The Socioecology of Infant Handling in Primates: Is the Current Model Convincing?

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ABSTRACT. A strong interest shown by females towards infants other than their own is one of the most consistent behavioral traits found in primates, including humans. Species differences exist, however, in the extent mothers allow other group members to interact with their offspring. Socioecological theory predicts that in species characterized by relaxed, egalitarian dominance relations mothers should allow extensive interactions between their infants and other individuals from the first weeks of life, while in species characterized by nepotistic and despotic dominance relations maternal tolerance of infant handling should be low. While this model received some support from a comparison between colobines and some cercopithecines, several other species, including the Barbary macaque, do not appear to fit easily into the framework. In fact, only about half of all well-studied species follow the predicted pattern, suggesting that other factors, associated with the costs and benefits of the behavior, must be invoked to explain the variation in mothering styles and infant handling found in primates.

Key Words: Infant handling; Socioecology; Dominance style; Barbary macaques; Primates.

INTRODUCTION

Infant handling, i.e. usually affiliative interactions between infants and individuals other than the mother (previously termed "aunting," ROWELL et al., 1964, or "alloparental care," WILSON, 1975), is extremely widespread in gregariously living primates. It occurs in lemurs, New World monkeys, Old World monkeys, and hominoids (see HRDY, 1976; MCKENNA, 1987; NICOLSON, 1987 for reviews). Although highly variable in its expression and frequency, two features appear to be fairly general. First, with the exception of a few taxa (especially the callithrichids and some small-bodied cebids) females appear to be much more interested in other females' infants than males (e.g. EDWARDS, 1993; HIGLEY & SUOMI, 1986; MAESTRIPIERI, 1994a). In fact, males of some species appear to avoid young infants (SIMONDS, 1974). Second, young infants are usually much more attractive than older ones (HIGLEY & SUOMI, 1986). The biological significance of the behavior appears to be less clear. No less than 14 different (but not entirely mutually exclusive) hypotheses have been advanced to explain the evolution and function of infant handling (MAESTRIPIERI, 1994a).

Obviously, any functional explanation for the evolution and maintenance of the phenomenon must take into account the evolved interests of all three individuals involved in infant handling episodes: the infant, the handler, and the infant's mother (VOGEL, 1984). Evidence supporting the view that the infants themselves benefit from being handled is limited, while the potential costs may be high. Kidnappings with a fatal result (the death of the infant) have been observed in several species (HRDY, 1976; MAESTRIPIERI, 1994a). Handlers may benefit either indirectly from such events via reduced fitness of other, unrelated females (SILK, 1980; WASSER & BARASH, 1981), or directly, via increased maternal competence (the "learning-to-mother" hypothesis: LANCASTER, 1971). Handlers may also benefit, however, if their behavior is benefi-

cial for the infants or their mothers, either through reciprocation (HRDY, 1976; STANFORD, 1992) or because infant handling reduces the costs of reproduction of related females, or, if the handler is a male, potential mates (HRDY, 1976; GARBER & LEIGH, 1997; MITANI & WATTS, 1997; ROSS & MACLARNON, 1995). There is little doubt that, for mothers, the main benefit lies in reduced costs of reproduction (MITANI & WATTS, 1997; ROSS & MACLARNON, 1995), but there is also little doubt that due to the risk of fatal abuse the potential costs are high.

While it appears that females from most or probably all primate species are strongly motivated to touch and to carry infants of other females, species differences in the degree of maternal permissiveness and, as a result, differences in the frequency of infant handling suggest that the cost-benefit ratio of these interactions for mothers may be quite different (HRDY, 1976). The reasons for these differences appear to lie in species-typical life history characteristics such as postnatal infant growth rates affecting the costs of reproduction (MITANI & WATTS, 1997; ROSS & MACLARNON, 1995), as well as in the feeding ecology affecting the competitive style of female primates (MAESTRIPIERI, 1994a).

THE SOCIOECOLOGY OF INFANT HANDLING

Building on the socioecological framework explaining social relationships amongst female primates of VAN SCHAIK (1989), MAESTRIPIERI (1994a) argued that mothering styles and patterns of infant handling should be ultimately related to species differences in feeding ecology which, in turn, cause differences in competitive regimes regulating female social relationships. Specifically, he predicted that "infant handling by adult females may be expected to involve a higher proportion of abusive interactions in species characterized by strong contest competition for food" (MAESTRIPIERI, 1994a, p. 542). Strong within-group contest competition (WGC) usually leads to the formation of highly asymmetrical (despotic) dominance relations and stable, linear and nepotistic hierarchies (VAN SCHAIK, 1989; STERCK et al., 1997). Due to the risk of infant abuse and the problems low-ranking mothers have to retrieve their offspring from higher-ranking conspecifics, MAESTRIPIERI (1994a) suggested that maternal tolerance of infant handling in such systems should be low. Conversely, species characterized by weak WGC and relaxed, egalitarian relationships are expected to tolerate other females' attempts to handle their infants since the risk of infant abuse is low and mothers have ample opportunity to retrieve their offspring. Although not explicitly considered by MAESTRIPIERI (1994a), a similar pattern should be expected in species characterized by strong WGC and strong between-group contest competition (BGC). Strong WGC still favours nepotistic hierarchies, but strong BGC enforces tolerant relationships, because dominant individuals need the help of subordinates (VAN SCHAIK, 1989; STERCK et al., 1997). Consequently, maternal tolerance of infant handling should be high in these species, too, and allow high rates of infant handling. The idea that mothering styles and patterns and frequency of infant handling may be related to status differences which are governed by species differences in feeding ecology, is not entirely new. As early as 1964 ROWELL and co-workers suggested that the "frequency of aunt-infant interaction is .. related to the .. status of the aunt" (ROWELL et al., 1964, p. 226). HRDY (1976) speculated that "if it turns out that female dominance hierarchies are as 'relatively unstable and poorly defined' among other Colobinae as JAY (1965, p. 233) found them to be among the langurs she studied, then several of the disadvantages of early (infant) sharing suggested in the case of rhesus macaques cease to apply, possibly predisposing members of this subfamily to the evolution of early aunting. Needless to say," she added, "this suggestion, if true, would lead to a host of questions" (HRDY, 1976, p. 137). MCKENNA (1979) proposed that differences in the feeding ecology between

colobines and cercopithecines may be ultimately responsible for differences in maternal permissiveness and, hence, for the amount of infant handling found in these two subfamilies. He argued that "food competition is much greater among and within groups of cercopithecines than it is within colobine groups." The digestive system of the folivorous colobines "had the effect of reducing the importance of dominance among females. This characteristic increased the chances that full infant transfer without the negative consequences experienced by cercopithecine females could be elaborated and successfully evolve" (MCKENNA, 1979, p. 274). Thus, in MCKENNA's view, the kind of treatment a primate infant receives is ultimately linked to "its species' stomach" (MCKENNA, 1987, p. 153). Similarly, MAESTRIPIERI's (1994a) analysis relied heavily on the differences in feeding ecology and social structure between colobines and cercopithecines. Indeed, the tolerance and permissiveness of female colobines who allow other females to handle their infants even shortly after birth for prolonged periods of time appears to be completely compatible with their egalitarian, individualistic dominance style. By contrast, the reluctance of the more frugivorous cercopithecine females to surrender their infants to other group members is easily explained by higher levels of WGC leading to more despotic and nepotistic rank relations. However, not all species appear to fit so neatly into the proposed framework. Barbary macaques, a species characterized by high frequencies of infant handling, may be one example.

