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## Infant handling and mortality in yellow baboons (*Papio cynocephalus*): evidence for female reproductive competition?

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**Abstract** This study examines negative and positive infant handling behavior in 24 free-ranging yellow baboon infants (*Papio cynocephalus*) studied over a 5-year period in Mikumi National Park, Tanzania. We test predictions of the female reproductive competition hypothesis to explain patterns of infant handling behavior by adult females (excluding the infant's mother) in relation to observed cases of infant mortality by age 3 months (25% of infants in this study). Results show that: (1) low-ranking infants received more negative infant handling than high-ranking infants; conversely high-ranking infants received more positive infant handling; (2) female kin engaged in higher levels of positive infant handling than did non-kin, whereas non-kin showed higher levels of negative infant handling; (3) rates of negative infant handling varied by season, with high levels at the onset of the rainy season; and (4) high level of negative infant handling was a significant predictor of infant mortality by age 3 months (infant rank and sex did not predict survival). We discuss how the occurrence and interpretation of infant handling behavior in the literature has likely been confused by different definitions of this behavior, as well as differences in the socio-ecological context in which this behavior occurs.

**Keywords** Infant handling · Reproductive competition · Infant mortality · Infanticide · Primates

### Introduction

Female–female reproductive competition has, historically, received far less attention than male–male competition (reviewed in Gowaty 1997; Blaffer Hrdy 1999), perhaps because the latter is more conspicuous. Sexual selection theory suggests that male–male competition is more often for quantity of offspring, whereas female–female competition is more often for quality of offspring (Wasser and Barash 1981). Thus, female competition has traditionally been researched under the paradigm of sexual selection with a primary focus on female choice for male mates (reviewed in Andersson 1994; Kokko et al. 2003). Over the past decade, a growing body of evidence across many taxa has reexamined the sexual selection paradigm and demonstrated male preference for female traits (for e.g. Amundsen and Forsgren 2001; Berglund and Rosenqvist 2001; Jones et al. 2001) and female–female competition in areas previously dominated by male-focused research, such as female size-mediated access to preferred mates in shrimp (Rahman et al. 2002) and female song in birds in response to biased sex ratios (Langmore et al. 2002).

One long recognized form of female–female competition in mammals is socially mediated reproductive suppression (Wasser and Barash 1981), with females competing to decrease the number and ages of competitors to their offspring (e.g. Wasser and Norton 1993). Infanticide by unrelated females represents the most overt form of such female–female competition, at the extreme resulting in pronounced variation in reproductive skew among females (Blaffer Hrdy 1999). Following the sexual selection paradigm, males benefit from infanticide by increased reproduction through enhanced access to newly receptive females (e.g. Hrdy 1976; Borries et al. 1999), whereas female infanticide is primarily driven by competition for limiting resources to offspring (e.g. in birds: Hanson et al. 1997, in rodents: Tuomi et al. 1997, in primates: Sterck et al. 1997; Wasser and Norton 1993). Like reproductive suppression, female infanticide is widespread among diverse taxonomic groups and has recently been proposed to explain a range of complex behavioral patterns including

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territoriality and gender-specific spacing patterns in voles (Fortier and Tamarin 1998; Wolff and Peterson 1998), temporary expulsion of group members among communal suricates (Clutton-Brock et al. 1998), timing of oviposition in beetles (Eggert and Mueller 2000), sexual mimicry in hyenas (Muller and Wrangham 2002), and communal nursing in mammals (Roulin and Hager 2003). Infant handling behavior in many primates may represent a more subtle form of such reproductive suppression, associated with far less risk than direct infanticide. This paper examines predictions of the female reproductive competition hypothesis for negative infant handling behavior by linking receipt of this behavior from non-related adult females to rates of infant mortality.

Infant handling in primates is widespread, yet its function has been hotly debated for more than a quarter of a century (Hrdy 1976; McKenna 1979; Quiatt 1979; Scollay and DeBold 1980; Wasser and Barash 1981; Maestripieri 1999; Manson 1999; Paul 1999; Silk 1999). At issue is the fact that not all infant handling appears to be affiliative, that is, some infant handling is rough, persistent and potentially abusive while other infant handling is gentle and potentially nurturing. Overtly aggressive infant handling (e.g. carrying the infant upside down, pulling it by its leg with its head bouncing on the ground) has been observed among multiparous females, or females that should already be skilled mothers (e.g., Wasser and Starling 1988), leading researchers to question the "learning to mother" or "aunting" hypotheses for some forms of infant handling.

Large, complex, multi-matrilineal primate groups such as terrestrial Old World primates produce many infants annually, all of whom grow up together and compete for age-specific resources (e.g., limited weaning foods, protection against predation, infanticide, getting lost during extensive troop movements, long-term social position) (Altman 1980; Wasser 1983; Dunbar 1984; Hausfater and Blaffer Hrdy 1984; Norton et al. 1987; Rhine et al. 1988). Social position may be particularly important because, as reflected by inheritance of dominance in females of large, matrilineal primate groups, early social positions that dramatically affect a female's competitive ability can last a lifetime. Negative handling of unrelated infants may be a form of competition that can modify the playing field, indirectly improving one's own infant's relative chances of acquiring each of the above limited resources.

