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ORIGINAL ARTICLE

# Patterns of infant handling and relatedness in Barbary macaques (*Macaca sylvanus*) on Gibraltar

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**Abstract** Among papionin primates, the Barbary macaque (*Macaca sylvanus*) shows the most extensive interactions between infants and group members other than the mother. Two different types of interactions occur: (1) long-lasting dyadic interactions between a handler and an infant, and (2) brief triadic interactions between two handlers involving an infant. Previous investigations showed that infant handling by males is best explained as use of infants to manage relationships with other males. In contrast, no adaptive explanation for infant handling by females emerged. Here, we compared the infant-handling pattern between subadult/adult males and subadult/adult females in a free-ranging group of 46 Barbary macaques on Gibraltar to test whether the relationship management hypothesis also applies to female handlers. We further investigated the infant-handling pattern of juveniles and used microsatellite markers to estimate relatedness between infant handlers and the infant's mother. We found that males, females and juveniles all participated extensively in triadic interactions using infants of above-average related females. In contrast, only males and juveniles were highly involved in dyadic interactions with infants of related females, while females rarely handled infants other than their own. The pattern of infant handling was entirely compatible with the predictions of the relationship management hypothesis for males and mostly so for females. Moreover, our genetic analysis revealed that males and females differ in their partner choice: while females preferred to interact with related females, males had no significant preference to interact with related males. We further discuss the observed above-average relatedness values between infant handlers and the infant's mother in the light of kin-selection theory.

**Keywords** Alloparental behaviour · Barbary macaque · Infant handling · Microsatellites · Relationship management

## Introduction

In most primate species the mother is the main handler and caretaker of her offspring (Nicolson 1987). In some species, however, males, females other than the mother and juveniles participate in infant handling (Sussman and Garber 1987; Goldizen 1990). Henceforth, we use the neutral term 'infant handling' to describe any type of interaction (ranging from potentially harmful to caring behaviour) showed by males, females other than the mother and juveniles towards infants. Apart from direct parental care, there are at least three ultimate explanations why infant handling might occur. First, infant handling might be an altruistic behaviour that benefits the infant and/or the infant's mother whilst being costly to the handler. Such altruistic behaviour can be selectively advantageous if the handler directs its interactions preferentially towards related infants and thereby gains inclusive fitness benefits (kin-selection theory: Hamilton

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1964; Riedman 1982). Second, infant handling could be a purely selfish behaviour that benefits the handler alone: (1) infant handling might be a form of reproductive competition among females, where handlers harm unrelated infants to increase the relative competitive advantage of their own offspring (Hrdy 1976; Silk 1980; Wasser 1983; Maestripieri 1994a). (2) Young females might handle infants to train maternal skills (learning-to-mother hypothesis: Landcaster 1971; Nicolson 1987; Maestripieri 1994a). (3) Males might use an infant to gain easier access to the infant's mother to increase mating success (mating effort hypothesis: Smuts 1985). (4) Infant handlers might use infants to test (Manson 1999) or manage (Hrdy 1976; Maestripieri 1994b; Paul et al. 1996) relationships with the mother or other group members. Relationship management is thought to be profitable as aggression between interacting individuals can be reduced, or increased access to resources (e.g. food, coalition partners) can be gained. Third, infant handling might be a non-adaptive byproduct, occurring because infants as novel objects simply attract the interest of group members (Manson 1999; Silk 1999) or because females are generally attracted to infants due to strong selection for mother–offspring bonding (Quiatt 1979).

Among papionin primates (baboons, macaques and mangabeys), the most extensive interactions between infants and other group members are shown by Barbary macaques (*Macaca sylvanus*) (Whitten 1987; Maestripieri 1998). This species is of particular interest because two different types of interactions between infants and handlers can be observed (Deag 1980). Dyadic interactions involve a single handler and an infant. During these interactions, behaviour directed towards the infant is usually gentle and closely resembles maternal behaviour, including carrying, holding, grooming, playing, monitoring and protecting (Taub 1984). A single interaction can continue for 20 min or even more (Deag and Crook 1971; Deag 1980; authors' personal observation). Triadic interactions involve two handlers and an infant, usually with the infant held between them. While the infant remains passive, the handlers often touch the infant's genitalia, showing typical facial expressions accompanying lip smacking and teeth-chattering. Triadic interactions rarely last longer than a minute (Deag and Crook 1971). While similar triadic interaction patterns have been reported for other primate species (Itani 1959; Silk and Samuels 1984; Smith and Whitten 1988; Ogawa 1995), the intensity and duration of dyadic interactions in Barbary macaques is unique among papionin primates (Whitten 1987). Moreover, it has been demonstrated that dyadic and triadic interactions are tightly linked in that a handler caring for a particular infant also preferentially uses this infant in triadic interactions (Taub 1980, 1984; Paul et al. 1996).

Several studies have aimed to test whether infant handling in Barbary macaques is altruistic, selfish or a non-adaptive byproduct. For dyadic interactions, it has been shown that males did not preferentially handle the infants they sired (Paul et al. 1992; Ménard et al. 2001) or maternally related infants (Paul et al. 1996). Combining these results with data on triadic interactions supported the view that infant handling by males is a selfish behaviour, with male handlers using infants to manage their relationships with other males (originally called the 'agonistic buffering' hypothesis: Deag and Crook 1971; Deag 1980; Taub 1980; Paul et al. 1996) or with males gaining increased mating opportunities with the infant's mother (Ménard et al. 2001). In contrast, females mostly handled maternally related infants, but with no apparent benefit to the infant or its mother (Paul and Küster 1996). The observed data were best explained through infant handling being a byproduct of strong selection for mother–offspring bonding (Paul and Küster 1996), although Paul and Küster (1996) acknowledged that there might be a yet untested functional explanation for infant handling by females.