THE BARBARY MACAQUE PUZZLE

Barbary macaques are both geographically and phylogenetically well separated from the other members of their genus (DELSON, 1980; MORALES & MELNICK, 1998). As their far-eastern relatives, the Japanese macaques, they are found beyond the tropics, with their present range being restricted to the mountaineous regions of Morocco and Algeria that experience harsh winters. Like other macaques, they live in multimale-multifemale groups which are characterized by male dispersal and female philopatry (PAUL & KUESTER, 1985, 1988; MÉNARD & VALLET, 1993). Although male dispersal occurs at lower rates than, for example, in rhesus monkeys, repeated suggestions that Barbary macaques are relatively inbred are unsubstantiated (MEHLMAN, 1986; PAUL & KUESTER, 1985; KUESTER et al., 1994). Barbary macaques are probably best known for their peculiar male-infant relations (WHITTEN, 1987), but as LAHIRI and SOUTHWICK stated more than 30 years ago, "all individuals in the social group exhibited the same intense interest in the infant" (LAHIRI & SOUTHWICK, 1966, p. 261). Infant handling in Barbary macaques has been studied by several observers in several different habitats (e.g. BURTON, 1972; LAHIRI & SOUTHWICK, 1966; DEAG, 1974, 1980; TAUB, 1978, 1984; SMALL, 1990). The most extensive data are available from a long-term study on a semifree-ranging population living in a large outdoor enclosure ("Affenberg Salem") in the southwest of Germany (KUESTER & PAUL, 1986; PAUL, 1984; PAUL & KUESTER, 1996; PAUL et al., 1996). Readers interested in full details and methods are referred to these papers, but information relevant here, including some hitherto unpublished results, will be reviewed below.

INFANT HANDLING

Unlike other macaques, Barbary macaque infants are carried by individuals other than the mother, including adult and subadult males, for prolonged periods of time shortly after birth. During their first three months of life, infants spent, on average, nearly 20% of the daytime in close physical contact (being held, groomed, and carried) with others (see Fig. 1 for an example of one cohort of 14 infants born in one year into one social group). On average, infants spent
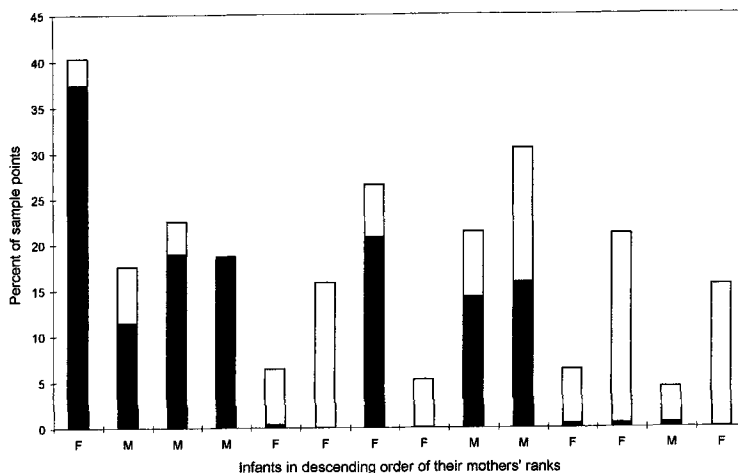
Fig. 1. Percentage of time one cohort of 14 Barbary macaque infants (M: males; F: females) born in one year (1988) into one social group (group C) spent in physical contact with other group members (black bars: males; blank bars: non-mother females) during their first 90 days of life; infants arranged in descending order of their mothers' ranks.

slightly more time with males than with females (9.9 vs 8.1% of the time in this sample), partly because a larger proportion of males than of females was involved with infants (PAUL & KUESTER, unpubl. data). However, while all infants were more or less frequently carried by non-mother females, half of them were ignored by males (see also PAUL et al., 1996; MÉNARD et al., 1992). Although infants which were ignored by males were not consistently carried more often by females, there was a significant negative correlation between time spent with males and time spent with females ($r_s = -0.52$, $n=14$, $p<0.05$, see Fig. 1). This suggests that there is a certain amount of competition over access to infants.

The frequency of infant handling was strongly dependent on the age of the handlers. Juvenile and young subadult males (younger than 5 yr of age) rarely handled infants, while males aged 6 yr and older handled infants more often than expected from their relative representation in the population (PAUL et al., 1996). In contrast, among females, 3- and 4-yr old adolescents were disproportionately involved (PAUL & KUESTER, 1996; see also DEAG, 1974).

As indicated by the observation that many infants were ignored by males, neither males nor females interacted randomly with infants. While adult males strongly preferred infants born to high-ranking females independent of the infants' sex, subadult males invariably preferred male infants − independent of their mothers' rank (KUESTER & PAUL, 1986; PAUL, 1984; PAUL et al., 1996). As a result, it was mainly daughters of low-ranking females who were ignored by males (Fig. 1). In contrast to earlier speculations (e.g. TAUB, 1984), males did not prefer to interact with closely related infants, including their own offspring. Paternity analyses by DNA typing revealed that males handled their own progeny exactly as often as would be expected by chance (PAUL et al., 1992, 1996). Behavioral observations and paternity analyses carried out in a wild population point into the same direction (MÉNARD et al., 1992, 1994). Similarly, special relationships or "friendships" between the males and the infants' mothers were not a prerequisite for the establishment of close male-infant associations (PAUL, 1984; SKAMEL, 1994). Females, on the other hand, showed a strong preference for closely related infants. Nevertheless, infant handling by females was not restricted to related infants. Out of 891 analyzed infant handling

episodes by females, 335 (i.e. nearly 40%) were directed at unrelated infants. In the majority of these cases and the involved dyads, the handler was higher-ranking than the infant's mother (PAUL & KUESTER, 1996).

