchi *et al.*, 1983; Cozzolino and Schino 1998). Wild Japanese macaques usually give birth to an infant every two years (in Rome, similarly to other captive or provisioned free-ranging groups, the normal inter-birth interval is one year; Takahata, 1980; Scucchi, 1984). Females reach sexual maturity at 3-4 years while males at 4-6 years. Females are the phylopatric sex and maintain close bonds with close relatives (i.e. member of the same matriline) through allo-grooming (hereafter, grooming) while males disperse from the natal group once reached sexual maturity. The Japanese macaque may live up to around 30 years in captivity and 20 years in the wild.

A review of the major findings of ethological research on the Japanese macaque colony

Soon after the macaques arrived to Rome Zoo, students from the Dipartimento di Genetica e Biologia Molecolare, Università La Sapienza di Roma, began to identify and name the monkeys and to conduct behavioural observations. This work was initially facilitated by Professor Luciano Bullini and the staff of Rome Zoo was happy to provide logistic support and collaboration throughout the years. In later years, research on the Japanese macaques has been supervised by two of us (GS and AT). Over the years, the colony has been a constant source of information and scientific data on the behaviour of the Japanese macaque (see the



Figure 2 - Grooming takes a conspicuous part of the daily activity of the Japanese macaques. In this picture, three closely-related females exchange grooming to tight their social bonds (photograph by Raffaella Ventura).

Reference list and the Appendix). At the same time, the colony has provided an excellent opportunity for students to get experience of ethological research for their Laurea degree (comparable to a MSc degree in other countries) and Dottorato di Ricerca (PhD degree).

For simplicity, we have divided the ethological studies so far conducted on the Japanese macaques into three different topics, although these are often interconnected. In the next three sub-sections we present our major findings and briefly discuss them in light of what other studies have found on Japanese macaques and/or on other primate species.

Mother-infant relationship

The study of mother-infant relationship has had a central role in the research conducted on the Japanese macaques of the Rome Zoo. These studies built on the seminal work of Harry and Margaret Harlow and Robert Hinde (Harlow *et al.*, 1963;

Hinde, 1974). The Harlows found that the artificial separation of the infant from its mother has detrimental effects on the expression of an appropriate social and sexual behaviour later in life. This effect becomes stronger when infants are completely socially deprived (i.e. they cannot interact with any other monkey). For example, an adult rhesus monkey socially deprived when infant, would respond with “abnormal” anxiety to social stimuli (e.g. the presence of conspecifics in the same cage) and would show inadequate sexual behaviour leading to incapacity to mate. Interestingly, Harlow and colleagues found that physical contact between mother and infant, rather than mere presence at a distance, was particularly important for the behavioural and physical development of the infant. This result supported similar conclusion drawn by contemporary theories in human psychology (Bowlby, 1971). Although fundamental in posing the bases of primatology

and comparative psychology, such invasive studies may be questioned from an ethical point of view and are now rarely, if ever, undertaken. Later studies by Rober Hinde and co-workers analysed in detail the development of mother-infant relationship over time (particularly in the rhesus macaque) and investigated the effects of brief mother-infant separations. They were instrumental in defining the methods and concepts underlying modern studies of mother-infant relationships.

Besides replicating some of the earlier findings on the development of mother-infant relationships (Schino *et al.* 1993b), research in Rome focused on the study of the causes and consequences of inter-individual variations in mother-infant relationships. We analysed the role of socio-demographic factors in influencing variation in the quality of mother-infant relationships using modern multivariate statistics (Schino *et al.*, 1995) and established the central role played by the mother's emotional reactivity in determining her maternal style (Troisi *et al.*, 1991). The consequences of these inter-individual variation in maternal style on the later behaviour of the infant were then analysed along successive time frames.

Maternal resumption of sexual behaviour is possibly the first stressor encountered by an infant macaque (at an age of about six months). Berman and colleagues (1994) considered maternal resumption of sexual behaviour as a "natural" form of mother-infant separation. When we analysed this topic in the Japanese macaques we found (Schino *et al.*, 2001a) that maternal sexual behaviour and consort activity (see above) did significantly reduce contact time between mothers and infants and increase maternal rejection. However, these effects were only temporary and did not result in an increase in the infant anxiety or decrease in social play. These results did not support the hypothesis that the effects of maternal sexual activity on the infant parallel those of mother-infant separation. Six months later in the infant life, the birth of a sibling has a stronger effect on infant behaviour (Schino & Troisi, 2001) as contact time between the mother and the yearling drops almost to zero. Yearling Japanese macaques responded to this sudden maternal unavailability in two different ways depending on the relationship they had with their mother prior to the birth of the sibling: yearlings that had spent a significant amount of

time in contact with their mothers (and thus presumably had a warmer relationship) showed an increase in grooming and other affiliative interactions with group mates, thus compensating maternal unavailability. Conversely, yearlings that had had less contact with their mothers (and had thus a tenuous relationship with her) did not increase affiliative interactions with group mates and showed a dramatic decrease in social play, indicative of a depressive reaction. Thus, paralleling what is observed in experimental mother-infant separations, and in agreement with attachment theory (Bowlby, 1971), the quality of mother-infant relationship predicted the yearling's response to the stress imposed by the birth of a sibling.