At least 16 hypotheses have been proposed to explain the function of infant handling in primates (summarized in Hrdy 1976, 1978; Quiatt 1979; Scollay and DeBold 1980; Wasser and Barash 1981; Wasser 1983; Maestripieri 1999; Silk 1999). It is beyond the scope of the present paper to address or distinguish among predictions of all hypotheses, but we provide a brief summary of the four major groups of hypotheses here: (1) maternal relief hypothesis (also called the aunting hypothesis: Poirer 1968; Hrdy 1976; Altman 1980): infant handling functions to reduce maternal demands, enabling mothers to spend time on other needs; (2) learning to mother hypothesis (Lancaster 1971; Hrdy 1976; Quiatt 1979): infant handling

provides nulliparous infant handlers with basic maternal skills prior to bearing their first offspring; (3) by-product hypothesis (Quiatt 1979): infant handling is the outcome of selection for behavioral orientation to young, promoting maternal attachment; and (4) female reproductive competition hypothesis (FRCH; Wasser and Barash 1981): infant handling functions to reduce the competitive abilities of handled infants relative to the handler's prospective offspring.

In this study, we examine predictions based on the FRCH for infant handling in free-ranging yellow baboons (*Papio cynocephalus*). We limit the analyses to infant handling behavior by adult females other than the mother, and test the following predictions: (1) the ratio of negative infant handling to positive infant handling increases with low maternal dominance rank (this prediction is based on the assumption that overt expression of abusive infant handling is constrained for high-ranking infants due to social protection; Altman 1980); (2) positive infant handling is more common by related adult females (e.g. aunts, female cousins, adult sisters) whereas negative infant handling is more common by unrelated adult females; (3) infants of the non-dispersing sex (females) are negatively handled more often than infants of the dispersing sex (males); (4) infants born earlier in the birth year are expected to receive more negative infant handling as females try to offset any age advantage of these earlier births in the birth cohort; and (5) negative infant handling is positively correlated with infant mortality.

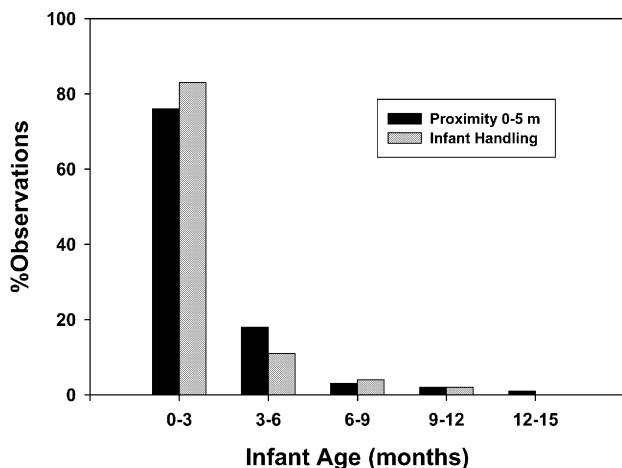
Our study population in Mikumi National Park, Tanzania, has been investigated since 1974 (Rhine 1986; Rhine et al. 2000). The present study complements a parallel study of determinants of lifetime reproductive success in this same troop of baboons (Wasser et al. 2004).

## Methods

### Study site and species

Twenty-four mother–infant dyads were studied in the Viramba 1 baboon troop (*P. cynocephalus*) at Mikumi National Park, Tanzania between 1983 and 1987. A detailed description of the study troop and ecology can be found in Rhine (1986) and Wasser and Norton (1993). The study troop is well habituated to the close proximity of observers on foot and has been studied since 1974. Details of the demography and female reproductive behavior of these baboons can be found in Rhine et al. (1988), Wasser and Starling (1988) and Wasser and Norton (1993).

Overall, 35 infants were born during the study period. Eleven mothers produced two offspring during this period. To avoid sampling bias, we included only the first born of these two infants in our analyses, providing a total sample size of 24 infants. These 12 male and 12 female infants stem from primiparous ( $n=8$ ) and multiparous ( $n=16$ ) females. The age at death (no. of days) of the infants that died during the study was: 3, 43, 47, 54, 78, 82. The age at death (no. of days) of the infants that died after the study period was: 201, 208, 285, 350, 361, 431, 478, 621, 642, 734, 1,303, 1,635, or >1,640 (missing values due to male transfer or continued survival). This clear cut-off in survival, with no mortality occurring between 3 and 6 months, was used as justification for examining infant survival to 3 months. We limit our analyses to infant handling behaviors that occur during the first 3 months of lactation, and



**Fig. 1** The mean proximity (shown as the relative percentage of cases during standardized protocols that other troop members were 0–5 m from mother–infant dyads) and the distribution of infant handling behavior in 3-month age blocks. Values are given as percentages of total observations for the infants' first 15 months.

show that 83% of mother–infant dyad social behavior is received during the infants' first 3 months of life (see Fig. 1). Maestriperi (1999) also found high levels of infant handling during the first 3 months of life in rhesus macaques, *Macaca mulatta*, which sharply declined thereafter, and Silk (1999) showed high levels of infant handling during the first 2 months of life in bonnet macaques *M. radiata*, which were still intermediate at 3 months, but very low by 5 months.