In the present study, we aim to examine the hitherto untested functional hypothesis that females, like males, use infants to manage relationships with other females and males. This seems plausible because females are known to be highly involved in triadic interactions as well (Small 1990; Timme 1995) and might gain the same benefits (reduced aggression, increased access to resources, alliance formation) from relationship management as males do. In addition, we aim to investigate the pattern of infant handling by juveniles, which has received little attention so far although it is known that juveniles participate in infant handling (Small 1990). The role of infant handling by juveniles seems important because all female juveniles and some male juveniles remain in their natal group (Küster and Paul 1999), such that relationship management may possibly influence their future status in the group.

We studied the infant handling pattern in a free-ranging group of Barbary macaques on Gibraltar to test five general predictions of the relationship management hypothesis, initially proposed by Paul et al. (1996) for male infant handlers (except for the additional prediction 4): (1) dyadic and triadic interactions are more frequent during periods of high group tension because there is more need to manage relationships between individuals; (2) dominants should be more often involved in triadic interactions than subordinates because dominants are expected to be approached most often by other individuals; (3) in triadic interactions between two males and two females, subordinates should more often initiate triadic interactions than dominants because subordinates have greater interest in regulating their relationships with dominants than vice versa; (4) triadic interactions between the mother and a handler should be more often initiated by the handler than by the mother because an infant handler needs to gain access to infants; (5) triadic interactions should occur more frequently between individuals with a small rank distance than between individuals with a large rank distance, because this corresponds to the social scale at which relationships need to be managed. Finally, we tested whether infants were a limited resource, which might lead to deviations from the expected pattern due to some handler categories potentially having restricted access to infants.

We further used polymorphic microsatellite loci to reveal fine-scale genetic relationships between infant handlers and the infant's mother and between participants in triadic interactions. In addition, we used the paternity analysis conducted by Modolo and Martin (2008) to test whether males preferentially interacted with their offspring or whether males that preferentially handled an infant of a given female had a higher probability of siring the female's subsequent offspring.

## Methods

### Study site

We conducted the study on Gibraltar (36°09′N, 5°21′W), where a long-term project was initiated in 1994. After 1995, all animals older than juveniles were individually recognisable. In 1999, when the present study was conducted, there were approximately 230 macaques living on Gibraltar, divided into seven social groups. Our research focussed on the Middle Hill group, which consisted of 46 animals during the study period (for age and sex composition, see Table 1). The home range of the Middle Hill group was located in a military area without public access. These animals were well habituated to humans but had little contact with tourists, unlike the other social groups (O'Leary and Fa 1993). All macaques were fed with fruits and vegetables once a day to prevent them from ranging down into town. As the provisioned food did not satisfy their daily needs, however, the animals spent considerable time feeding on natural resources such as seeds, roots, fruits and flowers.

**Table 1** Age and sex composition of the Middle Hill troop in July 1999, following the categories defined by Merz (1984)

| | Adult 7 years | Subadult 5–6 years | Juvenile 2 2–4 years | Juvenile 1 1–2 years | Infant | Total |
|---|---|---|---|---|---|---|
| Male | 5 | 4 | 5 | 5 | 6 | 25 |
| Female | 8 | 2 | 7 | 2 | 2 | 21 |
| Total | 13 | 6 | 12 | 7 | 8 | 46 |

### Behavioural observations

Over a period of 3 months (from July to October 1999), R.K. conducted a detailed comparison of infant-handling patterns of males, females and juveniles, taking all eight infants born in 1999 as focal individuals. Data were collected between 8.00 a.m. and 7.00 p.m., depending on visibility of the macaques. Barbary macaques on Gibraltar show strictly seasonal breeding. In 1997, the mean birth date for infants in the Middle Hill troop was 13 June ± 7.6 days (Chervet 1998). Therefore, the infants in our study were probably about 1 month old when observations began. Two adult females had no surviving infants, although they might have given birth to infants that died before data collection started. Focal animal sampling was conducted for 10-min periods, 2–3 times per day for each infant, noting the initiator, the type (dyadic or triadic) and the duration of the interaction. Dyadic interactions were recorded continuously and included interactions between an infant handler and an infant, in which infants were clinging dorsally or ventrally to the handler, or were located alongside (with body contact), resting with the handler in body contact, playing or being groomed by the handler. Triadic interactions included events that followed the behavioural pattern described by Deag 1980; (see description in the "Introduction"), which excluded unilateral interactions in which an individual attempted to inspect an infant while it was with the mother or another infant handler. Clear initiation patters were available for 59.6% of all triadic interactions, whereby carrier-initiated triads were those in which an infant handler approached another individual and non-carrier-initiated triads were those in which the non-carrier approached an individual accompanied by a baby. Focal sequences were randomised across the eight infants for each day and week, resulting in a total of 146 h of observation (18.2 ± 0.6 h per infant; mean ± SD).

Provision of food by the population management authority clearly influenced the daily activity pattern of the Middle Hill group. Because food was distributed in a clumped manner, it provoked considerable tension between group members and a significant increase in aggressive encounters (R.K., personal observation). We therefore tested whether the frequencies of dyadic and triadic interactions differed between the high-tension (feeding) and low-tension (non-feeding) periods. We defined the beginning of the high-tension period as the time when the animal caretaker's car arrived (between 8.00 and 9.30 a.m.). The macaques then started to feed and continued until there was no food left, which we defined as the end of the high-tension period (between 9.00 and 11.00 a.m.). The rest of the day (before and after feeding), we regarded as the low-tension period.