Variations in maternal style had long-lasting consequences on the infant. We analysed the behaviour of subjects, that had been previously observed as infants when they were 4-10 year-old (i.e., between late adolescence and full adulthood). Behaviour under baseline conditions was unrelated to maternal style experienced as infants. In contrast, analysis of behaviour shown under mild social stress (upon being approached by a dominant individual, or upon receiving an aggression) showed that subjects that had had more rejecting mothers were better able to cope with social stress, while subjects with less rejecting mothers showed higher anxiety (Schino *et al.*, 2001b). Thus, mothers that actively encouraged infant independence by means of a more rejecting maternal style promoted their later ability to cope with stressful social events.

Since the first birth season, some cases of maternal abuse and/or abandonment were observed. The cause and pattern of their occurrence was thus the subject of intense research. A wild-born female named Okame was observed to show high frequency of abusive behaviour towards her first infant, who eventually died. The same happened the following years. Abusive behaviour mainly consisted in the mother jumping on, dragging, throwing or stretching her infant (Troisi & D'Amato, 1983). In an attempt to determine whether maternal abuse may be considered an aggressive behaviour directed by the mother towards her own infant, Troisi & D'Amato (1983) analysed the morphological patterns of abusive behaviours. They found that maternal abuse is not similar or comparable to aggressive behaviour but it rather resembles the behaviours that macaques

display when manipulating inanimate objects. A similar conclusion had been drawn for maternal abuse in the rhesus macaque (Ruppenthal *et al.*, 1976). The next step was to compare the maternal style of the abusive monkey with that of non-abusive mothers. The abusive mother had higher frequencies of protectiveness and possessiveness (measured as the frequency of infant restraint by the mother) and lower frequencies of rejection towards her infant in comparison to non-abusive mothers (Troisi & D'Amato, 1984). These results suggested that maternal abuse may be due to an emotional disorder, comparable to what Bowlby defined as anxious attachment (Bowlby, 1971), which causes the mother to respond with abusive behaviours to anxiety-triggering situations. For example, the abusive mother would drag the infant as an anxious response when the infant did not want to follow her (Troisi *et al.*, 1982a). This conclusion was confirmed when Okame stopped being abusive and successfully reared an infant when treated with an anxiolytic drug (i.e. diazepam; Troisi & D'Amato, 1991).

Maternal abandonment of newborn infants is relatively frequent among the Japanese macaques of the Rome Zoo (i.e. 7.7% of total liveborn infants), particularly among primiparous females (i.e. 40% of total liveborn infants; Schino & Troisi, 2005). Maternal age and infant sex did not have a direct effect on abandonment while maternal experience and social rank significantly affected probability of abandonment: primiparous and, to a lesser extent, low-ranking females were more likely to abandon. Maternal abandonment, however, seems partly to be an adaptive strategy for inexperienced females if one considers that primiparous mothers who did not abandon their infant suffered a higher infant mortality, a subsequently longer inter-birth interval and thus a lower reproductive success than females who abandoned their first infant (Schino & Troisi, 2005). It remains unclear whether infant abandonment is more frequent in captivity than in wild populations of Japanese macaques, or it is simply more easily detected under captive conditions.

As a possible consequence of relatively frequent infant abandonment, a few cases of infant adoption have been observed over the years (Fuccillo *et al.*, 1983). Moreover, infant kidnapping has been observed in a female who had recently lost

her own infant and was dominant over the mother of the kidnapped infant (Schino *et al.*, 1993a). Adoption and kidnapping mainly involved gentle behaviours by the adoptive mother and successful infant weaning (Fuccillo *et al.*, 1983). Adoption may be due to a "reproductive error": females who are physiologically ready to lactate, whether they already have one lactating infant or they have recently lost one, are more likely to adopt another infant by mistake. An alternative view considers adoption as the by-product of an innate tendency of females to act in a gentle and affiliative way towards infants (Schino *et al.*, 1993a) regardless of their kin relationship with them (the "cute hypothesis"; Hrdy, 1999). Japanese macaque females often attempt to interact with infants both in captivity and in the wild (Majolo, pers. obs.) and adoption has also been observed in free-ranging Japanese macaques (Ogawa, 1998). Infant handling and allo-maternal behaviour is more frequently observed in juvenile nulliparous females (Schino *et al.*, 2003a) and it may potentially help inexperienced females learn the appropriate maternal skills.

Grooming distribution, aggression and competition

Grooming has an important hygienic function for primates, as it helps reduce parasite load, but it is also the main behaviour used to establish and maintain amicable social relationships (see Figure 2). Research on grooming interactions in Japanese macaques has mainly focused on females rather than on males both at the Rome Zoo and at other field sites (e.g. Nakamichi & Shizawa, 2003). This is because females of this species form long-lasting social relationships with their female group mates (with whom they live for their whole life) and indeed spend a considerable amount of time exchanging grooming. Conversely, male macaques often transfer to other groups during their lifetime and thus lack the possibility to establish long-term relationships. They generally maintain competitive relationships with one another for access to fertile females and rarely exchange grooming (although this may not be true for every population; Majolo *et al.*, 2005).