Dominance rank per adult female was calculated on an annual basis using cross-tabulations of agonistic behaviors (S.K. Wasser unpublished data). Infants were assigned the rank below that of their mothers (Hausfater 1975). For the analyses, we group the infants and their mothers into rank quartiles (1=highest ranked 25%, 4=lowest ranked 25% of adult females), since the absolute rank differs from year to year given variation in the number of troop members. There is a slight bias in favor of high-ranking females ( $n=6, 7, 7, 4$  for each rank quartile) in this study given longer inter-birth intervals and shorter life spans of low-ranking females (Wasser et al. 2004). The infants used in this study are descendants of 16 different matriline. Complete genealogical data are available for 17 infants, including their mothers and all aunts, uncles, cousins, and siblings (S.K. Wasser and G.W. Norton, unpublished data). In the analysis of kin versus non-kin for infant handling, we include only related adult females (aunt, adult sister, adult cousin). In the analysis of infant survival to age 3 months, we also include the variable "total number of relatives" (no. of kin: aunts, uncles, male and female siblings and cousins) alive per year for each infant.

Data are analyzed in relation to birth season (early wet, late wet, early dry, late dry) and birth order. Birth season refers to the following dates in any given year: 1 December–28 February (early wet); 1 March–31 May (late wet); 1 June–31 August (early dry), 1 September–30 November (late dry) (Rhine et al. 1988; Wasser and Norton 1993), which coincides with annual rainfall patterns in the study area (Wasser and Norton 1993). Birth cohort size refers to the number of infants born within a birth year (December–January). Birth order refers to the infant's order of birth within the cohort, whereas relative birth order is birth order divided by cohort size.

#### Data collection

Social behavior data were collected on the study troop 2 days a week during 1983–1987, except for two extended periods without field work from 5 January to 15 June 1985, and 15 September to 1 December 1987. Each mother–infant dyad was observed daily for

30 min on a rotating basis using focal animal sampling (Altman 1974). Proximity data (see below) were collected instantaneously three times per focal follow: at the start of the follow, at 15 min into the follow and at the end of the follow. Previous work (Wasser 1983) has shown the auto-correlation between samples to be minimal by 15 min. All behavior (see below) received or given by the mother was recorded on a continuous basis for two 15-min sessions, one session after each of the first two proximity data collections of the focal animal follow. For this study, we restrict the analyses to infant handling (see definitions below) of focal infants by adult females in the troop (excluding the mother). One additional behavioral category, aggression (threaten, chase, attack), is also analyzed. We note that this behavior is often directed at the mother–infant dyad, as opposed to just the infant, occurring predominantly when infants are on their mothers. All calculations of the frequency of infant handling behavior and mother–infant dyad behavior (aggression) were corrected for the number of follows per mother–infant dyad (mean $\pm$ SE number of follows per infant is: 16.2 $\pm$ 3.7). We use the frequency of infant handling as the unit of analysis, rather than the individuals performing the acts, to examine the effect of levels of infant handling on infant survivorship.

#### Definition of social behaviors

The definitions for behaviors examined in this study are as follows:

1. Proximity: number of individuals of a given age–sex class 0–1 m, 1–5 m, 5–15 m, and 15–25 m from the infant. The mean is calculated for three scores per focal observation (time 0 min, 15 min, 30 min) for each age–sex class and distance category.
2. Groom infant: calculated as a frequency per focal sampling period.
3. Negative infant handling: a composite behavior including rough handling, rough carrying and grab-pulling the infant off the mother. This variable is calculated as: negative handling = (number of rough handle + number of rough carry + number of grab-pull).
4. Rough infant handling: occurs when a baboon other than the mother briefly (<5 s) pushes, drops or shoves the infant. This includes pushing the infant's face to the ground and pushing the infant sideways (separate from tearing or pulling at the infant).
5. Rough infant carry: occurs when a baboon other than the mother awkwardly carries the infant (e.g. upside down, drags it by one leg) for  $\geq 5$  s.
6. Grab-pulling: occurs when a baboon tears or pulls the infant from its mother while the infant attempts to hold on.
7. Positive infant handling: a composite behavior including gentle touch, gentle handling, and gentle carry. This variable is calculated as: positive handling = (number of gentle touch + number of gentle handling + number of gentle carry).
8. Gentle infant touch: when a baboon other than the mother gently touches the infant (typically very brief <1 s duration).
9. Gentle infant handling: when a baboon other than the mother caresses (i.e. tactile exploration without probing) and/or holds the infant without dropping or abusing it in any obvious way for  $\geq 1$  s.
10. Gentle infant carry: when a baboon other than the mother carries the infant in a head-forward, secure position.
11. Aggression: a composite behavior including the variables threat (looking directly at the mother or infant while bobbing the head down, yawning, showing the pink of the eyelids and/or slapping the ground), chase (a running pursuit of the retreating mother–infant dyad) and attack (hitting or biting the infant, mother, or mother–infant dyad). The score is calculated as: (number of threats + number of chases + number of attacks).