For analysis of the behavioural data, we divided the infant handlers into four age and sex categories: (1) males (adult and subadult males; all ≥5 years), (2) females (adult and subadult females; all ≥5 years), (3) juvenile males and (4) juvenile females (both 2–4 years). For some analyses, the latter two categories were combined as there was no difference in the infant-handling pattern between juvenile males and females (see "Results"). We excluded 1-year-old juveniles from the analysis because they very rarely interacted with infants and could not be distinguished at the individual level. We pooled adult and subadults of each sex in a single category because of the limited number of individuals involved. However, we report statistical comparisons between subadults and adults whenever analyses were possible. Pooling of adult and subadult females is in fact entirely reasonable because both subadult females had an infant in the study year.

We established pairwise rank relationships among males and females based on 592 "ad libitum" dyadic agonistic interactions collected mainly during the feeding period throughout the study using only dyadic clear dominance interactions (including aggressive and submissive behaviour) (Semple 1998; Kümmerli and Martin 2005). We calculated pairwise rank distances for male and female dominance hierarchies separately. We defined a rank distance of 1–2 as small, a rank distance of 3–5 as medium and a rank distance >5 as large. Males had on average 3.3 small, 3.3 medium and 1.3 large rank relationships with other males. Females had on average 3.4 small, 3.6 medium and 2.0 large rank relationships with other females.

## Genetic analyses

In September 1999, 32 members of the Middle Hill group were trapped and sedated in a large cage using a blowpipe (Telinject, Oftringen, Switzerland) and the anaesthetic Ketaminol 100 mg/ml (0.2 ml/kg body weight). EDTA-blood samples were obtained by venipuncture from the femoral vein, taking a quantity of 25 ml from each subadult/adult and the reduced quantity of 15 ml from each juvenile. After a blood sample had been collected, each anaesthetised animal was placed in a separate large cloth bag and kept in a warm, dark room near the trapping site. This permitted each animal to recover in a quiet environment without being exposed to other group members or environmental stress factors (e.g. hot sunlight, extraneous noise, etc.). Earlier trapping experience (von Segesser 1999) had shown that, under these circumstances, Barbary macaques recover in 2–3 h. After this recovery period had elapsed, we released the animals, who immediately joined other group members without showing any adverse effects of capture and/or anaesthesia.

The collected samples included all mothers and all infant handlers in the group. Because of potential risks and other considerations, we were unable to trap the eight focal infants. However, we were able to use the paternity analyses conducted by Modolo and Martin (2008), which was based on samples collected following this study. This allowed us to test whether males preferentially interacted with their offspring or whether males that preferentially handled an infant of a given female had a higher probability of siring the female's subsequent offspring.

Fission of the Middle Hill group had occurred previously in the summer of 1998. Hair samples were available from 22 individuals of the splinter group. Thus, we were able to genotype a total of 54 individuals from the original Middle Hill group. This provided us with a good estimate of allele frequencies at the group level, which is important for accurate estimates of relatedness.

Microsatellites were successfully amplified using 13 pairs of oligonucleotide primers. One primer pair (MFGT17) had been designed for Japanese macaques (Inoue and Takenaka 1993). The remaining 12 systems all involved human primers. Nine of those systems (D1S207, D2S141, D6S311, D7S503, D8S1106, D11S925, D16S420, D17S791 and D18S536) were already known to show variation in Barbary macaques (von Segesser 1999; von Segesser et al. 1999; Lathuillière et al. 2001). The three remaining systems (D2S305, D3S1279 and D4S243) were known to show polymorphism in other Old World monkeys (Nair et al. 2000; F.M. von Segesser, personal communication) and were successfully amplified in *Macaca sylvanus*. We have described PCR and electrophoresis protocols in detail elsewhere (Kümmerli and Martin 2005). Number of alleles per locus ranged from two to five with expected heterozygosity between 0.22 and 0.76.

## Statistical analyses

In all analyses, we report data for dyadic and triadic interactions as the percentage of total observation time and as the number of triadic interactions per observation hour, respectively. For analyses that aimed to investigate relationships between specific infant–handler pairs, we determined the main handlers that preferentially interacted with a given infant in dyadic and triadic interactions (see Paul et al. 1996 for a similar approach). We regarded an individual as a main handler if it interacted at least 1% of the total observation time in dyadic interactions and/or was involved in at least three triadic interactions with a given infant. For analyses that aimed to investigate the interaction between infants and a class of group members (e.g. males), all observed infant-handling bouts were used.

We used the computer program RELATEDNESS 5.0.8 (Queller and Goodnight 1989) to estimate pairwise relatedness between any pair of group members. Relatedness estimates range between −1 and 1, with the average relatedness between individuals within a population being zero by definition. $R$-values above or below 0, respectively, indicate that animals are more or less related than expected by chance. Pairwise relatedness estimates based on only a few loci can lead to erroneous values (Csilléry et al. 2006; van Horn et al. 2008). To test whether our genetic data produced reliable relatedness estimates, we compared known pedigree relationships (expected $R_{\text{mother–offspring}} = 0.5$, expected $R_{\text{half-sibling}} = 0.25$) with average pairwise genetic relatedness estimates between the same individuals. We found no significant differences between expected pedigree and observed genetic relatedness values (mother–offspring: $R = 0.47 \pm 0.05$, $t_{15} = 0.63$, $P = 0.54$; half-siblings: $R = 0.23 \pm 0.08$, $t_{15} = 0.28$, $P = 0.78$), demonstrating that our genetic data generated reliable relatedness estimates. For dyadic interactions, we tested whether relatedness between main handlers and an infant's mother is significantly different from relatedness between mothers and individuals that did not handle their infants. For triadic interactions, we compared whether the relatedness between two main handlers of a given infant is significantly different from the average relatedness between pairs of group members of the corresponding category that did not interact in triadic interactions with each other.