DEAG (1974, p. 321) suggested that interactions between males (and non-mother females) and infants "closely resembled maternal behaviour." Superficially, this appears to be true. Males and females carry infants, they groom infants, they protect infants, and sometimes they also punish them (aggression toward infants by males and females has been observed as early as during the infants' second month of life: PAUL, unpubl. data). "Allonursing" is rare (cf. PACKER et al., 1992), but at least in one case a non-mother female successfully adopted and reared a kidnapped infant (PAUL & KUESTER, 1996). A closer examination revealed, however, that the behavior of males (and non-mother females) towards infants differs in subtle but important ways from maternal behavior. Analyses of HINDE's contact indices (HINDE & ATKINSON, 1970) over the course of the first two years of life of a small subsample of six infants revealed that, in the mother-offspring dyad, during the infants' first two months the mothers were responsible for maintaining phys-ical contact with their infants. During the infants' third month of life, the index changed from negative to positive values, i.e. the infants became responsible for maintaining physical contact with their mothers (see, e.g. BERMAN, 1980 for similar values in rhesus macaques). In male-infant dyads, the situation was quite different. Here, the indices became positive only during the infants' second year of life, and during their first year they were much lower than in the mother-infant dyads (PAUL, 1984). HINDE's index has not been quantified for non-mother females, but it is not unusual to see males and non-mother females restraining distressed infants. Thus, males and non-mother females are much more restrictive than mothers are. As a consequence, mothers often had difficulties to retrieve their offspring from higher-ranking females and males. Several early infant deaths in this population were attributed to extensive infant handling or "kidnap-ping" by males and females, sometimes even close relatives (PAUL & THOMMEN, 1984; PAUL & KUESTER, 1988, 1996, unpubl. obs.).

While it is beyond the scope of this paper to discuss the functional significance of infant handling in Barbary macaques (see PAUL & KUESTER, 1996; PAUL et al., 1996), one result is worth mentioning here. There was no indication that mothers (or the infants themselves) bene-fited from the infant handling activities of other individuals. In particular, frequent infant handling did not allow mothers to reproduce at a faster rate as it has been observed in captive vervet monkeys (PAUL & KUESTER, 1996; see FAIRBANKS, 1990 for vervet monkeys; ANDERSON, 1992 for free-ranging mountain baboons). In light of the apparent tolerance of Barbary macaque mothers toward infant handling, this result remains surprising.

DOMINANCE STYLE

The apparent deviation from the "typical" macaque mothering style has been explained by the less despotic and more socially tolerant "dominance style" (DE WAAL, 1989) of Barbary macaques (MAESTRIPIERI, 1994a). Barbary macaques have a long reputation of being more peaceful or "nicer" than, for example, rhesus, pigtail, or Japanese macaques, whose intragroup relationships are characterized as less "easygoing" (e.g. CALDECOTT, 1986; LAHIRI & SOUTHWICK, 1966; MOORE, 1992). This impression is based on several observations: (1) aggression appears to be less frequent and less severe than in other macaques (LAHIRI & SOUTHWICK, 1966; but see AURELI et al., 1997; KUESTER & PAUL, 1992); (2) the sex ratio of the sexually mature members of Barbary macaque groups is more balanced than in most other macaques, suggesting that male-male competition may be less severe (e.g. MOORE, 1992); (3) they "are known for exhibiting highly ritualized behaviors that seem to function to regulate agonistic behavior" (MOORE, 1992,

p. 370). Moreover, Barbary macaques fail to follow the so-called "KAWAMURA principle" (the age-inversed rank order among matrilineal sisters found in several cercopithecines, see CHAPAIS, 1992 for review; PAUL & KUESTER, 1987; PRUD'HOMME & CHAPAIS, 1993 for Barbary macaques) — a fact that has been related to relatively weak within-group contest competition (HILL, 1999) and a more individualistic rank system (THIERRY, 1990).

In fact, although Barbary macaques have been characterized as "generalist herbivores" (FA, 1994) or "eclectic feeders" (MÉNARD & VALLET, 1996), they appear to be more adapted to a folivorous diet than most other macaques (FA, 1994). Hence, it seems plausible to speculate that within-group feeding competition may be less severe than in other macaques, favouring a more relaxed dominance style.

However, the picture of the "nice" Barbary macaques appears to be both oversimplified and male-biased. While it is true that males during conflicts with potentially dangerous rivals (i.e. adult males) exhibit a rather egalitarian dominance style, probably because adult males are potentially valuable partners in coalitions against other males (PREUSCHOFT et al., 1998; PREUSCHOFT & PAUL, in press), females are much more despotic. Their agonistic interactions are highly asymmetrical, counter-aggression is almost non-existent (it rarely occurs in dyads involving young females engaged in the process of rank acquisition), and the female hierarchy is highly linear, stable, and nepotistic (PAUL & KUESTER, 1987; PREUSCHOFT et al., 1998). Indications for a more individualistic hierarchy (THIERRY, 1990) are restricted to within-family relationships. At least from the food-enhanced colony at Salem, there is also ample evidence that WGC is an important regulator of female social relationships (HEINZ, 1995; HEINZ & PAUL, 1996). The significance for WGC in wild Barbary macaques remains to be evaluated, but reports from different field sites suggest that, here too, females are characterized by rather despotic rank relations (e.g. DEAG, 1977). There seems to be little reason to regard female Barbary macaques as egalitarian or even "tolerant," therefore.

Strong evidence for a less despotic dominance style of Barbary macaques appears to be rather limited. In the only comparative study to date, AURELI et al. (1997) found that in a captive one-male group unrelated Barbary macaques reconciled more often after conflicts than Japanese and long-tailed macaques did. Their data also indicate that Barbary macaques receive more agonistic support from unrelated individuals than long-tailed and Japanese macaques (but see PRUD'HOMME & CHAPAIS, 1993, who related the fact that Barbary macaques do not follow the "KAWAMURA principle" to the lack of nonkin support). Moreover, in contrast to the highly despotic rhesus and long-tailed macaques, Barbary macaques use an aggressive signal (the "rounded mouth threat face," DEAG, 1974) as a formal status indicator, instead of the submissive "silent bared-teeth display" (PREUSCHOFT et al., 1998). Thus, Barbary macaques may be not as despotic as rhesus, long-tailed and Japanese macaques are. Whether this is due to a relatively high level of between-group competition, as AURELI et al. (1997) suggest, remains to be proven (although strong BGC has been observed in the Salem colony, see PAUL & KUESTER, 1988, 1996; for wild populations see DEAG, 1973; MEHLMAN & PARKHILL, 1988). Nevertheless, the high level of infant handling and maternal tolerance in spite of the highly asymmetrical and nepotistic rank relations among female Barbary macaques appears to be inconsistent with the proposed socioecological framework.