### Age–sex class definitions

Data on each of the above proximity and behavioral categories were analyzed in relation to adult females in the troop. We distinguished among age–sex classes in the following way:

1. Adult females: females who already experienced their first menstrual cycle, generally 5 years or older. In specific cases, adult females are analyzed separately with regard to parity status (nulliparous, primiparous, multiparous).
2. Immature females: all females prior to experiencing their first menstrual cycle, generally less than 5 years and excluding infants (0–1 year).
3. Infant females: females aged 0–1 year.
4. Infant males: males aged 0–1 year.

### Statistics

Both parametric and non-parametric tests were used in the data analysis. Data were  $\log_{x+1}$  transformed to satisfy requirements of parametric tests. Analysis of variance and multiple regression were used to examine levels of infant handling for different characteristics of handlers and infants, and to examine the role of birth season, birth order and birth cohort size in relation to levels of infant handling.

## Results

### Troop demography 1983–1987

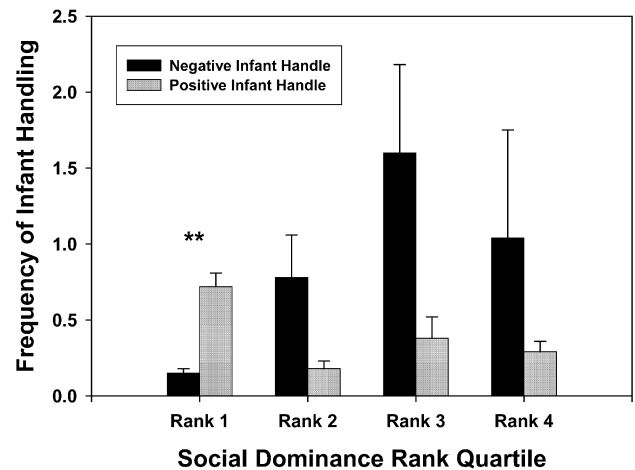
Troop composition was relatively constant for all age–sex classes during the period of analysis, 1983–1987. The annual mean±SD number of individuals per age–sex class is as follows: adult females: 20±2.6; adult males: 9±2.3; immature females: 12±4.2; immature males: 17±3.2; infant females: 4±2.1; infant males: 3±0.9. Mean troop size during 1983–1988 was 66±5.7 individuals. Troop size began to show a decline following 1988 that stabilized by 1994 (see Wasser et al. 2004).

### Proximity and behavior as a function of infant age

Figure 1 shows the mean proximity of other troop members to a mother–infant dyad as the percentage of cases that troop members were within 0–5 m of the mother–infant dyad, and the proportion of infant handling behavior, each as a function of the handled infant's age. Clearly, most proximity and infant handling occurs during the infant's first 3 months of life compared with all subsequent 3-month age blocks.

### Maternal dominance rank and infant handling

Infant handling by adult females (other than the mother) was examined as a function of maternal dominance rank. A multiple regression analysis examined rank quartile as the dependent variable against the following independent variables: groom, negative infant handling, positive infant handling, and aggression. We found an overall effect of



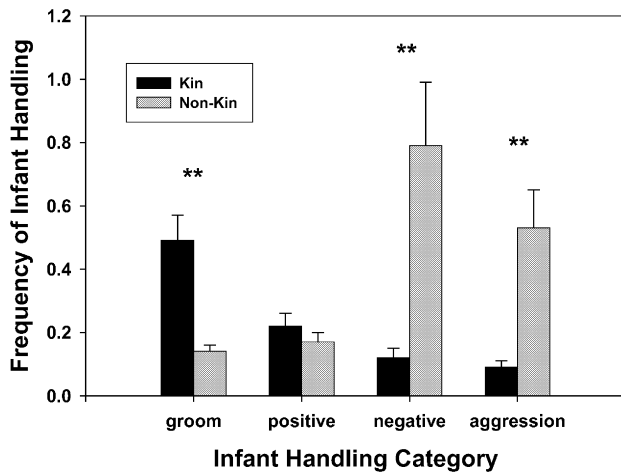
**Fig. 2** Infant handling behavior (means±SE) according to the dominance rank quartile ( $I$ = highest, 4= lowest) of the infant ( $n=6, 7, 7, 4$  respectively). Results are shown as mean frequency per 30 min of observation per infant

dominance rank on infant handling behavior ( $R^2=0.44$ ,  $P<0.03$ ). Infants of low-ranking mothers received higher levels of negative infant handling ( $r_{\text{partial}}=0.46$ ,  $\beta=0.39$ ,  $t=2.2$ ,  $P<0.04$ ) and aggression ( $r_{\text{partial}}=0.49$ ,  $\beta=0.49$ ,  $t=2.5$ ,  $P<0.03$ ) compared with infants of high-ranking mothers (Fig. 2).

Within each dominance rank quartile we compared levels of negative infant handling with positive infant handling using a Student's  $t$ -test (Fig. 2). The difference in infant handling was significant only for the top rank ( $t=4.157$ ,  $df=5$ ,  $P<0.01$ ) with higher levels of positive infant handling ( $0.72\pm 0.09$ ) compared with negative infant handling ( $0.15\pm 0.03$ ). Within ranks 2–4, negative infant handling occurred at non-significantly higher levels compared with positive infant handling, with high variance in negative infant handling behavior (rank 2:  $t=2.02$ ,  $df=6$ ,  $P=0.09$ ; rank 3:  $t=2.18$ ,  $df=6$ ,  $P=0.07$ ; rank 4:  $t=1.4$ ,  $df=3$ ,  $P>0.2$ ) (Fig. 2).