Troisi and colleagues (1982b) found that the amount of time allocated to grooming was not affected by climatic variables (i.e. ambient temperature and relative humidity) in the Japanese

macaques of the Rome zoo while this was true for the long-tailed macaque (*Macaca fascicularis*; Troisi & Schino, 1986). They speculated that the adaptation of the Japanese macaque to the temperate/cold climate of Japan (where temperature may vary significantly during the day or the year) required grooming to become independent from climatic factors, given its important hygienic and social function. Long-tailed macaques retained the effect of climatic factors on grooming as they are adapted to a tropical habitat where temperature and humidity are relatively stable. Recently, the independence of grooming from climatic factors has been confirmed in wild Japanese macaques (Ventura *et al.*, 2005). The mating season, however, has a negative effect on social relationships and grooming exchange among females as a possible consequence of the increased inter-sexual grooming during consortships (D'Amato *et al.*, 1982). Again, data on wild macaques support this picture (Majolo & Koyama, in press).

In the Rome colony, females tend to significantly bias their grooming towards close kin and/or high-ranking monkeys (Schino *et al.*, 2003b) as it has been observed in other studies in captivity or in the wild (e.g. Nakamichi & Shizawa, 2003). This bias seems to be due to the benefits of grooming close relatives and/or high-ranking females (who may represent better allies or provide tolerance over valuable resources; Ventura *et al.*, submitted; Schino *et al.*, submitted). Inter-individual preferences do not seem to be a consequence of a transmission of rules of grooming preferences over generations through social learning (Schino *et al.*, 2004).

Various models attempted to predict the pattern of grooming interactions among group members (for one of the most influential models see: Seyfarth, 1977). Very controversial is the hypothesis that grooming may be exchanged for other benefits, be them tolerance over food or agonistic support (Henzi & Barrett, 1999). Conclusive data on a cause-effect relationship between grooming and such benefits are still lacking so that some authors consider reciprocation the main benefits of giving grooming (because of its hygienic and stress-releasing function, see below). A female, however, has more chances to be tolerated while interacting with an infant if she has

previously groomed the mother's infant than if she has not (Henzi & Barrett, 2002). Moreover, the fact that female macaques prefer giving grooming to partners ranking higher than themselves is an indirect evidence that grooming may be exchanged for other rank-related benefits (Schino, 2001). The recent biological market theory compares social groups where animals exchange grooming and other social interactions to markets where individuals trade various goods (Noë & Hammerstein, 1995). It predicts that group members will exchange similar amount of grooming when no other goods are available (e.g. when food is abundant for every group member), or if grooming partners belongs to the same class of traders (i.e. they have similar rank and resource holding potential). Grooming will thus be mostly exchanged for itself and reciprocated. When key resources are limited and their access is rank-related, the degree of grooming reciprocation will decrease with the increasing rank distance between grooming partners. Low-ranking animals will give more non-reciprocated grooming to high-ranking partners than vice-versa, in an attempt to "buy" access to those resources. These predictions have been confirmed for wild baboons (Barrett *et al.*, 1999) using data on immediately reciprocated grooming interactions. The reasoning behind this methodological approach is that traders should exchange goods on an immediate or short-term basis to avoid cheating, particularly if animals are unable to remember past interactions with group members and modify their grooming interactions accordingly. Data on the Japanese macaques in Rome, however, show that grooming is highly reciprocated, in accordance with the predictions of the biological market theory, when total grooming exchanged per dyad is analysed but not when single grooming interactions are analysed (Schino *et al.*, 2003b). This result, although not conclusive, suggests that monkeys may remember past-interaction and are able to match total grooming exchanged over a relatively long period of time although single grooming episodes may not be immediately reciprocated.

Research on the Japanese macaque colony has indeed shown that this species is capable of relatively complex social interactions. First, redirection (defined as the aggressive behaviour that one animal, previously involved in a conflict,