THE POSSIBLE ROLE OF PROVISIONING

Due to the huge, ubiquitous, inescapable, and mostly destructive influence of human activities on virtually all aspects of life on earth, presumably few, if any, nonhuman primates live in completely "natural" settings. Yet, while captivity or provisioning does not necessarily produce

"unnatural" or abnormal behavior, it is clear that environmental factors like these may influence various aspects of life history, demography, behavior, and social relationships (FA & SOUTHWICK, 1988; see also HILL, 1999), including mothering styles (BERMAN, 1980). Thus, the behavior of the Barbary macaques at "Affenberg Salem" may not be typical for the species in general. Although the Salem macaques live in a semi-natural setting where food (including provisioned food items) is widely dispersed, they also live in a predator-free environment where the available space is restricted to about 18 ha, and the constant food supply allows for early sexual maturation, high female fertility, and low rates of mortality (PAUL & KUESTER, 1988). While differences to wild populations should not be neglected, these do not appear to be as large as may be expected (MÉNARD & VALLET, 1996). Moreover, as in the wild, the Salem Barbary macaque population consists of several social groups with frequent male transfer, and the composition (but not the size) of the groups, including their sex ratio, resembles those of wild groups.

As noted above, a systematic comparison of the behavior and social relationships of wild and semifree-ranging Barbary macaques has still to be done. Yet, some already available informations may be significant here. Although WGC may be stronger in the Salem environment, it appears that − due to the restricted space and the close co-existence of several social groups − BGC is also stronger than in wild populations. The fact that the Salem macaques deviate from the KAWAMURA principle further suggests that their dominance style does not differ significantly from that of their wild living conspecifics. Interestingly, AURELI (1992) found a remarkable similarity in the frequency of reconciliation, i.e. one important component of dominance style, between wild and captive long-tailed macaques.

It is of course possible that wild and captive populations differ in their rates of infant handling. HAUSER and FAIRBANKS (1988, p. 810) noted that in vervets, rates of infant handling "were lower in the field habitats and the behaviour of allomothers probably had less impact on the mother-infant relationship." Yet, in his study of wild Barbary macaques, DEAG (1974) found that the (two only) babies in his study group were carried by others for 20 to 50% of the observation time − values quite similar to those reported here. Since interbirth intervals of wild Barbary macaque females are typically longer than those of the Salem macaques (MÉNARD & VALLET, 1996) it remains possible that in field habitats infant handling has a stronger effect on the reproductive performance of mothers than in our study (PAUL & KUESTER, 1996; see also OGAWA, 1995 for Tibetan macaques). If so, this could explain why Barbary macaque mothers are tolerant toward the infant handling attempts of others. Unfortunately, comparative data on infant handling frequency and its potential effect on maternal breeding performance under different living conditions are neither for Barbary macaques nor for any other species available.

THE BROADER PERSPECTIVE

Barbary macaques do not appear to fit neatly into the socioecological framework explaining different patterns of infant handling and mothering styles proposed by McKENNA (1979) and MAESTRIPIERI (1994a). Moreover, although the model received support from the behavior of several female colobines and papionines, Barbary macaques do not appear to be the only species which deviates from the expected pattern. NICOLSON (1987) already noted that the high amount of infant handling displayed by female vervet monkeys does not fit the pattern McKENNA (1979) [and MAESTRIPIERI (1994a)] suggested. Vervet monkeys are usually considered as a "resident-nepotistic" species (sensu STERCK et al., 1997) exhibiting a rather despotic dominance style. Yet, infant handling is common, with rates of infant handling in captivity

approaching on average 10% of the time during the infants' first two months of life (FAIRBANKS, 1990). Moreover, although female vervet monkeys disproportionately handle close kin, infant handling is not restricted to related infants, and cases of infant handling-to-death have been observed (HAUSER & FAIRBANKS, 1988).

A preliminary survey of the available information on infant handling and female social relationships in a larger sample of nonhuman primates (Table 1) suggests that similar deviations are even more common than usually acknowledged. Common squirrel monkeys (*Saimiri sciureus*) are a further example of a species characterized by nepotistic and despotic dominance relationships (MITCHELL et al., 1991), but high rates of infant handling (NICOLSON, 1987), although during the first few weeks of their infants' life, squirrel monkey mothers have been characterized as quite restrictive (SWARTZ & ROSENBLUM, 1981). Infant handling is presumably not restricted to close kin (see WILLIAMS et al., 1994 for bolivian squirrel monkeys), and cases of infant handling-to-death have also been observed (ROSENBLUM, 1971). Whether the egalitarian

Table 1. Female social relationships and the occurrence of infant handling among nonhuman primates with multi-female groups.

Species[1]	Social category[2]	Infant handling[3]	References
Lemur catta	DE	Yes	GOULD, 1992
Alouatta caraya	DE?	Yes	CALEGARO-MARQUES & BICCA-MARQUES, 1993
A. palliata	DE?	Yes?	SERIO-SILVA & RODRIGUEZ-LUNA, 1994 (categorized as "No" by MITANI & WATTS, 1997)
Ateles geoffroyi	DE	No	MITANI & WATTS, 1997
Cebus albifrons	RN	Yes	MITANI & WATTS, 1997
C. apella	RN	Yes	MITANI & WATTS, 1997
C. olivaceus	RN	Yes	O'BRIEN & ROBINSON, 1991
Saimiri sciureus	RN	Yes	NICOLSON, 1987
Cercopithecus aethiops	RN	Yes	MITANI & WATTS, 1997
Erythrocebus patas	RE	Yes	MITANI & WATTS, 1997
Cercocebus torquatus	RE	Yes	BERNSTEIN, 1976
Macaca sylvanus	RN	Yes	MITANI & WATTS, 1997
M. silenus	RNT?	Yes	PREUSCHOFT & BECKMANN, 1995 (social category); KUMAR & KURUP, 1981 (infant handling)
M. nemestrina	RN	No	MAESTRIPIERI, 1994b ("Kidnapping" of young infants about as rare as among rhesus monkeys)
M. maurus	RNT	No	MATSUMURA, 1997
M. tonkeana	RNT	Yes	THIERRY et al., 1994
M. fascicularis	RN	No	MITANI & WATTS, 1997
M. arctoides	RNT	No	MITANI & WATTS, 1997
M. radiata	RN	No	SILK, 1980; SIMONDS, 1965
M. mulatta	RN	No	MITANI & WATTS, 1997
M. fuscata	RN	No	MITANI & WATTS, 1997
Theropithecus gelada	RN	No	MITANI & WATTS, 1997
Papio cynocephalus	RN	No	MITANI & WATTS, 1997
P. hamadryas	DE	No	MITANI & WATTS, 1997
Colobus badius	DE	No	CLUTTON-BROCK & HARVEY, 1984
C. guereza	RE?	Yes	MITANI & WATTS, 1997
Presbytis entellus	RE?	Yes	MITANI & WATTS, 1997
P. pileata	DE	Yes	STANFORD, 1992
Gorilla gorilla beringei	DE	No	MITANI & WATTS, 1997
Pan troglodytes	DE	No	MITANI & WATTS, 1997
Pan paniscus	DE	No	MITANI & WATTS, 1997