### Kinship and infant handling

Figure 3 presents the results for infant handling shown by adult female kin versus adult female non-kin. The difference in infant handling behavior for kin versus non-kin was tested using two-way ANOVA against the variables infant handling category (groom, positive infant handling, negative infant handling, aggression) and kin (kin, non-kin). Both variables and their interaction were significant in explaining the difference in levels of infant handling (ANOVA: category:  $F=2.7$ ,  $df=3$ ,  $P<0.05$ ; kin:  $F=8.04$ ,  $df=1$ ,  $P<0.005$ ; interaction effect category  $\times$  kin:  $F=13.18$ ,  $df=3$ ,  $P<0.001$ ). Overall, adult female kin engaged in more affiliative behavior (groom and positive infant handling) whereas adult female non-kin engaged in more agonistic behavior (negative infant handling and aggression).



**Fig. 3** The frequency of infant handling behavior per 30 min by adult female kin and non-kin. Means $\pm$ SE are shown for all infants ( $n=24$ )

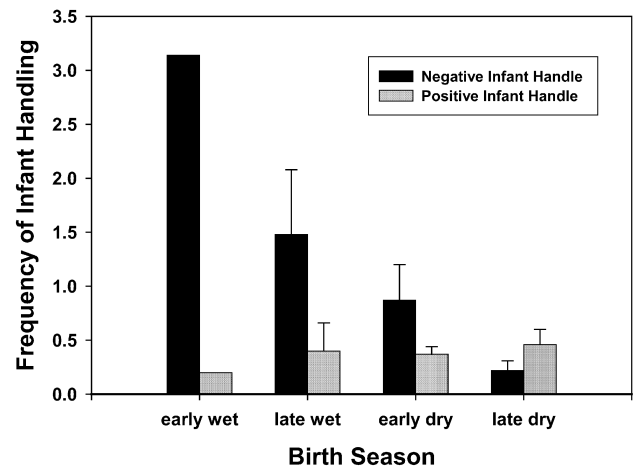
The number or type of kin (no. of siblings, no. of aunts, no. of uncles, no. of cousins, total no. of kin) present in the troop was not related to receipt of any of our behavioral measures of infant handling (regression analysis, all  $P>0.3$ ). Thus, number of kin alone may not buffer against behaviors such as negative infant handling or aggression.

#### Infant sex and infant handling

The sex of the infant was examined in relation to the variables groom, positive infant handling, negative infant handling, and aggression. Using multiple regression analysis, only the variable groom was significant ( $r_{\text{partial}}=0.44$ ,  $\beta=0.5$ ,  $t=2.1$ ,  $P<0.05$ ) in relation to infant sex. In a two-way ANOVA we compared groom with infant sex and rank. Adult females groomed infant females at higher levels than infant males (males:  $0.42\pm 0.35$ ; females:  $0.83\pm 0.52$ ) ( $F=5.5$ ,  $df=1$ ,  $P<0.05$ ). However, there was no interaction effect between infant sex and rank for grooms received.

#### Seasonal effects on infant handling

We found a significant effect of birth season on negative infant handling, with high negative handling in the early wet season (but  $n=1$ ) at the beginning of the ecological year, and progressive decline in negative handle over the next 12 months ( $R^2=0.35$ ,  $r_{\text{partial}}=-0.53$ ,  $\beta=-0.511$ ,  $t=-2.72$ ,  $P<0.02$ ) ( $n=1, 4, 13, 6$  for each season respectively; Fig. 4). This was tested using multiple regression analysis, with negative infant handling as the dependent variable tested against the independent variables birth season, birth order, cohort size and relative cohort position. There was no effect of birth order, cohort size or relative cohort position on receipt of negative infant



**Fig. 4** The frequency of infant handling behavior per 30 min is shown in relation to birth season (means $\pm$ SE for all infants,  $n=24$ ). The onset of the rains (*early wet*) corresponds roughly with the calendar month December. Sample sizes for each season are  $n=1, 4, 13, 6$  respectively

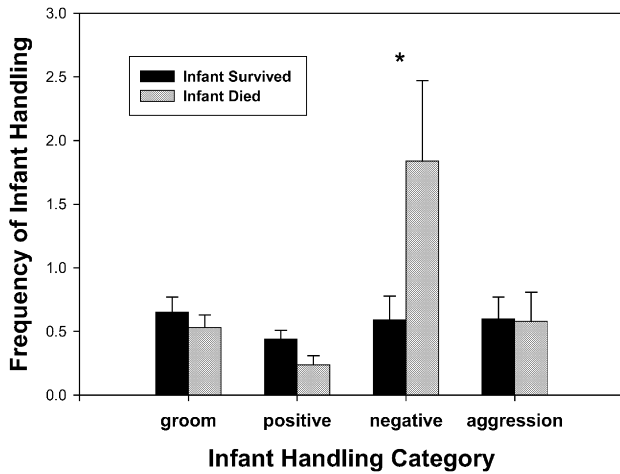
handling, and no effect of any of the variables for positive infant handling.