Behavioural data and relatedness estimates deviated significantly from a normal distribution. We therefore used Spearman's rank correlation coefficient for correlation analyses and permutation analyses (Manly 1997) for analysis-of-variance (ANOVA)-like designs. For ANOVA designs, we first applied a parametric ANOVA computation to our data set and extracted the resulting $F$ values, which were classified as the observed values of our analysis ($F_{\text{obs}}$). Whenever appropriate, we introduced individual identity as a factor into our model to account for repeated measures taken from the same individual (Sokal and Rohlf 1995). We then performed 1,000 random permutations on our data set and calculated the $F$ values after each permutation using the computer program R 2.2.0 (available on http://www.r-project.org/). We counted the number of cases in which $F$ values obtained from the permutation were greater or equal to the observed $F$ values ($n_{F \geq F_{\text{obs}}}$). Finally, we calculated the probability of obtaining $F$ values greater or equal to the observed $F$ values by using the formula $P = (1 + n_{F \geq F_{\text{obs}}})/1000$. We regarded $P$ values ≤0.05 as significant. In pairwise post hoc comparisons, we adjusted the nominal $\alpha = 5\%$ by using the sequential Bonferroni correction method (Rice 1989).

**Table 2** Percentage of time focal infants spent with their mothers and with the different categories of infant handlers (males, females and juveniles) in dyadic interactions

| Infant (sex) | Mother | Infant handlers | | |
|---|---|---|---|---|
| | | Males | Females | Juveniles |
| Clea (f) | 52.7 | 0.0 (0) | 0.2 (0) | 7.3 (2) |
| Gromit (m) | 63.9 | 4.3 (2) | 0.2 (0) | 1.8 (1) |
| Jes (m) | 80.0 | 0.0 (0) | 0.5 (0) | 5.8 (2) |
| Lloyd (m) | 55.1 | 3.9 (2) | 0.7 (0) | 3.9 (1) |
| Nemo (m) | 56.4 | 16.0 (3) | 0.1 (0) | 0.6 (0) |
| Minus (m) | 57.6 | 13.0 (4) | 0.8 (0) | 0.6 (0) |
| Austin (m) | 39.8 | 12.7 (3) | 0.2 (0) | 3.3 (2) |
| Rabea (f) | 62.0 | 18.1 (2) | 1.0 (0) | 0.0 (0) |

The number of main infant handlers is given in parentheses

## Results

### Patterns of dyadic infant handling

All infants were involved in infant handling, with total interaction times accounting for 6.3–19.1% (11.9 ± 5.2%; mean ± SD) of total observation time (Table 2). Infants had two to five (median = 3) main infant handlers. Seven out of nine (78%) males were main handlers of one to three infants each, with adult males being significantly more often involved in infant handling than subadult males (ANOVA permutation test: $n = 9$, $P = 0.021$). Of the 12 juveniles, 8 (67%) were main handlers of one infant each, with no significant difference existing between male and female juveniles in their handling rate (ANOVA permutation test: $n = 12$, $P = 0.34$). The rates of infant handling for all females were very low, such that there were no main handlers for any infant. When all dyadic interactions between females and an infant were considered together, non-mothers did not handle infants more often than mothers (ANOVA permutation test: $n = 10$, $P = 0.98$).

Handling rates differed significantly between males, females and juveniles (Fig. 1a; ANOVA permutation test: $n = 31$, $P = 0.001$). Post hoc pairwise comparisons revealed that males spent significantly more time handling infants than both females (ANOVA permutation test: $P = 0.003$) and juveniles ($P = 0.003$). Furthermore, juveniles spent significantly more time handling infants than females ($P = 0.007$).

### Patterns of triadic infant handling

All infants were involved in triadic interactions with the number of triadic events per infant ranging from 32 to 110 (66.4 ± 29.3; mean ± SD). Infants had between three and ten (median = 5.5) main handlers. Out of 531 evaluated

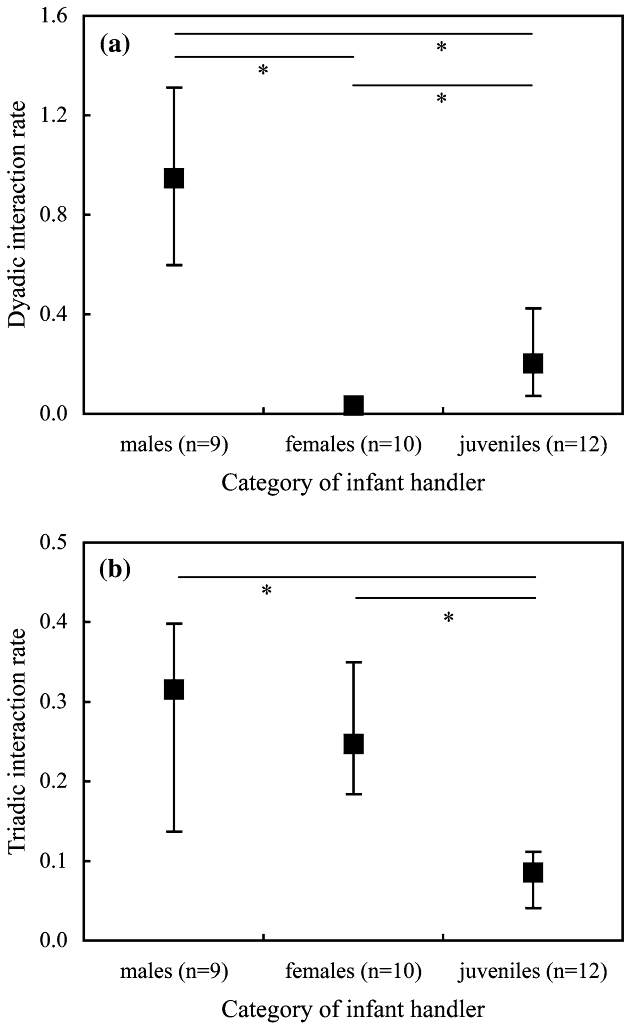

**Fig. 1** Rates of infant handling (median with 1st and 3rd quartiles) of males, females and juveniles in dyadic (**a**) and triadic (**b**) interactions. Dyadic infant handling rates are given as percentages (i.e. the time each group member spent with infants relative to the total observation time). Triadic infant handling rates are given as the number of triadic interactions per hour in which each group member was involved