1) Macaques arranged in order of their phylogenetic relationships (see MORALES & MELNICK, 1998); 2) following STERCK et al., 1997; DE: Dispersal-egalitarian; RE: Resident-egalitarian; RN: Resident-nepotistic; RNT: Resident-nepotistic-tolerant; 3) based on MITANI & WATTS, 1997, and additional references given in the references column.

Costa Rican squirrel monkeys (*S. oerstedi*, see MITCHELL et al., 1991) show similar high levels of infant handling (or even higher ones, as the model would predict) is not known.

Stumptail macaques, on the other hand, are a prime example for a species exhibiting a relaxed, egalitarian dominance style (DE WAAL & LUTTRELL, 1989). Female stumptail macaques direct a great deal of affiliative contacts toward the troop's infants, but infant carrying is surprisingly rare (ESTRADA & ESTRADA, 1984; MAESTRIPIERI, 1994b). Similarly, MATSUMURA (1997) observed that in moor macaques — a species also characterized by highly egalitarian female relationships — mothers holding their infants were often approached by other females, but that females never carried infants other than their own. MITANI and WATTS (1997), who categorized such species as showing no infant handling (see Table 1), also wondered why among some species, such as gorillas, female interest in infants and attempts to handle them are high, but infant carrying is nevertheless rare.

There are two possible solutions to this problem, although both would obviously raise a host of further questions. Either strong interest in infants is not equivalent to a strong motivation to carry infants of other females, or females with egalitarian relationships are not always as socially tolerant as usually acknowledged. Bonnet macaques may represent an example for the latter solution. This species is often characterized as one "of the more socially tolerant species" (MAESTRIPIERI, 1994a, p. 548), and early laboratory studies indeed reported that bonnet macaque mothers (in comparison to pigtail macaque mothers) "frequently permit others to explore, handle, and groom their newborn without removing it from them" (ROSENBLUM & KAUFMAN, 1967, p. 35). Other studies, however, described bonnet macaque mothers as being much more restrictive. SIMONDS (1965) observed that females often approached new mothers, but were not allowed to hold the infant. Similarly, SILK (1980) reported that out of 196 "kidnapping attempts" (defined as any "active attempt to obtain physical possession of an infant who was in physical contact with its mother") only 13 were successful, and that mothers resisted virtually all kidnapping attempts. The fatal attack on an infant by a female Tonkean macaque (MUROYAMA & THIERRY, 1996) further suggests that female-infant interactions in egalitarian species at least sometimes may represent a serious risk.

Even among colobines the relationship between egalitarianism and infant handling is not as straightforward as might be expected. Black-and-white colobus monkeys (*C. guereza*) are known for high levels of infant handling, while red colobus monkeys (*C. badius*) are known for its absence. This difference has been related to different modes of dispersal. In contrast to black-and-white colobus females, red colobus females usually emigrate from their natal group and are therefore seldom related to each other (CLUTTON-BROCK & HARVEY, 1984). Thus, kinship relations may be at least as important regulators of maternal style as differences in competitive style (see also MATISOO-SMITH et al., 1997, for data on infant handling in a captive group of closely related spider monkeys). This would explain why infant handling in several species characterized by female dispersal and egalitarian relationships is rather rare (Table 1). However, this argument, too, does not appear to be the whole story, since there are also species characterized by female dispersal and egalitarian relationships *and* high rates of infant handling (see STANFORD, 1992 for *Presbytis pileata*).

CONCLUSION

Although it is clear that the available data on infant handling, mothering style and social structure must be interpreted with caution since they are mostly based on qualitative compar-

isons, it seems that the current socioecological model explaining variations in infant handling is of little predictive value. Nearly half of all well-known species listed in Table 1 do not follow the predicted pattern. Neither do tolerant or egalitarian female relationships necessarily favour high rates of infant handling, nor do nepotistic-despotic female relationships necessarily preclude them. In order to better understand variations in infant handling and mothering style within and across species we need more information on the benefits and costs associated with the behavior.

REFERENCES

ANDERSON, C. M. 1992. Male investment under changing conditions among chacma baboons at Suiker-bosrand. *Amer. J. Phys. Anthropol.*, 87: 479–496.

AURELI, F. 1992. Post-conflict behaviour among wild long-tailed macaques (*Macaca fascicularis*). *Behav. Ecol. Sociobiol.*, 31: 329–337.

AURELI, F.; DAS, M.; VEENEMA, H. C. 1997. Differential kinship effect on reconciliation in three species of macaques (*Macaca fascicularis, M. fuscata,* and *M. sylvanus*). *J. Comp. Psychol.*, 111: 91–99.

BERMAN, C. M. 1980. Mother-infant relationships among free-ranging rhesus monkeys on Cayo Santiago: a comparison with captive pairs. *Anim. Behav.*, 28: 860–873.

BERNSTEIN, I. S. 1976. Activity patterns in a sooty mangabey group. *Folia Primatol.*, 26: 185–206.

BURTON, F. D. 1972. The integration of biology and behavior in the socialization of *Macaca sylvana* of Gibraltar. In: *Primate Socialization,* POIRIER, F. E. (ed.), Random House, New York, pp. 29–62.

CALDECOTT, J. O. 1986. Mating patterns, societies and the ecogeography of macaques. *Anim. Behav.*, 34: 208–220.

CALEGARO-MARQUES, C.; BICCA-MARQUES, J. C. 1993. Allomaternal care in the black howler monkey (*Alouatta caraya*). *Folia Primatol.*, 61: 104–109.

CHAPAIS, B. 1992. The role of alliances in social inheritance of rank among female primates. In: *Coalitions and Alliances in Humans and Other Mammals,* HARCOURT, A. H.; DE WAAL, F. B. M. (eds.), Oxford Univ. Press, Oxford, pp. 29–59.