#### Maternal parity and infant handling

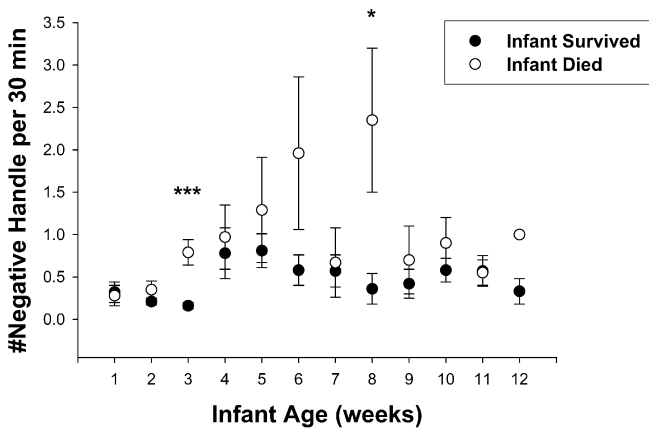
Maternal parity was not related to how frequently a female's infant was handled (groom, positive infant handling, negative infant handling, and aggression; Student's  $t$ -test, all  $P>0.2$ ; primiparous:  $n=6$  vs multiparous:  $n=16$ ). Offspring of primiparous females did not have fewer kin (no. of aunts, no. of uncles, no. of cousins, total no. of kin) compared with multiparous females (Mann-Whitney  $U$ -test, all  $P>0.3$ ), except for the variable no. of siblings, which was significant.

#### Infant mortality and infant handling

Six of 24 infants died by 3 months of age in the study (25%). Their ages (in days) at death were: 3, 43, 47, 54, 78, 82 (mean $\pm$ SE:  $51.2\pm 11.7$ ). The rank quartile distribution for these six infants was as follows: two infants each per rank quartile 2–4 (none of the infants that died was rank 1). Two of the infants were female, four were male. We do not have data on the direct cause of death in these infants. However, one infant in this study, Siku, received extremely high levels of negative infant handling on 14 February 1983 (42 grab-pulls in 1 h), and has the second highest mean level of negative infant handling ( $3.12\pm 1$  per 30 min) of all infants analyzed in this study. Siku died on 1 March 1983 (age 47 days), direct cause unknown, and continued to be carried by her mother Mwaka. Although Siku was dead, four adult females repeatedly tried to pull the infant away from the mother for several hours after its death (Wasser and Starling 1988). The cause of death was not observed for the five other



**Fig. 5** The frequency of infant handling behavior per 30 min for infants that survived to age 3 months ( $n=16$ ) versus those that died by age 3 months ( $n=6$ ). Shown are mean  $\pm$ SE for all infants



**Fig. 6** Negative infant handling in relation to infant age in weeks. Shown are mean  $\pm$ SE per week for infants that survived ( $n=4, 5, 11, 9, 13, 13, 12, 9, 11, 17, 8, 8$ ) and died ( $n=6, 5, 5, 5, 5, 3, 2, 2, 2, 1$ )

infants in this study. Four infants were missing from the troop on sequential days of observation (the mean gap in observational days was  $3 \pm 1.3$  days) with their mothers still present in the troop; one infant was missing with its mother (that is, both mother and infant were likely victims of predation). Negative infant handling cannot be inferred as the direct cause of death without more information.

Figure 5 shows the difference in average infant handling behavior between infants that survived to age 3 months ( $n=16$ ) and those that died ( $n=6$ ). Only negative infant handling differed significantly between these groups (Student's  $t$ -test:  $t=-2.58$ ,  $df=22$ ,  $P<0.02$ ); there was a higher, though not significant, level of positive infant handling in infants that survived (Student's  $t$ -test:  $t=1.8$ ,  $df=22$ ,  $P=0.1$ ). To examine if infants that die by age 3 months are on a different infant handling trajectory compared with infants that survive, we examined mean levels of negative infant handling per week (Fig. 6). Levels of negative infant handling were signifi-

cantly higher in infants that died compared with infants that survived by age 3 weeks (Mann Whitney  $U$ -test:  $z=-3.118$ ,  $P<0.002$ ) and at 8 weeks ( $z=-2.225$ ,  $P<0.04$ ), with a non-significant result at age 6 weeks ( $z=-1.7$ ,  $P=0.09$ ).

To examine effects of both demographic (e.g. sex, rank, no. of kin, no. of aunts) and behavioral (e.g. groom, positive infant handling, negative infant handling, aggression) variables on infant mortality by age 3 months, we conducted logistic regression analysis. The dependent variable was survival to 3 months (0=survived, 1=died). We first examined the relative significance of each variable in relation to infant survival. For the continuous variables we used univariate logistic regression analysis: groom (odds ratio,  $OR=0.554$ ,  $P>0.5$ ), negative handling ( $OR=2.58$ ,  $P<0.05$ ), positive handling ( $OR=0.049$ ,  $P>0.2$ ), aggression ( $OR=0.35$ ,  $P=0.09$ ), no. of kin ( $OR=0.52$ ,  $P>0.1$ ), no. of aunts ( $OR=0.29$ ,  $P>0.1$ ); and for the categorical variables we used chi-squared tests: infant sex ( $\chi^2=0.68$ ,  $df=1$ ,  $P>0.4$ ) and rank quartile ( $\chi^2=3.4$ ,  $df=3$ ,  $P>0.3$ ). The only significant variable in these single comparisons was the variable negative infant handling; aggression was not significant. Using multiple logistic regression for these two variables, only negative infant handling was significantly related to infant survival ( $OR=2.58$ ,  $P<0.05$ . Nagelkerke  $R^2=0.284$ ; for aggression  $P>0.2$ ).