direct towards an animal not involved in that conflict) is relatively frequent in the Japanese macaque (Scucchi *et al.*, 1988). Interestingly, monkeys significantly prefer close kin of their former opponents as victims of their redirected aggression (Aureli *et al.*, 1992). Redirection may function as a form of “revenge” against the former opponent and/or to reduce the chances that it will act aggressively in the future (as redirection may result in an attack to the opponent’s close kin). Second, the recruitment behaviour (i.e. an attempt made by one monkey to obtain agonistic support from another) during conflicts was analysed to assess the criteria macaques used to select potential supporters. Both mature and immature macaques preferentially directed their recruitment attempts to individuals ranking higher than, and/or that were not closely related to, their opponent (Schino *et al.*, in press). Moreover, macaques are able to combine the two criteria, giving more importance to the kin relationship between the recruited monkey and the former opponent than to their relative rank. These findings indicate that Japanese macaques can recognize third-party rank and kin relationships, and have some sort of “understanding” of the social network linking group members. This capacity is not exclusive of primate species (e.g. Paz-y-Miño *et al.*, 2004), although the extent to which it is due to complex cognitive abilities or to some simple form of associative learning is far from being understood. Grooming is also related to another key aspect of primate social behaviour: conflict management. De Waal and van Roosmalen (1979) were the first to demonstrate that reconciliation is the main post-conflict means that primates use to manage conflicts. Reconciliation has been observed in many primates and, when studied, in a few non-primate social species (e.g. dolphins and goats; see Aureli & de Waal, 2000 for a review). Reconciliation is defined as the “post-conflict friendly reunion of former opponents that restores their social relationship disturbed by the conflict” (Aureli & de Waal, 2000: p. 387). Primates thus use grooming to establish amicable relationships (that may potentially give them some benefits; see above) and reconciliation function to re-establish the tenure of such relationships when a conflict is unavoidable. A study on the Rome colony (Schino

et al., 1998) analysed intra-group variations in conciliatory tendency, and identified a number of factors underlying such variation. Of paramount importance were kinship and relationship quality: monkeys reconciled preferentially with their kin and with group mates with whom they had more friendly relationships. Other studies conducted in captivity, in provisioned groups and in the wild support these findings, although with different strength (Aureli *et al.*, 1997; Kutsukake & Castles 2001; Majolo, 2004).

Grooming and reconciliation also have a calming effect as monkeys show a significant decrement in stress-related behaviour during or immediately after a grooming interaction or a reconciled conflict (Schino *et al.*, 1988; Aureli *et al.*, 1997). Various studies have shown that scratching, self-grooming, body-shake and yawning are all behaviours affected by the emotional state of a monkey and thus valid behavioural indicators of anxiety (Maestriperi *et al.*, 1992). For example, monkeys show a significant increase in scratching rate during periods of social instability (e.g. when a conflict is not reconciled and/or when the risk of aggression is high; Schino *et al.*, 1988; Maestriperi *et al.*, 1992). The same happens to mothers when their infant is handed by non-kin/dominant females who may potentially harm it (Maestriperi 1993). These results have been supported by studies providing behavioural, physiological and pharmacological data on various primate species (Johnson *et al.*, 1996; Schino *et al.*, 1996; Kutsukake & Castles 2001).

Demography and life histories

In comparison to the previous two topics, a lower number of studies have been conducted on the life history variables of the Japanese macaques in Rome. This is partly due to the longer time necessary to collect sufficient data in comparison to behavioural studies. Various studies have been conducted to analyse which factors affect birth timing. Scucchi (1984) found that lactation determines post-partum menstrual cycle but not inter-birth spacing, if one excludes from the analysis females who had a late birth during the previous birth season (Scucchi *et al.*, 1983). These results partly contrast with what is found in wild populations, where there is a direct effect of

lactation in inter-birth spacing (Takahata, 1980), and are probably due to the fact that captive macaques rely on a higher nutritional and health standard than in the wild. In the Rome colony, seasonal birth timing is not affected by age of the females, their social status, temperature and humidity during the previous mating season, and group size (Cozzolino & Schino, 1998). However, operational sex ratio (the ratio between fertile males and females in a group) influenced seasonal birth timing. Cozzolino and Schino hypothesised that when operational sex ratio is high, competition among males for fertile females may increase the disruption of consortships and delay the birth season.

One of the most debated topics in behavioural ecology is whether females are able to bias the sex ratio of their offspring according to demographic and social factors. Trivers and Willard (1973) hypothesised that, in species with polygynous mating systems, if mothers in good conditions (e.g., high-ranking) produce offspring in above average condition then they should invest preferentially in male offspring as they will have a higher reproductive success than females (because they may potentially mate with several females in a short period of time) Aureli *et al.* (1990) and Schino *et al.* (1999) added to the conflicting primatological literature by showing that the Japanese macaques of Rome conformed to Trivers and Willard's predictions. Later reviews have partially clarified the reasons underlying the heterogeneity of the literature on primate sex allocation (Brown & Silk 2002; Schino 2004).

Animal behaviour research in zoos

Captive studies and field work: to what extent does captivity affect behaviour?

As far as we are aware, the colony of Japanese macaques in Rome is one of the best (in terms of amount of data collected) and longest studied group of primates in a zoo environment. Comparable amounts of data and a similar or longer length of study have been obtained by few other zoos or research centres. To cite just a few examples, in the Netherlands, the chimpanzees colony of Arnhem Zoo has been studied for several years and has been the source of many publications

(e.g. de Waal, 1998). In France, the Centre d'Ethologie des Primates (Strasbourg) houses various primate species and run various researches on social behaviour. In the U.S.A. the Japanese macaques have been studied in two research centres in Oregon and Texas. Moreover, a large colony of rhesus macaques (*Macaca mulatta*) has been established around 70 years ago on the island of Cayo Santiago, off Puerto Rico, and studied since then.