interactions, 33.7% were male–infant–male triads, 24.1% were mother–infant–female triads, 20.9% were mother–infant–male triads and 14.5% were mother–infant–juvenile triads. In this context, the term 'mother' refers to the mother of the infant being handled. Note that there were no female–infant–female interactions in which none of the females was the mother of the infant involved. Other combinations of partner categories (mostly including 1-year-old juveniles) accounted for only 6.8% of all triads and were not considered in subsequent analyses. All males were involved in triadic interactions, being main handlers of 1–4 infants, with adult males participating significantly more often in triadic interactions than subadult males (ANOVA permutation test: $n = 9$, $P = 0.029$). Apart from their own infants, 7 out of 10 females were main handlers of 1–3 other infants with subadult females being involved in triadic interactions as often as adult females (ANOVA permutation test: $n = 10$, $P = 0.92$). Rates of triadic interactions did not differ between mothers (without their own infant) and non-mothers (ANOVA permutation test: $n = 10$, $P = 0.71$), while mothers were marginally significantly more often involved in triadic interactions when including interactions with their own infant (ANOVA permutation test: $n = 10$, $P = 0.069$). Ten out of 12 (83%) juveniles were main handlers in triadic interactions of one or two infants, with no difference existing between male and female juveniles in their triadic interaction rates (ANOVA permutation test: $n = 12$, $P = 0.69$).

There were significant differences between males, females (including interactions with their own infants) and juveniles in the frequency with which they were involved in triadic interactions (Fig. 1b; ANOVA permutation test: $n = 31$, $P = 0.007$). Post hoc analyses revealed that males and females interacted in triads significantly more often than juveniles (ANOVA permutation test, male–juvenile comparison: $P = 0.003$, female–juvenile comparison: $P = 0.005$), whereas there was no significant difference in triadic interaction rate between males and females (ANOVA permutation test: $P = 0.68$).

Consistent with findings from other studies, there was a significant positive correlation between the time male and juvenile handlers spent with their main partner infants and the number of triadic interactions they performed with them (Spearman rank correlation for male main handlers: $r_s = 0.88$, $n = 9$, $P = 0.002$; for juvenile main handlers: $r_s = 0.70$, $n = 10$, $P = 0.025$).

## Testing predictions of the relationship management hypothesis

A comparison between the five predictions of the relationship management hypothesis and the test results for male, female and juvenile infant handling is provided in Table 3.

Infants spent significantly more time with males during the high-tension than the low-tension period (ANOVA permutation test: $n = 6$, $P = 0.007$, Table 4). The diametrically opposite pattern was found for dyadic interactions with juveniles, in that infants spent significantly more time with juveniles during the low-tension than the high-tension period (ANOVA permutation test: $n = 8$, $P = 0.011$, Table 4). For infant handling by females, the frequencies did not differ significantly between the low-tension and high-tension period (ANOVA permutation test: $n = 8$, $P = 0.26$, Table 4). Frequency comparisons of triadic interactions between the high-tension and low-tension periods differed greatly depending on the categories of individuals involved in the interaction (Table 4). There

**Table 3** Predictions of the relationship management hypothesis and the results of tests for infant-handling patterns of males, female and juveniles

| Prediction | Males | Females | Juveniles |
|---|---|---|---|
| (1) Frequency of dyadic and triadic interactions increases when group tension is high | + | − | − |
| (2) Frequency of triadic interactions increases with rank | + | + | x[a] |
| (3) Subordinates initiate triadic interactions more often than dominants | + | − | x |
| (4) Handlers initiate triadic interactions more often than mothers | + | + | + |
| (5) Triadic interactions occur mostly between handlers with small rank distances | + | + | x |

[a] As juveniles have no clear rank position within the social group, some predictions could not be tested (x)

+ Support, − no support

**Table 4** Comparison of handling frequencies in dyadic and triadic interactions between the high-tension and the low-tension period

| | High-tension period | Low-tension period |
|---|---|---|
| Dyadic interactions | Total observation time (%) | |
| Male–infant* | 22.3 ± 4.7 | 8.3 ± 1.8 |
| Female–infant | 0.8 ± 0.3 | 0.4 ± 0.1 |
| Juvenile–infant* | 1.7 ± 0.7 | 3.1 ± 0.9 |
| Triadic interactions | Interactions per hour | |
| Mother–infant–male | 0.79 ± 0.31 | 0.71 ± 0.20 |
| Mother–infant–female* | 0.37 ± 0.10 | 0.69 ± 0.15 |
| Mother–infant–juvenile | 0.59 ± 0.18 | 0.52 ± 0.09 |
| Male–infant–male$^{+}$ | 2.29 ± 1.02 | 0.98 ± 0.42 |

* $P < 0.05$, $^{+}$ marginal significant difference

were no significant differences between the two periods in the frequencies of mother–infant–male interactions (ANOVA permutation test: $n = 8$, $P = 0.64$) or of mother–infant juvenile interactions (ANOVA permutation test: $n = 8$, $P = 0.72$). In contrast, mother–infant–female triadic interactions occurred significantly more often during the low-tension than the high-tension period (ANOVA permutation test: $n = 8$, $P = 0.049$), while there was a tendency for the opposite pattern in male–infant–male triadic interactions (ANOVA permutation test: $n = 6$, $P = 0.068$). During the high-tension period, triadic interactions occurred significantly more often between two males and an infant than between other partner categories (ANOVA permutation test: $n = 28$, $P = 0.015$), whereas there was no difference in frequency of triadic interactions between different partner combinations during the low-tension period (ANOVA permutation: $n = 28$, $P = 0.59$).