## Discussion

Results of this study support predictions of the female reproductive competition hypothesis (FRCH) to explain patterns of infant handling behavior in this population. The main findings that lend support to FRCH are as follows: (1) low-ranking infants were negatively handled at higher rates than were high-ranking infants (Fig. 2); (2) female kin engaged in higher levels of positive infant handling than did non-kin, and conversely female non-kin engaged in higher levels of negative infant handling than did kin (Fig. 3); (3) we found a strong seasonal effect of negative infant handling, with high levels at the onset of the rainy season in December (Fig. 4); (4) high level of negative infant handling was a significant predictor of infant mortality by age 3 months (Fig. 5), and (5) by age 3 weeks, infants that died were on a different negative infant handling trajectory compared with infants that survived (Fig. 6). We found no effect of maternal rank or infant sex on survival to 3 months, and no effect of infant sex on incidence of negative infant handling. However, female infants received higher levels of groom than did male infants.

### Maternal dominance rank and infant handling

Social dominance rank was clearly related to patterns of infant handling (Fig. 2). Low-ranking infants received higher levels of negative infant handling and aggression,

but with high variance, compared with high-ranking infants, whereas the opposite pattern was found for positive infant handling. Maestripieri (1999) found a virtually identical pattern among rhesus macaques, *M. mulatta*. While negative infant handling and aggression were negatively correlated with infant survival, dominance rank alone did not predict infant mortality. Clearly the social environment of infants is affected by their rank quartile (Cheney 1977; Wasser 1983; Cheney et al. 1986; Fairbanks and McGuire 1986; Wasser and Wasser 1995). More restrictive mothering styles have been associated with low rank and more permissive mothering styles with high rank in baboons (Altman 1980). This has been argued to arise from a more socially hostile environment experienced by low-ranking mothers that is compensated for by restrictive mothering (Altman 1980; Berman 1990; Wasser and Wasser 1995; Berman et al. 1997). Our results support this assertion, with evidence of higher levels of aggression and negative infant handling for low-ranking infants. Multivariate statistical analysis showed that the level of negative infant handling (and aggression) was a better predictor of infant mortality than was maternal dominance rank. In this population, maternal dominance rank effects on lifetime reproductive success occurred largely through impacts on offspring production (e.g. interbirth interval, reproductive life span) and only weakly on offspring survivorship to 4 years, for male infants only (Wasser et al. 2004).

#### Birth season, relative cohort position and infant handling

The FRCH begs the question: what are young baboons competing for? Altman (1980) suggested that limited weaning foods were tied to reproductive competition among females. Norton et al. (1987) examined resource distribution and food use among the Mikumi baboons, and documented preferred weaning foods that are available only in the wet season (infants are weaned at around 8 months after birth, Rhine et al. 1985). Rhine et al. (1988) showed a seasonal shift in patterns of infant mortality; infant mortality was highest in the late dry season when the amount and diversity of foods is lowest and the troop is most mobile, infant mortality was lowest in the late wet season when the opposite holds true (Norton et al. 1987; Rhine et al. 1988). Rhine et al. (1988) and Wasser and Norton (1993) also documented increased mortality probability with increased birth cohort sizes. Combined, these results suggest that there is competition for limited age-specific resources among immature baboons (e.g. weaning foods). Our results show that birth season was related to levels of negative infant handling, with high levels during the early rainy season. This is expected by the FRCH as females should be trying to offset any age advantage of these earliest born infants, including those born late in the prior birth year (see also Wasser and Norton 1993). An alternative hypothesis to explain this pattern is that female time budgets are less constrained in the wet season, making it less costly to

handle infants. However, this does not explain why we find a peak in negative infant handling during the wet season, and not in positive infant handling. Moreover, food is more abundant in the late than early wet season (Rhine et al. 1988), whereas negative infant handling was highest in the early wet season.

#### Infant mortality and infant handling

We do not propose that negative infant handling directly causes mortality, although some instances of this have been observed in our study troop (Wasser and Starling 1988). Rather, high levels of harassment may result in diminished competitive abilities of handled infants through increased physiological stress, disrupted lactation, increased maternal time budget, lower feeding opportunities and occupation of more peripheral troop locations by mother–infant dyads. We suspect that nutritional insufficiency due to interrupted lactation (see Wasser and Barash 1981), as well as increased predator susceptibility and higher probabilities of infant's getting lost are the most significant causes of the observed mortality patterns associated with negative infant handling found in this study. Rhine et al. (1988) found that the amount of rain in the first month of the rainy season was highly correlated with infant survival in the first year of life. They hypothesized that early rain causes grass to grow taller faster, increasing the probability of infants getting lost and/or experiencing predation. Predation and risk of getting lost could be tied to social harassment if negative social behavior forces recipient females and their infants to more peripheral locations in the troop. When our baboon population crashed following this study, suspected leopard depredation accounted for 23.8% of all observed mortality cases in these baboons (Wasser et al. 2004).