Field primatologists and researchers working on captive animals are sometimes pictured as in contrast. Field primatologists may be thought of as viewing their findings as more reliable because they come from animals in "natural" conditions. Students working with captive animals may be thought seeing field work as largely inaccurate (due to the often adverse field conditions) and considering zoo- or lab-based research as more reliable because the effect of confounding variables may be artificially controlled (particularly in the lab). Contemporary primatology, however, emphasizes how the integration of data from wild and captive primates greatly improves our understanding of the behaviour and evolution of our closest relatives.

Field work is essential, even when adverse conditions make it a bit inaccurate, for a complete understanding of the behavioural ecology of a species. For example, dispersal and ranging patterns, the effect of food abundance on group size and social relationships, and population dynamics are all aspects that may only be addressed in wild populations. It is however important to remember that both human overpopulation and the consequent habitat destruction may affect the quality of data collected in the wild. For example, the disappearance or rarity of some predators of primates (e.g. tigers) affects the capacity of field studies to properly analyse the importance of predation risk on social behaviour and ranging patterns. Moreover, the fact that primates (and many other species) often live in small populations confined to separate areas makes the study of dispersal patterns difficult to be fully addressed (Cowlshaw & Dunbar, 2000). Given the rapid loss of species and wilderness, it is time to question to what extent field studies are indeed analysing "natural" patterns of behaviour.

In captivity, the occurrence of unpredictable and undesired events that may alter the results of a study (e.g. the immigration of a new male causing a period of social instability in the study group) is limited if not impossible. Furthermore, accessibility and easy visibility make the collection of large amounts of data much easier in captivity than in the wild (compare for example the data on alliance formation in Japanese macaques collected in the Rome Zoo and in the wild by Schino *et al.* (submitted) and Ventura *et al.* (submitted)). Finally, captivity offers the possibility to run invasive experiments (e.g. injecting animals with drugs) and to control for the effects of various variables to an extent that is often impossible in the wild. In this regard, laboratories rank higher than zoos where (ideally) the welfare of the animals represents a priority. Zoo animals, however, are more frequently housed in "natural" groupings that provide more valid data on their social behaviour. Consider, for example, the case of common marmosets who are usually housed in family groups in zoos (their most common grouping pattern in the wild) but are often housed in same-sex pairs in the lab to control breeding (as this species usually produces two sets of twins per year).

In support of an integration of captive and field research is the fact that when the findings of studies conducted in the wild and in captivity are compared, it turns out that they more often disagree quantitatively rather than qualitatively. To make a simple example, the weaning process occurs more quickly in captive Japanese macaques than in the wild (see above). However, the gradual development in the mother-infant relationship that this process implies (from continuous contact during the first days of the infant's life to the complete nutritional and social independence) is maintained (Tanaka, 1989; Schino *et al.*, 1993b). An additional aspect to consider is that even an abnormal behaviour displayed as a consequence of captivity may provide useful insights on the function of more natural behaviour (e.g. Harlow *et al.*, 1963).

Three key aspects have to be controlled for to make sure that zoo research provides valid data (see for a more detailed discussion: Kleiman *et al.*, 1996). First, animals have to be housed in breeding groupings that resemble in size and

composition those of wild conspecifics. Second, enclosures have to be of sufficient size and designed to stimulate "natural" behaviour (e.g. by providing trees and branches for species living in the forest canopy). Third, zoo visitors have not to influence the behaviour of the animals. If this happens, data should be collected in off-exhibit enclosures and/or when visitors are absent.

In conclusion, we consider research in captivity and in the wild as complementary rather than in opposition, each of them having its benefits and drawbacks (e.g. Kummer, 1984). The decision on whether to run a field- or a zoo-based study should depend on the research question one wants to address and on various logistic factors (e.g. funding or time available for the study).

The importance of long-term studies

Long-term studies are essential to fully understand the degree of flexibility that a species, a population or a single animal has in adapting its behaviour to variable ecological and/or social conditions. Moss (1988), for example, conducted her first study on elephants in Tanzania during a 6 years draught period. She found that elephants live in families, composed of various females and juveniles, which rarely interact with other families. It was only when a long period of rain arrived and food became abundant that she observed elephants forming large aggregations composed of several families and differing in size and composition. She then comprehended that elephants remain separated in families when food is scarce (as a way of reducing food competition) but may aggregate and interact with many other families when food is abundant. The complex social structure of African elephants would thus have not been clarified with a short-term study.