CLUTTON-BROCK, T. H.; HARVEY, P. H. 1984. Comparative approaches to investigating adaptation. In: *Behavioural Ecology: An Evolutionary Approach* (2nd ed.), KREBS, J. R.; DAVIES, N. B. (eds.), Blackwell Scientific, Oxford, pp. 7–29.

DEAG, J. M. 1973. Intergroup encounters in the wild Barbary macaque *Macaca sylvanus* L. In: *Comparative Ecology and Behaviour of Primates,* MICHAEL, R. P.; CROOK, J. H. (eds.), Academic Press, London, pp. 315–373.

DEAG, J. M. 1974. A study of the social behaviour and ecology of the wild barbary macaque, *Macaca sylvanus* L. Ph.D. Diss., Univ. of Bristol, England.

DEAG, J. M. 1977. Aggression and submission in monkey societies. *Anim. Behav.*, 25: 456–474.

DEAG, J. M. 1980. Interactions between males and unweaned Barbary macaques: testing the agonistic buffering hypothesis. *Behaviour,* 75: 54–81.

DELSON, E. 1980. Fossil macaques: phyletic relationships and a scenario of deployment. In: *The Macaques: Studies in Ecology, Behavior and Evolution,* LINDBURG, D. G. (ed.), Van Nostrand Reinhold, New York, pp. 10–30.

DE WAAL, F. B. M. 1989. Dominance "style" and primate social organization. In: *Comparative Socioecology: The Behavioural Ecology of Humans and Other Mammals*, STANDEN, V.; FOLEY, R. A. (eds.), Blackwell Scientific, Oxford, pp. 243–263.

DE WAAL, F. B. M.; LUTTRELL, L. M. 1989. Toward a comparative socioecology of the genus *Macaca*: different dominance styles in rhesus and stumptail monkeys. *Amer. J. Primatol.*, 19: 83–109.

EDWARDS, C. P. 1993. Behavioral sex differences in children of diverse cultures: the case of nurturance to infants. In: *Juvenile Primates: Life History, Development, and Behavior*, PEREIRA, M. E.; FAIRBANKS, L. A. (eds.), Oxford Univ. Press, New York, pp. 327–338.

ESTRADA, A.; ESTRADA, R. 1984. Female-infant interactions among free-ranging stumptail macaques (*Macaca arctoides*). *Primates*, 25: 48–61.

FA. J. E. 1994. Herbivore intake/habitat productivity correlations can help ascertain re-introduction potential for the Barbary macaque. *Biodiversity Conserv.*, 3: 309–317.

FA, J. E.; SOUTHWICK, C. H. (eds.). 1988. *Ecology and Behavior of Food-enhanced Primate Groups*. Alan R. Liss, New York.

FAIRBANKS, L. A. 1990. Reciprocal benefits of allomothering for female vervet monkeys. *Anim. Behav.*, 40: 553–562.

GARBER, P. A.; LEIGH, S. R. 1997. Ontogenetic variation in small-bodied New World primates: implications for patterns of reproduction and infant care. *Folia Primatol.*, 68: 1–22.

GOULD, L. 1992. Alloparental care in free-ranging *Lemur catta* at Berenty Reserve, Madagascar. *Folia Primatol.*, 58: 72–83.

HAUSER, M. D.; FAIRBANKS, L. A. 1988. Mother-offspring conflict in vervet monkeys: variation in response to ecological conditions. *Anim. Behav.*, 36: 802–813.

HEINZ, U. 1995. Konkurrenz zwischen adulten Berberaffenweibchen. Diploma thesis, Univ. of Innsbruck, Austria.

HEINZ, U.; PAUL, A. 1996. Food competition and social relationships in female Barbary macaques (*M. sylvanus*) at Affenberg Salem. *Primate Report*, 44: 18.

HIGLEY, J. D.; SUOMI, S. J. 1986. Parental behaviour in non-human primates. In: *Parental Behaviour*, SLUCKIN, W.; HERBERT, M. (eds.), Blackwell, Oxford, pp. 152–207.

HILL, D. A. 1999. Effects of provisioning on the social behaviour of Japanese and rhesus macaques: implications for socioecology. *Primates*, 40: 187–198.

HINDE, R. A.; ATKINSON, S. 1970. Assessing the roles of social partners in maintaining mutual proximity, as exemplified by mother-infant relations in monkeys. *Anim. Behav.*, 18: 169–176.

HRDY, S. B. 1976. Care and exploitation of nonhuman primate infants by conspecifics other than the mother. In: *Advances in the Study of Behavior, Vol. 6*, ROSENBLATT, L.; HINDE, R. A.; SHAW, R.; BEER, C. (eds.), Academic Press, New York, pp. 101–158.

JAY, P. 1965. Field studies. In: *Behavior in Nonhuman Primates, Vol. 2*, SCHRIER, A. M.; HARLOW, H. F.; STOLLNITZ, F. (eds.), Academic Press, New York, pp. 525–591.

KUESTER, J.; PAUL, A. 1986. Male-infant relationships in semifree-ranging Barbary macaques (*Macaca sylvanus*) of Affenberg Salem/FRG: testing the "male care" hypothesis. *Amer. J. Primatol.*, 10: 315–327.

KUESTER, J.; PAUL, A. 1992. Influence of male competition and female mate choice on male mating success in Barbary macaques (*Macaca sylvanus*). *Behaviour*, 120: 192–217.

KUESTER, J.; PAUL, A.; ARNEMANN, J. 1994. Kinship, familiarity and mating avoidance in Barbary macaques, *Macaca sylvanus. Anim. Behav.*, 48: 1183–1194.

KUMAR, A.; KURUP, G. U. 1981. Infant development in the lion-tailed macaque, *Macaca silenus* (LINNAEUS): the first eight weeks. *Primates*, 22: 512–522.

LAHIRI, R. K.; SOUTHWICK, C. H. 1966. Paternal care in *Macaca sylvana. Folia Primatol.*, 4: 257–264.

LANCASTER, J. 1971. Play-mothering: the relation between juvenile females and young infants among free-ranging vervet monkeys (*Cercopithecus aethiops*). *Folia Primatol.*, 15: 161–182.

MAESTRIPIERI, D. 1994a. Social structure, infant handling, and mothering styles in group-living Old World monkeys. *Int. J. Primatol.*, 15: 531–553.

MAESTRIPIERI, D. 1994b. Mother-infant relationships in three species of macaques (*Macaca mulatta, M. nemestrina*, and *M. arctoides*), II. The social environment. *Behaviour*, 131: 97–113.

MATISOO-SMITH, E.; WATT, S. L.; ALLEN, J. S.; LAMBERT, D. M. 1997. Genetic relatedness and alloparental behaviour in a captive group of spider monkeys (*Ateles geoffroyi*). *Folia Primatol.*, 68: 26–30.