The ordinal rank of males and females (rank #1 refers to the highest-ranked individual) were significantly negatively correlated with the frequency with which they were involved in triadic interactions (Spearman rank correlations for males: $r_s = -0.80$, $n = 9$, $P = 0.01$, for females including interactions with their own infants: $r_s = -0.75$, $n = 10$, $P = 0.013$, for triadic interactions without their own infants: $r_s = -0.70$, $n = 10$, $P = 0.024$).

Male–infant–male triadic interactions were initiated significantly more often by the subordinate male than by the dominant (59 versus 38, binomial test: $P = 0.042$). This was, however, not the case in female–infant–female triadic interactions (which always included the mother of the infant being handled), where there was no difference in the initiation frequency between subordinates and dominants (41 versus 43, binomial test: $P = 0.91$). Triadic interactions involving the mother were initiated significantly more often by the infant handler than by the mother (mother–infant–male: 13 versus 46, mother–infant–female: 5 versus 79, mother–infant–juvenile: 5 versus 50; binomial tests: all $P < 0.001$).

The frequencies of triadic male–infant–male and mother–infant–female interactions were not evenly distributed among different categories of rank distances, but were significantly skewed towards infant handler pairs with a small rank distance (Table 5).

We found two lines of evidence for infants being a limited resource, with males being the most successful competitors. First, juveniles tended to handle infants that were handled by males only rarely or not at all, which is reflected by a significant negative correlation between the rates at which an infant was handled by males as opposed to juveniles (Spearman rank correlation: $r_s = -0.95$, $n = 8$, $P < 0.0001$). Second, infants were significantly less often together with their mothers during the high-tension period (42.0%) than during the low-tension period (63.2%, ANOVA permutation test: $n = 8$, $P = 0.001$), while a three-fold increase in interaction time with males was observed during the high-tension period compared to the low-tension period (see Table 4).

### Infant handling and relatedness coefficients

In dyadic interactions (Fig. 2a) involving either males or juveniles, the average relatedness between main handlers and the infant's mother was significantly higher than the relatedness between the remaining mother–non-handler dyads (ANOVA permutation test, male main handlers: $P = 0.002$; juvenile main handlers: $P = 0.007$).

**Table 5** Expected and observed frequencies of male–infant–male and mother–infant–female triadic interactions with respect to the rank distance between the interacting individuals

| Type of triad | Frequency | Rank distance | | | $\chi^2$ | *P* |
|---|---|---|---|---|---|---|
| | | Small[a] | Medium | Large | | |
| Male–infant–male ($N = 179$) | Expected[b] | 75 | 75 | 30 | 21.1 | <0.0001 |
| | Observed | 88 | 84 | 7 | | |
| Female–infant–female ($N = 128$) | Expected | 48 | 51 | 28 | 80.3 | <0.0001 |
| | Observed | 96 | 30 | 2 | | |

[a] *Small* rank distance of 1–2, *medium* rank distance of 3–5, *large* rank distance >5

[b] See "Methods" for the average number of males and females in each category on which basis the expected values are calculated

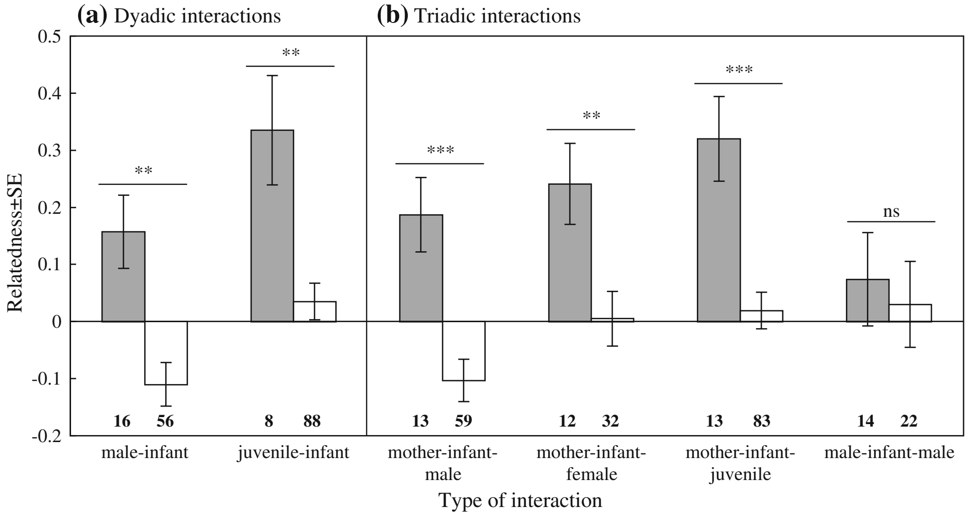

**Fig. 2** Mean pairwise relatedness (*R* ± SE) between (**a**) the main handlers in dyadic interactions and the infant's mother, and (**b**) two individuals that were involved at least three times in triadic interactions with the same infant. These relatedness values (*grey bars*) were compared to the relatedness values between any pair of group members that were not main handlers (*white bars*) of a given infant in the corresponding handler category. *Numbers* below the *bars* indicate the number of pairs of group members in each category. $^{**}P \leq 0.01$, $^{***}P \leq 0.001$, *ns* not significant

In triadic interactions (Fig. 2b) between the mother, her infant and a main handler, average relatedness between the mother and the handler was significantly greater than relatedness between the remaining mother-non-handler dyads (ANOVA permutation tests: mother–infant–male: $P = 0.001$; mother–infant–female: $P = 0.010$, mother–infant–juvenile: $P = 0.001$). By contrast, in male–infant–male triadic interactions, relatedness between two main male handlers did not differ significantly from the average relatedness between two males in the group (ANOVA permutation tests: $P = 0.70$).