#### Evidence for female reproductive competition

There is considerable evidence for female reproductive competition in the Mikumi baboons (Wasser and Starling 1988; Wasser and Norton 1993; Wasser et al. 1998, 2004). High-ranking females have significantly higher lifetime reproductive success than do low-ranking females. They reach menarche earlier, have shorter interbirth intervals, fewer abortions, shorter lactation periods, and longer reproductive and total life spans than do subordinate females (Wasser et al. 2004).

At the proximate level, Wasser and Starling (1988) showed that adult females selectively target other females in agonistic interactions based on reproductive states. These interactions are correlated with the suppression of reproduction in targeted females (and may explain the observed rank-related temporal shifts in birth peaks) (Wasser 1996). The frequency of this female–female agonistic behavior is positively correlated with predictors of increased birth cohort size (i.e., number of estrous and pregnant females) (Wasser and Starling 1988). Previous

studies have shown that infant mortality increases with birth cohort size, and this is especially the case for female infants (Rhine et al. 1988; Wasser and Norton 1993). All cases of infant killing by adult females, which were preceded by prolonged periods (usually days) of attacks on infants (i.e. negative infant handling), were observed during the early wet season (Wasser and Starling 1988). The highest rates of negative infant handling in our study also occurred among infants born during the wet season. Negative infant handling, a behavior that shows variation in relation to ecological and social conditions, thus appears to contribute to the pronounced skew in female reproductive success in this species.

## Conclusion

Wild populations of mammals are likely to differ in the extent of reproductive competition between females, as well as in access to one another's offspring, due to parameters such as resource distribution, group size and group composition (Smuts et al. 1987; Dunbar 1988). Combined, these differences may explain part of the variation in patterns of infant handling found across primate species and studies. For example, among langur, patas, cebus and vervet monkeys the handling and care of young infants is often characterized by relaxed and friendly contacts by non-mothers (Poirier 1968; Lee 1983; Nicolson 1987; Fairbanks 1990; Stanford 1992; Muruyama 1994; Garber and Leigh 1997; Manson 1999). In contrast, among several species of macaques, baboons, and chimpanzees, infant handling is often abusive (Silk 1980; Silk et al. 1981; Hiraiwa 1981; Lee 1983; Nishida 1983; Collins et al. 1984; Nicolson 1987; Wasser 1983; Wasser and Starling 1988; Maestriperi 1993, 1999). Indirect female infanticide due to abusive infant handling occurs in other taxonomic groups, such as hyenas *Crocuta crocuta* (M. East, personal communication; Hofer and East 1995); yet, this is challenging to systematize given its potentially sporadic occurrence during brief periods of relative resource scarcity. Paul and Kuester (1996) write that kidnapping led to the death of 12 of 37 infants during their first 3 months of life in barbary macaques, *M. sylvanus*, with frequent negative infant handling over a few days probably contributing to infant death in four cases. Paul and Kuester (1996) suggested this could not be explained by the reproductive competition hypothesis since overall there was no clear pattern of infant mortality associated with infant handling. However it is not clear how these authors measured infant handling during kidnapping events given the definition of infant handling as holding, carrying or grooming infants (Paul and Kuester 1996). This points to the role of definitions of infant handling in data interpretation, which vary considerably from one study to the next. For example, in Silk (1999) infant handling is restricted to the variables greet, muzzle, touch, groom, inspect, pull, carry, hold. In this case, pulling is the only variable that approaches a measure of negative handle since it involves resistance from the mother (all

other variables in essence score for positive handle). Maestriperi (1999) provides detailed measures of infant abuse (eight in total), and scores aunting as touch, hold, carry or groom infants. Thus, many authors include groom as a measure of infant handling and assume that it represents positive infant handling. In this study, we attempted to provide symmetrical measures of positive and negative infant handling, and treated groom and aggression as separate variables.

Suppression of negative infant handling behavior in females may be due to male vigilance and interference in order to protect the male's offspring (Klein 1983; Collins 1986), making it difficult to find clear patterns of overt female aggression in the form of sustained negative infant handling. Risk of infanticide is proposed to explain the evolution of male-female associations in primates (van Schaik and Kappeler 1997), and may be a significant factor influencing group size regulation in Thomas's langurs, *Presbytis thomasi* (Steenbeek and van Schaik 2001). Based on such results, it is clear that patterns of abusive infant handling need to be similarly understood within a socio-ecological framework including parameters like paternity certainty and group composition (single male vs multi-male groups, number of related adult females). In large multi-male groups, paternity certainty is lower and average group size is larger thereby decreasing the likelihood that males will observe specific acts of infant handling or be concerned with such behavior among females. These conditions create more opportunities for overt female competition without male interference. Also, large multi-male groups have more adult females and hence more unrelated female competitors, in addition to more mouths to feed. We suspect that infant handling, like grooming (Dunbar 2003), is a behavior that has multiple functions and associated consequences. Thus, the multifunctional role of infant handling behavior complicates attempts to tease apart hypotheses for its expression without considering the multiple needs and constraints facing the various individuals involved in this behavior.

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