MATSUMURA, S. 1997. Mothers in a wild group of moor macaques (*Macaca maurus*) are more attractive to other group members when holding their infants. *Folia Primatol.*, 68: 77–85.

McKENNA, J. J. 1979. Aspects of infant socialization, attachment, and maternal caregiving patterns among primates: a cross-disciplinary review. *Yrbk. Phys. Anthropol.*, 22: 250–286.

McKENNA, J. J. 1987. Parental supplements and surrogates among primates: cross-species and cross-cultural comparisons. In: *Parenting Across the Life Span: Biosocial Dimensions*, LANCASTER, J.; ALTMANN, J.; ROSSI, A. (eds.), Aldine de Gruyter, New York, pp. 143–184.

MEHLMAN, P. 1986. Male intergroup mobility in a wild population of the Barbary macaque (*Macaca sylvanus*), Ghomaran Rif Mountains, Morocco. *Amer. J. Primatol.*, 10: 67–81.

MEHLMAN, P. T.; PARKHILL, R. S. 1988. Intergroup interactions in wild Barbary macaques (*Macaca sylvanus*), Ghomaran Rif Mountains, Morocco. *Amer. J. Primatol.*, 15: 31–44.

MÉNARD, N.; SCHEFFRAHN, W.; VALLET, D. 1994. Paternity certainty, relatedness and parental investment: a test in a natural population of Barbary macaques (*Macaca sylvanus*). *Folia Primatol.*, 62: 204–205.

MÉNARD, N.; SCHEFFRAHN, W.; VALLET, D.; REBER, C. 1992. Application of blood protein electrophoresis and DNA fingerprinting to the analysis of paternity and social characteristics of wild Barbary macaques. In: *Paternity in Primates: Genetic Tests and Theories*, MARTIN, R. D.; DIXSON, A. F.; WICKINGS, E. J. (eds.), Karger, Basel, pp. 155–174.

MÉNARD, N.; VALLET, D. 1993. Population dynamics of *Macaca sylvanus* in Algeria: an 8-year study. *Amer. J. Primatol.*, 30: 101–118.

MÉNARD, N.; VALLET, D. 1996. Demography and ecology of Barbary macaques (*Macaca sylvarnus*) in two different habitats. In: *Evolution and Ecology of Macaque Societies*, FA, J. E.; LINDBURG, D. G. (eds.), Cambridge Univ. Press, Cambridge, pp. 106–131.

MITANI, J. C.; WATTS, D. 1997. The evolution of non-maternal caretaking among anthropoid primates: do helpers help? *Behav. Ecol. Sociobiol.*, 40: 213–220.

MITCHELL, C. L.; BOINSKI, S.; VAN SCHAIK, C. P. 1991. Competitive regimes and female bonding in two species of squirrel monkeys (*Saimiri oerstedi* and *S. sciureus*). *Behav. Ecol. Sociobiol.*, 28: 55–60.

MOORE, J. 1992. Dispersal, nepotism, and primate social behavior. *Int. J. Primatol.*, 13: 361–378.

MORALES, J. C.; MELNICK, D. J. 1998. Phylogenetic relationships of the macaques (Cercopithecidae, *Macaca*), as revealed by high resolution restriction site mapping of mitochondrial ribosomal genes. *J. Human Evol.*, 34: 1–23.

MUROYAMA, Y.; THIERRY, B. 1996. Fatal attack on an infant by an adult female Tonkean macaque. *Int. J. Primatol.*, 17: 219–227.

NICOLSON, N. 1987. Infants, mothers, and other females. In: *Primate Societies*, SMUTS, B. B.; CHENEY, D. L.; SEYFARTH, R. M.; WRANGHAM, R. W.; STRUHSAKER, T. T. (eds.), Univ. of Chicago Press, Chicago, pp. 330–342.

O'BRIEN, T. G.; ROBINSON, J. G. 1991. Allomaternal care by female wedge-capped capuchin monkeys: effects of age, rank, and relatedness. *Behaviour*, 119: 30–50.

OGAWA, H. 1995. Bridging behavior and other affiliative interactions among male Tibetan macaques (*Macaca thibetana*). *Int. J. Primatol.*, 16: 707–729.

PACKER, C.; LEWIS, S.; PUSEY, A. 1992. A comparative analysis of non-offspring nursing. *Anim. Behav.*, 43: 265–281.

PAUL, A. 1984. Zur Sozialstruktur und Sozialisation semi-freilebender Berberaffen (*Macaca sylvanus* L. 1758). Ph.D. diss., Univ. of Kiel, Kiel.

PAUL, A.; KUESTER, J. 1985. Intergroup transfer and incest avoidance in semifree-ranging Barbary macaques (*Macaca sylvanus*) at Salem (FRG). *Amer. J. Primatol.*, 8: 317–322.

PAUL, A.; KUESTER, J. 1987. Dominance, kinship and reproductive value in female Barbary macaques (*Macaca sylvanus*) at Affenberg Salem. *Behav. Ecol. Sociobiol.*, 21: 323–331.

PAUL, A.; KUESTER, J. 1988. Life-history patterns of Barbary macaques (*Macaca sylvanus*) at Affenberg Salem. In: *Ecology and Behavior of Food-enhanced Primate Groups*, FA, J. E.; SOUTHWICK, C. H. (eds.), Alan R. Liss, New York, pp. 199–228.

PAUL, A.; KUESTER, J. 1996. Infant handling by female Barbary macaques (*Macaca sylvanus*) at Affenberg Salem: testing functional and evolutionary hypotheses. *Behav. Ecol. Sociobiol.*, 39: 133–145.

PAUL, A.; KUESTER, J.; ARNEMANN, J. 1992. DNA fingerprinting reveals that infant care by male Barbary macaques (*Macaca sylvanus*) is not paternal investment. *Folia Primatol.*, 58: 93–98.

PAUL, A.; KUESTER, J.; ARNEMANN, J. 1996. The sociobiology of male-infant interactions in Barbary macaques, *Macaca sylvanus*. *Anim. Behav.*, 51: 155–170.

PAUL, A.; THOMMEN, D. 1984. Timing of birth, female reproductive success and infant sex ratio in semi-free-ranging Barbary macaques (*Macaca sylvanus*). *Folia Primatol.*, 42: 2–16.

PREUSCHOFT, S.; BECKMANN, F. 1995. "Smiling" and "Laughter" in lion-tailed macaques (*Macaca silenus*): a preliminary analysis of their bared-teeth displays. In: "Laughter" and "Smiling" in Macaques. Ph.D. thesis by PREUSCHOFT, S., Univ. of Utrecht, Utrecht, pp. 111–136.

