



Infants as costly social tools in male Barbary macaque networks

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ARTICLE INFO

Article history:

Received 5 August 2009

Initial acceptance 6 October 2009

Final acceptance 28 January 2010

Available online 1 April 2010

MS. number: 09-00519R

Keywords:

Barbary macaque

GC level

glucocorticoid

grooming

Macaca sylvanus

male–infant interaction

nonhuman primate

social network analysis

In mammals, females are the main caretakers of offspring. In a number of species, however, males also care for young, and may spend considerable time with infants. In various nonhuman primates, male interactions with infants appear to benefit mainly the males, who use them to regulate their relationships, particularly with other male group members. We studied whether interactions with infants were related to glucocorticoid output in male Barbary macaques, *Macaca sylvanus*, at the enclosure 'La Forêt des Singes', France. We used a combination of behavioural observations, social network analysis and measures of faecal glucocorticoid metabolites as an indicator of physiological stress, and compared the results for the birth season in spring, during a time of intense interactions with infants, with a period in autumn, when males interacted less frequently with infants. Social network analyses revealed that infant carriers had stronger ties with other males than noncarriers. Overall, male relationships were stronger in spring than in autumn. Infant care was unevenly distributed among males and not related to rank, suggesting that the motivation to invest in infant carrying depends on the position in the social network and the current constellation of relationships. Despite the correlation of infant carrying with male interactions, the time spent with infants alone explained most of the variation in glucocorticoid levels, suggesting that access to the male–male network is paid for by an increase in stress hormone levels. Taken together, these results show that Barbary macaque infants can be viewed as costly social tools that facilitate networking among males.

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Owing to gestation and lactation, females bear the largest share of the cost of reproduction in mammals (Clutton-Brock 1991). In a number of mammal species, however, males also contribute to the rearing of young. In cooperatively breeding tamarins, for instance, males carry infants more frequently than mothers (Wright 1990; Schradin & Anzenberger 2001), while in cooperatively breeding meerkats, male group members provide young with food (Doolan & Macdonald 1999; Hodge 2007). In addition to food provisioning and carrying, males may defend young against infanticide (Pusey & Packer 1994; Palombit et al. 1997; Van Schaik & Kappeler 1997). The occurrence of male care is typically explained by kin selection (Trivers 1972), but it has also been related to the direct benefit of increasing one's chances of survival with increasing group size (Clutton-Brock et al. 2001).

In nonhuman primates, interactions between males and infants occur in a number of species (reviewed in Paul et al. 2000), including baboons, *Papio* spp. (Smuts 1985; Palombit et al. 1997; Buchan et al. 2003) and Tibetan macaques, *Macaca thibetana*

(Zhao 1996). One of the most notable cases is, however, found in the Barbary macaque, *M. sylvanus*, where males interact extensively and intimately with infants soon after birth (Deag & Crook 1971; Deag 1980; Taub 1984). The initial hypothesis that this extensive caretaking behaviour constitutes paternal investment (Taub 1980) was refuted by DNA fingerprinting (Paul et al. 1992, 1996). Likewise, the 'male reproductive tactic' hypothesis, which suggested that males increase their mating success by signalling willingness to invest in a female's offspring, found no support (Paul et al. 1996). Present evidence bolsters the 'agonistic buffering' hypothesis, which posits that males use infants to regulate their social relationships and to facilitate male–male coalitions (Deag & Crook 1971; Paul et al. 2000). Coalition formation is a common strategy to increase an individual's competitive ability temporarily (Harcourt 1989) and is found in various primate species (e.g. baboons: Noe & Sluijter 1990; chimpanzees: De Waal 1982). In Barbary macaques, coalition formation was shown to be strongly related to male mating success (Küster & Paul 1992) and to foster rank maintenance (Widdig et al. 2000) or improvement (Witt et al. 1981). Direct evidence linking infant care to male coalition formation and eventually reproductive success is, however, still lacking.

In addition, it remained unclear whether the social consequences of infant care, such as increased male–male interaction or

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a decrease in aggression received, are associated with changes in male physiology. A number of recent studies have shown that nonhuman primates respond with elevated glucocorticoid output to changes in social dynamics in their environment (e.g. Engh et al. 2006; Crockford et al. 2008). We therefore determined glucocorticoid output in male Barbary macaques, based on analysis of faecal samples, to study the effects of male–infant interactions and the associated changes in male social dynamics on the adrenal axis, both in spring (intense interactions with infants and other males) and autumn (fewer interactions with infants and other males). As previous studies indicated that grooming can influence glucocorticoid output in primates (Gust et al. 1993; Shutt et al. 2007; Wittig et al. 2008), we also considered how the amount of grooming given and received affects glucocorticoid levels. Furthermore, because the frequency of aggression received could also influence glucocorticoid levels (e.g. Ostner et al. 2008), this variable was included in the model as well.