Studies focusing on life history patterns can only be conducted when long-term data are available. This is particularly true for species with a long life span. In order to understand the relation between age and reproductive success, for example, females have to be studied ideally for their whole period of reproductive activity. This may last more than 20 years in macaques. The same happens when the research focus is on how social tactics varies with age: male sub-adult macaques may postpone direct agonistic interactions with fully

adult males until they reach adulthood and the associated benefits for fighting abilities (i.e. full body size and canine length). Long-term studies are also required when data on various generations are necessary or to analyse relatively rare events. This is the case, for example, of the study on inter-generational transmission of social preferences conducted on the Rome colony (Schino *et al.*, 2004). Also, Cozzolino and Schino (1998) were only able to effectively analyse the factors affecting birth timing after 18 years of data collection, when sufficient births had been observed. The same example applies to other relatively rare events, such as maternal abandonment or infant abuse (Schino & Troisi, 2005). Here, zoo research has the advantage that long-term or intensive observations are often easier to be conducted than in the wild: animals do not transfer and groups do not move to an inaccessible new home range while you are fighting with statistics at home.

What relationship exists between animal behaviour research and the management of zoo animals?

In 1993, the Consortium of Aquariums, Universities and Zoos conducted a survey on the research conducted in 120 zoos from different countries (Hardy, 1996). The survey gave the following results: 72% of zoos were conducting behavioural research; mammals were the most studied among the animal Classes and primate studies accounted for almost 44% of total research on mammal species. These data indicate that primate studies represent a significant proportion of the research activity in zoos. This brings us to the consequent question: to what extent does behavioural research interfere with, or improve the management of primate species in zoos? We believe behavioural research rarely interfere with colony management. Behavioural research in zoos mainly consists of observational studies where the student must avoid affecting the behaviour of his/her study animals and thus he/she does not interfere with daily management routine. Even when studies involve some experimental manipulation, such as providing the animals with enrichment devices or tasks to solve, this gives very few problems to zoo keepers (for example, they have to remove the enrichment device once the experiment is over).

Conversely, research may be extremely useful for the proper management of captive primates.

Studies on social organisation and dispersal patterns, in captivity and/or in the wild, help zoos house a species in the most stable social group (see example above) and to set criteria for the transfer of animals. As regards the Japanese macaque, for example, the fact that females are organised into closely-bonded matriline and that males are the dispersing sex tell us that housing this species in groups of related females increases social stability and decrease the probability of injurious fighting. It also tell us that any transfer of animals is most successful when it involves a whole matriline or juveniles/sub-adult males (as this resembles what happens in the wild and as transferring young males receive less aggression from dominant males than adults). The benefits of research for colony management are particularly evident if one considers the findings of the studies conducted on behavioural indicators of stress (including studies on the Japanese macaques of Rome). The fact that scratching and other behaviours may reliably indicate the emotional state of an animal (Maestriperi *et al* 1992; Troisi, 2002) is extremely useful as it allows us to measure the animal response to stressful events (e.g. change of enclosure, excessive presence of visitors, or transfer into a new group) in a non-invasive, relatively quick and easy way. Before such studies were conducted, the only way to assess the emotional condition of an animal was through blood samples (whose collection is stressful in itself) or urine samples (which require a long training of the animals).

Inter-disciplinary implications of primate behaviour studies

Primateology is an unusual research field: students have different backgrounds (mainly anthropology, psychology, or zoology, depending on the country of origin) but still would define themselves as primatologists. Primate behaviour research is often published or presented in primate-devoted journals and meetings so that contacts between primatologists and students of other animal species are sometimes difficult to be maintained. This low level of mutual interaction and exchange of ideas may be partly related to our still anthropocentric view of science. Primates are sometimes considered (both by primatologists and

by non-primatologists) as too complex and close to humans to be compared to non-primate species. Some psychologists, conversely, view primate species as lacking the most important characteristics of the human mind (e.g. a theory of mind or language) and thus as “non-adequate” study subjects. A good example of the need of more exchange of ideas between apparently unrelated disciplines is the importance of kinship for social relationships. Primate behaviour research has clearly demonstrated (particularly in macaques) that kin relationships between group members represent the basic unit of social groups. A troop of macaques, for example, is composed of various females having different genetic relationships with one another. Each female interacts longer and in a more amicable way with its close kin, particularly with its offspring and mother, less with distantly related females, and rarely or never with unrelated females. In other words, by knowing kin relationships among females one may predict the type of social relationships between dyads, the formation of sub-units (i.e. matriline) within the group, and thus the average level of social cohesion of the group. This analytical and somehow “hierarchical” approach is very similar to what ethnologists refer to as structuralism and use to describe traditional human societies (Levi-Strauss, 1963). Following this approach, human societies may be subdivided in basic structures (the most important one being the mother-infant dyad) whose analysis helps us understand various aspects of the society, such as patterns of cultural transmission and type and quality of social bonds. Clearly, both ethnology and primatology would benefit from an integration of data and conceptual approaches from these two disciplines. In light of these considerations, in this final section we aim to discuss the inter-disciplinary implications of primate behaviour research to help bridge the gap between primatology and related fields. Primate behaviour research has important implications for many different areas. To exemplify this, we briefly discuss the importance of research on primates for psychiatry and for studies on human parental behaviour. In the rest of this section, however, we particularly focus on the hypotheses proposed for the evolution of brain size and cognitive abilities for their implications for anthropology and psychology.