Paternity data were available for six out of the eight focal infants (Modolo and Martin 2008). Two out of the six infants (0.33) were sired by one of their main infant handlers. This matches exactly the expected probability of a father interacting with its infant by chance. We further tested whether males that preferentially handled an infant of a given female in 1999 fathered the female's subsequent offspring in 2000. This was indeed the case for four out of five (0.80) infants born to mothers that had infants with male main handlers in 1999 (a total of nine infants were born in 2000, see Modolo and Martin 2008). This proportion is higher than the expected probability (0.37) of a male preferentially handling a female's infant and siring the female's next offspring by chance. Because males handled infants of related females, the association between infant handling and reproductive success leads to increased levels of inbreeding in those specific cases (pairwise relatedness between the four mother–father pairs = 0.15 ± 0.02). However, there was no overall indication of inbreeding at the group level, where average relatedness between fathers and mothers was close to zero ($R = 0.03 \pm 0.07$, $n = 15$) and was not significantly different from the relatedness between the males and females that did not have infants together ($R = -0.05 \pm 0.03$, $n = 76$, ANOVA permutation tests: $P = 0.37$).

## Discussion

Males spent significantly more time with infants than female and juvenile infant handlers and had the highest triadic interaction rate (Fig. 1). The pattern of infant handling by males was fully consistent with the view that males use infants to manage relationships with other group members (Table 3). Males, similar to females and juveniles, predominantly handled infants of related females and used these infants in triadic interactions with the infant's mother and unrelated males. This suggests that males generally manage relationships with females of their own matriline and with unrelated males. The former interaction is possible because females are strictly philopatric and a large proportion of males also remain in their natal group (Ménard and Vallet 1993, for Algeria; Küster and Paul 1999, for outdoor enclosure in Salem/Germany; L. Modolo, R.D. Martin, C.P van Schaik, M. Krützen (manuscript submitted) for Gibraltar).

Consistent with previous studies (Paul et al. 1992, 1996; Ménard et al. 2001), males did not handle their own offspring more often than expected by chance, which refutes the paternal investment hypothesis. The behavioural pattern of infant handling by males was largely consistent with previous findings from an outdoor enclosure in Salem, Germany (Paul et al. 1996). This consistency suggests that the observed male infant-handling pattern is a general characteristic of Barbary macaques that can be observed in different populations living under different environmental conditions. However, there were also differences between the two studies, particularly in the genetic relationships between interacting individuals. In Salem, male infant handlers did not preferentially handle maternally related infants (Paul et al. 1996), whereas in our study there is evidence that males handled infants of related females, which presumably results in some elevation of relatedness between infant handlers and infants above the average level. There are several possible explanations for this difference. First, Paul et al. (1996) compared observed with expected handling frequencies of different categories of relatives based on pedigree relationships. This method has less statistical power compared to our analyses that tested the general prediction whether infant handlers were above-average related to the infant's mother and did not distinguish between different categories of relatives. Thus, Paul et al.'s (1996) method might have impeded the detection of limited but significant relatedness relationships between handlers and infants. Second, the proportion of infants available per male was markedly lower in Salem (0.30–0.55) than in Gibraltar (0.89) and the social groups in Salem contained twice as many group members compared to our study group. Hence, in Gibraltar males probably had more scope to select infants of specific (related) mothers than in Salem.

Female infant handlers very rarely interacted in dyadic interactions with infants other than their own, whereas they were engaged in triadic interactions as often as males were. The low infant-handling rate in dyadic interaction can best be explained by the fact that eight out of ten females were mothers. Hence, most females had no need to handle other infants because they already had access to an infant (their own) with which they could interact in triads. This suggests a causal connection between dyadic and triadic interactions in which handlers first need to have access to infants (dyadic interactions) before they can interact in triadic interactions. The fact that females were much less involved in dyadic infant handling than males contrasts with the pattern found in several other papionin primate species (Maestripieri 1999; Silk 1999; Ross and MacLarnon 2000; Henzi and Barrett 2002). The low dyadic infant-handling rate found for females also contrasts with the hypotheses that infant handling reflects reproductive competition among females or that infant handling is a byproduct of strong selection for mother–offspring bonding, as both hypotheses predict higher handling rates for females than for males (Silk 1999). Moreover, the finding that non-mothers were not more often involved in dyadic and triadic infant handling than mothers further contradicts the byproduct hypothesis. This latter finding could also indicate that non-mother females have limited access to infants as a result of being inferior in competition with males. Altogether, our findings suggest that the infant-handling pattern shown by female Barbary macaques (low dyadic interaction but high triadic interaction rates) has an adaptive explanation.