We determined the males' position in the social group and the influence of interactions with infants on the number and quality of social relationships using a social network analysis approach. Social network analyses are attracting increasing attention in studies of animal behaviour (Croft et al. 2008; Krause et al. 2009; Lusseau & Conradt 2009). The social network approach extends simple matrix statistics, as it allows one to track connections between individuals to second and higher degrees, and to study the social organization of individuals at different levels (Krause et al. 2009). In addition, a number of statistics have been developed to characterize an animal's position in the social network, the substructure ('cliquishness') of a group, as well as population dynamics. In our analysis, we applied a statistical measure derived from social network analysis that captures the centrality of a given individual, based on the number of partners and number of interactions with these partners. Furthermore, we made use of the graphical representations derived from the network analysis to provide intuitive illustrations of the social structure of the group.

If interactions with infants help to alleviate stress, possibly by reducing the amount of aggression received, this should be reflected in a reduced stress response in males that are mainly involved in caretaking. Following the notion that males use infants to regulate their social relationships, we further expected that males who invest heavily in caretaking have stronger ties to other males than individuals who do not take care of infants.

METHODS

Study Site and Animals

The study was conducted at the outdoor enclosure 'La Forêt des Singes' in Rocamadour, France, a visitor park where monkeys range freely, while visitors are restricted to a path (Turckheim & Merz 1984). Barbary macaques live in multimale multifemale groups, in which females remain in the natal group with their offspring (Küster & Paul 1999). They are seasonal breeders with a birth season in spring and a mating season in autumn (Small 1990). Data were collected from the beginning of May to the end of June and from the end of August until the end of October 2007 in the largest group ('PB'), which comprised 53–54 individuals over 1 year of age (one male died during the study period). All animals of the group could be identified individually. During the study, there were 19 males between 5 and 27 years of age in the group, from which we chose 12 aged 5–20 years as focal animals (Table 1). Males were selected with the aim of covering all rank classes (high, middle, low) and the broad range of the age distribution, while excluding very old males who have a tendency to withdraw from the group (J. Fischer, personal observation). By the start of the observations in

Table 1

Identity (ID), age, rank in spring and autumn, and weighted degree (male contacts/h) in spring and autumn for the 12 focal males

ID	Age (years)	Rank spring	Rank autumn	Degree spring	Degree autumn
A340	10	1	1	9.25	2.22
A337	10	2	4	1.69	2.16
O202	19	3	3	7.19	1.08
R250	17	4	5	8.06	2.97
C361	8	5	2	11.88	3.19
C360	8	6	7	2.63	5.24
Z321	11	7	9	0.50	0.60
M189	20	8	6	7.00	2.43
E380	6	9	11	0.81	0.65
T265	16	10	10	1.25	0.43
D370	7	11	8	0.94	1.03
F391	5	12	12	4.81	3.30

May, two babies (a female born 11 April 2007 to female M189 and a male born 19 May 2007 to female G400) were already intensely cared for by males; another male baby was born 7 July 2007 to female L170 after the first period of observations had finished. Neither female G400 nor L170 had male maternal relatives in the group. M189 was the mother of A340, the alpha male, who was the brother of E380, another male in our sample. All other males were maternally unrelated. Relatedness data were obtained from E. Merz (personal communication).

Behavioural Observations

For each focal male, we conducted 69 half-hour protocols (32 in spring and 37 in autumn) with the focal animal sampling method, resulting in a total observation time of 414 h. The order in which males were observed was pseudorandomized with the stipulation that no animal was observed twice on the same day, and each animal was observed equally frequently at the different times of the day. During focal observations, all agonistic (threat, chase away, chase and attack), submissive (avert, retreat, scream, flee, present, teeth chatter), affiliative (grooming, sitting in contact, mount, chatter, hug, support) and male–infant interactions (carry baby, triadic interaction) were recorded continuously using a Palm handheld computer (Model Zire; Palm Inc., Sunnyvale, CA, U.S.A.) running a custom program created with Pendragon Forms (Pendragon Software Cooperation, Libertyville, IL, U.S.A.). A complete description of the Barbary macaque ethogram can be found in Hesler & Fischer (2007). We used MatMan 1.1 (Noldus, Wageningen, Netherlands) to construct a dominance matrix using ad libitum and focal data of dyadic agonistic encounters and approach–retreat interactions ($N = 369$ interactions).

Faecal Sample Collection and Glucocorticoid Analysis

We analysed 287 faecal samples (147 in spring, 140 in autumn, 5–16 faecal samples per focal animal and season, median = 12). Samples were collected directly after defecation, placed on ice for up to 4 h until transferred to a freezer and stored at -20°C until hormone analysis. All analysed samples were collected after noon (1200–1700 hours) as in this time period no effect of collection time on glucocorticoid levels was found (data not shown). Prior to analysis, samples were lyophilized and pulverized and a portion of the faecal powder was extracted with 3 ml of 80% methanol (Heistermann et al. 2004). Faecal extracts were analysed for immunoreactive 11β -hydroxyetiocholanolone ($3\alpha,11\beta$ -dihydroxy-CM), a group-specific measurement of 5-reduced $3\alpha,11\beta$ -dihydroxylated cortisol metabolites which has been proven to provide

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