Recently, a book has been published with the clear aim of using data available on macaques as a model to understand the evolution of social behaviour in mammals (Thierry *et al.*, 2004). The genus *Macaca* is an ideal taxon for such a task given that macaques live under highly variable ecological conditions. They may thus help us determine how habitat characteristics affect behaviour. Although we are far from having sufficient data on macaques to fully address this question, research on this taxon has provided valuable comparative data for other species and/or for other research fields. This may be exemplified by briefly focusing on three research topics that have been extensively analysed in the Japanese macaques of Rome (and in other non-human primates in various research centres as well). First, the importance of physical contact and of an appropriate mother-infant relationship for the behavioural development of infant macaques, determined by observational and experimental studies (Harlow *et al.*, 1963; Troisi *et al.*, 1989; Schino *et al.*, 1995) has also been demonstrated for other species and particularly for humans (e.g. Bowlby, 1971). Second, research conducted mainly on macaques suggests that non-human primates may represent a good model for human child abuse and emotional disorders (Troisi & D’Amato, 1983; Maestripieri, 2005). This is important in consideration of the difficulties to run such studies on human beings. Third, since reconciliation has been described in chimpanzees and various macaques (Aureli & de Waal, 2000) a great effort has been made to determine its occurrence in other species. Reconciliation has been described in both humans and in various non-primate species (e.g. Schino, 1998; Ljungberg *et al.*, 1999). Interestingly, the occurrence of reconciliation cannot be simply explained by considering phylogenetic relationships, habitat characteristics or cognitive abilities. Rather, reconciliation is observed in those species where group members maintain stable amicable relationships that may be disrupted by aggression and competition. This is a good example of how comparative data are essential to understand the main factors that led to the evolution of a particular character or behaviour. From its distribution and from its relative independence from phylogenetic relationships, we may hypothesise that long-term

social relationships among group members are a prerequisite factor for the evolution of reconciliation.

The former examples highlight two ways in which the study of nonhuman primates can help us understand human behaviour and evolution: the use of models and the abstraction of principles (Hinde 1982, 1986). Models are simplified versions of an object of scientific enquiry that, by virtue of their simplicity or easiness of manipulation, help understand the mechanisms underlying the biological process under investigation. The study and experimental manipulation of mother-infant relationships in monkeys has been instrumental in the development of attachment theory and in our understanding of both normal and pathological human development (e.g. Bowlby, 1971). Principles can be abstracted by careful comparative analyses. For example, comparing milk composition and nursing patterns in a variety of mammalian species, it can be noted that species having the highest milk fat content tend to nurse their infants less frequently. This principle can be applied to humans to derive expected nursing patterns. On the basis of the low fat content of human milk, it can be assumed that human babies are adapted to a rather continuous access to the mother's breast (Blurton-Jones 1972).

The possibility to abstract principles useful for illuminating human behaviour and evolution requires an understanding of the ecological and social context in which a particular behavioural/psychological trait evolved (e.g. Crawford, 1998; Daly & Wilson, 1999). Thus, extant species are one of the best research "tools" we possess to study the relationship between ecology, social behaviour and evolution in primates. For example, the genus *Papio* represents a good model for analysing the importance of the ecological context on the evolution of the first hominids, as *Papio* and *Homo* both appeared when climatic changes led to the emergence of the African savannah (Henzi & Barrett, 2005).

As another example of how the abstraction of principles derived from the study of nonhuman primates can help us understand human evolution, we may look at what is probably the most notable aspect of human evolution: the extraordinary increase in brain size. Several theories have been proposed to explain the functional

significance (i. e. the selective value) of increased brain size (e.g. Jerison, 1973). For example, some theorists proposed that the increase of the ratio brain size / body size (which is thought to be associated to an increase of cognitive abilities) during the course of primate evolution was related to the need to solve ecological problems (e.g. foraging on food requiring extractive skills) and/or to support cooperative hunting and tool use (Jerison, 1973). As an alternative, Byrne and Whiten (1988) proposed the so called social brain hypothesis stating that the necessity to survive in a complex social environment was at the root of the neocortex increase in primates. To test this hypothesis a series of analyses were run using modern statistical methods that control for phylogenetic effects. In these analyses, brain size (or, more correctly, neocortex size controlled for body size) was the dependent variable while the predictor variables were group size, diet and foraging behaviour. Group size was found to be the best predictor of neocortex size in primates. Later analyses extended this relationship to other taxa such as carnivores and insectivores (Barton, 1996; Dunbar, 1995, 2003; Dunbar and Beaver, 1998).

According to Dunbar (2003), the social brain hypothesis assumes the following evolutionary pathway: group living evolved in ancestral primates as a means to reduce predation risk. With the emergence of the African savannah, some primate species began to spend increasing and significant proportions of their time on the ground and in open habitats. For these species, the benefits of living in larger groups (i.e. improved predator detection and mobbing) were greater than for arboreal/forest species. This is because predators of primates are mainly terrestrial animals, at least for Old World monkeys. Larger groups, in turn, represented more complex social environments where a good coordination of movements and activities among the various group members is essential to maintain coherent social units. Group-living also represented an opportunity for additional benefits, some of them being mainly obtained through the formation of social bonds with other group members (see above). Under this condition, larger neocortices, and the increased cognitive capacity that this involved, were "necessary" for each group member to maintain stable and long-

lasting amicable relationships, to recognise each group companion, to memorise past interactions with the other animals or among third individuals, and to integrate the various individuals into its mental social world (Dunbar, 2003).