PREUSCHOFT, S.; PAUL, A. in press. Dominance, egalitarianism, and stalemate: an experimental approach to male-male competition in Barbary macaques. In: *Primate Males*, KAPPELER, P. M. (ed.), Cambridge Univ. Press, Cambridge.

PREUSCHOFT, S.; PAUL, A.; KUESTER, J. 1998. Dominance styles of female and male Barbary macaques (*Macaca sylvanus*). *Behaviour*, 135: 731–755.

PRUD'HOMME, J.; CHAPAIS, B. 1993. Rank relations among sisters in semi-free-ranging Barbary macaques (*Macaca sylvanus*). *Int. J. Primatol.*, 14: 405–420.

ROSENBLUM, L. A. 1971. Infant attachment in monkeys. In: *The Origins of Human Social Relations*, SCHAFFER, H. R. (ed.), Academic Press, New York, pp. 85–113.

ROSENBLUM, L. A.; KAUFMAN, I. C. 1967. Laboratory observations of early mother-infant relations in pigtail and bonnet macaques. In: *Social Communication among Primates*, ALTMANN, S. A. (ed.), Univ. of Chicago Press, Chicago, pp. 33–41.

ROSS, C.; MACLARNON, A. 1995. Ecological and social correlates of maternal expenditure on infant growth in haplorhine primates. In: *Motherhood in Human and Nonhuman Primates*, PRICE, C. R.; MARTIN, R. D.; SKUSE, D. (eds.), Karger, Basel, pp. 37–46.

ROWELL, T. E.; HINDE, R. A.; SPENCER-BOOTH, Y. 1964. "Aunt"-infant interaction in captive rhesus monkeys. *Anim. Behav.*, 12: 219–226.

SERIO-SILVA, J. C.; RODRIGUEZ-LUNA, E. 1994. Howler monkey (*Alouatta palliata*) behavior during the first weeks of life. In: *Current Primatology, Vol. 2: Social Development, Learning and Behaviour*, ROEDER, J. J.; THIERRY, B.; ANDERSON, J. R.; HERRENSCHMIDT, N. (eds.), ULP Press, Strasbourg, pp. 309–313.

SILK, J. B. 1980. Kidnapping and female competition among captive bonnet macaques. *Primates*, 21: 100–110.

SIMONDS, P. E. 1965. The bonnet macaque in South India. In: *Primate Behavior: Field Studies of Monkeys and Apes*, DEVORE, I. (ed.), Holt, Rinehart & Winston, New York, pp. 175–196.

SIMONDS, P. E. 1974. Sex differences in bonnet macaque networks and social structure. *Archives of Sexual Behav.*, 3: 151–166.

SKAMEL, U. 1994. Zur Struktur und Funktion zwischengeschlechtlicher Beziehungen bei Berberaffen (*Macaca sylvanus* L. 1758) außerhalb der Paarungszeit. Diploma thesis, Univ. of Goettingen, Germany.

SMALL, M. F. 1990. Alloparental behaviour in Barbary macaques, *Macaca sylvanus*. *Anim. Behav.*, 39: 297–306.

STANFORD, C. B. 1992. Costs and benefits of allomothering in wild capped langurs (*Presbytis pileata*). *Behav. Ecol. Sociobiol.*, 30: 29–34.

STERCK, E. H. M.; WATTS, D. P.; VAN SCHAIK, C. P. 1997. The evolution of female social relationships in nonhuman primates. *Behav. Ecol. Sociobiol.*, 41: 291–309.

SWARTZ, K. B.; ROSENBLUM, L. A. 1981. The social context of parental behavior: a perspective on primate socialization. In: *Parental Care in Mammals*, GUBERNICK, D. J.; KLOPFER, P. H. (eds.), Plenum Press, New York, pp. 417–454.

TAUB, D. M. 1978. Aspects of the biology of the wild Barbary macaque (Primates, Cercopithecinae, *Macaca sylvanus* L. 1758): biogeography, the mating system and male-infant associations. Ph.D. diss., Univ. of California, Davis.

TAUB, D. M. (ed.). 1984. Male caretaking behavior among wild Barbary macaques (*Macaca sylvanus*). In: *Primate Paternalism*, Van Nostrand Reinhold, New York, pp. 20–55.

THIERRY, B. 1990. Feedback loop between kinship and dominance: the macaque model. *J. Theor. Biol.*, 145: 511–521.

THIERRY, B.; ANDERSON, J. R.; DEMARIA, C.; DESPORTES, C.; PETIT, O. 1994. Tonkean macaque behaviour from the perspective of the evolution of Sulawesi macaques. In: *Current Primatology, Vol. 2, Social Development, Learning and Behaviour*, ROEDER, J. J.; THIERRY, B.; ANDERSON, J. R.; HERRENSCHMIDT, N. (eds.), ULP Press, Strasbourg, pp. 103–117.

VAN SCHAIK, C. P. 1989. The ecology of social relationships amongst female primates. In: *Comparative Socioecology: The Behavioural Ecology of Humans and Other Mammals*, STANDEN, V.; FOLEY, R. A. (eds.), Blackwell Sci., Oxford, pp. 195–218.

VOGEL, C. 1984. Patterns of infant-transfer within two troops of common langurs (*Presbytis entellus*) near Jodhpur: testing hypotheses concerning the benefits and risks. In: *Current Primate Researches,* ROONWAL, M. L.; MOHNOT, S. M.; RATHORE, N. S. (eds.), Jodhpur Univ. Press, Jodhpur, India, pp. 361–379.

WASSER, S. K.; BARASH, D. P. 1981. The selfish 'allomother': a comment on SCOLLAY and DEBOLD (1980). *Ethol. Sociobiol.,* 2: 91–93.

WHITTEN, P. L. 1987. Infants and adult males. In: *Primate Societies,* SMUTS, B. B.; CHENEY, D. L.; SEYFARTH, R. M.; WRANGHAM, R. W.; STRUHSAKER, T. T. (eds.), Univ. of Chicago Press, Chicago, pp. 343–357.

WILLIAMS, L.; GIBSON, S.; MCDANIEL, M.; BAZZEL, J.; BARNES, S.; ABEE, C. 1994. Allomaternal interactions in the Bolivian squirrel monkey (*Saimiri boliviensis boliviensis*). *Amer. J. Primatol.,* 34: 145–156.

WILSON, E. O. 1975. *Sociobiology: The New Synthesis.* Belknap Press of Harvard Univ. Press, Cambridge, Massachusetts.

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