For females, three out of the five tested predictions of the relationship management hypothesis were upheld (Table 3). The observation that females had more triadic interactions during periods of low rather than high group tension seemingly contradicts the relationship management hypothesis. However, infants tended to be with males during the high group tension period and spent significantly less time with their mothers, which might explain the decrease in mother–infant–female triadic interaction rate, as triadic interactions between females always included the infant's mother. This further suggests that infants were a limited resource and were monopolised by males during periods of high group tension. At first sight, the observation that dominant females initiated triadic interactions as often as subordinates also seems to be incompatible with the relationship management hypothesis. However, this deviation from expectation can also be logically explained because social rank in females correlates with kinship, such that triadic interactions between females occurred mainly between relatives of the same matriline (Fig. 2b). Although mothers are always ranked higher than their daughters (Fa and Lind 1996), the relationship between female members of matrilines are quite relaxed and it is conceivable that mothers and daughters have equal interest in engaging in triadic interactions with one another. Given these arguments, our data indicates that not only males but also females seem to use infants to manage relationships with other group members. However, while males seem to use infants to manage relationships with related females and unrelated males, female relationship management seem to occur mainly with related individuals of their matriline. This latter pattern is consistent with findings from various Old World primates with female philopatry, where benign infant-handling interactions preferentially occur between females of the same matriline (e.g. *Cercopithecus aethiops*, Fairbanks 1990; *Papio cynocephalus*, Kleindorfer and Wasser 2004; for reviews see: Nicolson 1987; Paul 1999; Ross and MacLarnon 2000).

Juveniles handled infants in both dyadic and triadic interactions, showing the same behavioural elements as male and female handlers. However, juveniles spent significantly less time with infants than males and were less often involved in triadic interactions than both males and females. Our relatedness analyses, combined with our knowledge of matriline membership (Kümmerli and Martin 2005), clearly showed that juveniles exclusively handled infants of their own matriline and used these infants mainly in triadic interactions with the infant's mother. Whether and to what extent juveniles use infants to manage relationships with members of their matriline remains somewhat speculative. This is because juveniles have no clear rank position within the social group, such that only two out of five predictions of the relationship management hypothesis could be tested. Furthermore, it seemed that juveniles suffered from competition for access to infants, such that juvenile infant handling was restricted to infants that were handled by males only rarely or not at all. This restricted access to infants might also explain why juveniles were involved in fewer triadic interactions with infants than males and females. But the most important point to note here is that, if most female juveniles and some male juveniles stay in their natal group [as observed by L. Modolo et al. L. Modolo, R.D. Martin, C.P van Schaik, M. Krützen (manuscript submitted)] and continue to handle mostly infants of their own matriline, this would translate directly into the infant-handling pattern of subadult/adult males and females observed in this study.

We can envisage at least three benefits that handlers might gain from relationship management through infant handling. First, having strong relationships with other group members might increase an individual's access to food and other resources, which might improve its body condition and hence its reproductive competitiveness and/or success. Second, relationship management through infant handling might be part of a stress-coping mechanism, whereby reduced stress could improve body condition and lead to an extended reproductive lifespan and increased lifetime fitness (Strum 1984). Third, relationship management might lead to the formation of alliances, which are known to be important to maintain dominance positions (Widdig et al. 2000). Moreover, males might obtain an extra benefit from established relationships with females through increased mating opportunities as reported by Ménard et al. (2001). In this study, we found that four out of five (0.80) infants born to mothers in 2000, which had infants with male main handlers in 1999, were sired by a main handler. Although the sample size is too low to draw firm conclusions, our finding supports the idea that males might increase reproductive success with a given female through infant handling.

As males preferentially handle infants of related females, such increased reproductive success due to infant handling could potentially lead to inbreeding. However, we detected no significant inbreeding across mother–father pairs of the 15 infants born in 1999 and 2000. This is probably because a high proportion (55%) of mothers in 2000 had either no infant or their infants had no male main partner in 1999 and therefore no related male could obtain increased mating opportunities through infant handling.

Our observation that infant handlers showed a significantly above-average degree of genetic relatedness with mothers of the infants concerned could be interpreted as evidence for infant handling being subject to kin selection (Hamilton 1964). However, there are reasons for inferring that infant handling in Barbary macaques is unlikely to be a kin-selected behaviour because; (1) triadic interactions do not seem to have any benefits for infants and/or their mothers because of their short duration and their sometimes harmful nature (Küster and Paul 1986); (2) infant handling did not result in a detectable increase in infant survival or female fecundity in Salem (Paul and Küster 1996) and did not lead to increased feeding opportunities for mothers in Gibraltar (Chervet 1998). Such benefits for the mother or the infant in terms of increased survival, shortened interbirth intervals, longer reproductive lifespans or healthier and/or heavier offspring would however be expected if infant handling were a kin-selected behaviour (Woodroffe and Vincent 1994; Mitani and Watts 1997). The question remains whether such benefits occur under natural conditions in Morocco and Algeria, where ecological conditions impose real constraints (Ménard and Vallet 1996). Hence, the kin-selection hypothesis cannot be completely discounted until infant handling and its fitness consequences are examined under more natural conditions.

In conclusion, our study provides evidence that infant handling by males and by females other than the mother is a selfish behaviour, whereby handlers use infants for relationship management. Although Barbary macaques have always been regarded as a special case within Old World primates with respect to the high intensity of infant handling, infant handling by both males and females is widespread in primates. However, its function in Old World primates is subject to intense debate (Strum 1984; Ogawa 1995; Maestripieri 1999; Paul 1999; Silk 1999; Kleindorfer and Wasser 2004) because infant handling has been variously observed to have positive as well as negative consequences for the infant (Schino et al. 2003; Kleindorfer and Wasser 2004). Hence, this raises the question why mothers should tolerate infant handling when it may harm their infants. Our results now provide a possible explanation to this problem because infant handlers mostly handled infants of related mothers. Hence, although handlers seem to act selfishly, kin relationships might reduce the risk of infant abuse by handlers.

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