The social brain hypothesis is particularly useful for its implications on human social evolution. Dunbar (2003) applied the equation obtained from the regression analysis between group size and neocortex ratio in living primates to derive expected group size in modern humans (using available data on neocortex ratio). It turned out that the maximum number of people with whom we may form a cohesive group, according to this analytical approach, is approximately 150 individuals. Interestingly, this figure is in between the two social units of traditional human societies: the overnight camps of foraging people (usually formed by 30-40 people) and the tribal units (i.e. 1500-2000 people). Moreover, the conclusion that this figure (i.e. 150 individuals) roughly represents the maximum number of personal relationships we are able to maintain (as opposed to impersonal or formal relationships) is supported by studies that have analysed the size of human conversational networks or the number of friendly relationships that each person may maintain (e.g. Hill & Dunbar, 2003).

Finally, the principles derived from the social brain hypothesis and the modelling approach used by Dunbar (2003) were applied in an attempt to indirectly analyse group size of extinct hominoids and to formulate hypotheses about the emergence of language (Aiello & Dunbar, 1993; Dunbar, 1993). Given the relationship between brain size and group size, data on brain size of extinct hominoids suggests that the progressive increase in human group size began around one million years ago. It was this increase in group size that clearly distinguished the grouping patterns of early humans from those of apes, although we still cannot definitely say whether such increase was the cause or the effect of the neocortex enlargement. We may hypothesise that individuals living in larger groups not only required sufficient cognitive abilities to cope with this complex social environment but also a more effective means to maintain social bonds and to exchange information (about, for example, the

location of food) with the other group companions (Dunbar, 2003). Indeed, the larger the group, the greater the amount of time that group members have to devote to foraging activities (as food depletion rate for a given area increases proportionately with group size). Nonhuman primates use grooming as the main social tool to maintain social bonds, and increase the time allocated to grooming as group size increases (Dunbar 1991). According to Dunbar (2003), during human evolution the increase in group size reached a point where a conflict occurred between the need to increase foraging time and that to increase grooming time to service social relationships. This conflict in the allocation of time to social versus foraging activities was solved by evolving a more efficient way of communicating and maintaining social bonds: language. Morphological changes in the larynx allowed hominids to produce complex sounds that (once "supported" by a sufficiently large neocortex) eventually evolved into a proper language. Language is much more effective than grooming in maintaining group cohesion and amicable social relationships, and for information exchange, for four main reasons (Dunbar, 2003). First, it gives the possibility to interact with many more than one individual at the same time. Second, individuals may speak while being engaged in something else (e.g. foraging) whereas grooming is a basically exclusive activity. Third, language does not require close proximity between two individuals and thus allows a more effective group cohesion and coordination of movements. Fourth, and related to the previous point, language allows us to obtain information about events that happened during our absence and it may convey detailed information, for example, on the exact location of food. Thus, the application of principles derived from the comparative study of nonhuman primates allowed the formulation and initial testing of new hypotheses about the evolution of increased brain size and of language, that is, two of the most prominent characteristics of modern humans.

In conclusion, in this paper we have attempted to present the major findings of our research on the Japanese macaques of Rome in light of what is currently known about primate behaviour and evolution. Primate studies may

greatly benefit from different methodological approaches and a mutual exchange of ideas between zoologists, ecologists, anthropologists, psychiatrists and psychologists.

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Info on the Web

<http://www.asab.org>

web page of the Association for the Study of Animal Behaviour containing details of conferences and a list of jobs.

<http://www.animalbehavior.org>

web page of the Animal Behavior Society containing a list of jobs in animal behaviour, mainly in the U.S.A.

<http://pin.primate.wisc.edu>

web page maintained by the National Primate Research Center, (University of Wisconsin, U.S.A.) and probably the most comprehensive web site for primatology. Among many other things, here you can find a list of jobs in primatology (primate jobs), the contact details of primatologists all over the world (international directory of primatology), the web page of the International Society of Primatologists, and you may consult Primate Lit, an excellent bibliographical database for primatology.

<http://www.waza.org>

web page of the World Association of Zoos and Aquariums.

<http://www.bioparco.it>

here you can find the full list of research projects currently conducted at the Bioparco.

<http://www.biaza.org.uk>

web page of the British and Irish Association of

Zoos and Aquariums. Here you can download the guidelines for behavioural research in zoos, and for monitoring stress in, and the effect of visitors on, zoo animals.

<http://www.leakeyfoundation.org>

web page of the Leakey Foundation, one of the main funding agencies for anthropological research with a tradition of supporting studies on both human and nonhuman primates.

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