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Gabriele Schino · Alfonso Troisi

Mother-infant conflict over behavioral thermoregulation in Japanese macaques

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Abstract This study evaluated the effects of time of day, ambient temperature, and relative humidity on mother-infant interactions in captive Japanese macaques (*Macaca fuscata*). Unlike time of day and relative humidity, temperature influenced mother-infant interactions. Even though total time spent in ventroventral contact did not change, lower temperatures were associated with greater attempts by the infants to maintain contact with their mothers and with more frequent maternal rejection. Effects of temperature on mother-infant interactions were not mediated by the effects of temperature on mothers' general activity. These results are interpreted in light of the different thermoregulatory needs of mothers and infants, and highlight a previously neglected cause for mother-infant conflict.

Key words Mother-infant conflict · Behavioral thermoregulation · Temperature · *Macaca fuscata*

Introduction

In 1974, Robert Trivers introduced the concept of mother-offspring conflict (Trivers 1974). He argued that, due to different genetic interests, mothers and infants should conflict over the amount of maternal care. More recently, it has been proposed that in nonhuman primates, mother-infant conflict should occur more over the timing than over the amount of maternal care. In fact, both Altman (1980) and Barrett et al. (1995) observed that maternal rejection is often context dependent, and hypothesized that mothers attempt to structure infant contact time so as to minimize disturbance during foraging. Thus, while conflict may occur because of differences between mothers and infants in long-term genetic interests, at a proximate level it may depend on differences in immediate ecological needs (e.g., foraging vs nursing).

Among the ecological variables likely to generate mother-infant conflict is ambient temperature. In fact, adult and infant primates, due to their different size, have different thermoregulatory needs and their thermoregulatory behaviors are therefore expected to differ. Quite surprisingly, although an influence of climatic factors has been demonstrated on a variety of primate social and nonsocial behaviors (e.g., Bernstein 1975, 1976, 1980; Troisi and Schino 1986, 1987), to our knowledge, no study has investigated possible climatic influences on primate mother-infant relationships.

In this paper we report data on the effects of time of day, ambient temperature, and relative humidity on mother and infant behavior in captive Japanese macaques. Our results suggest that the different thermoregulatory needs of mothers and infants can lead to a previously neglected cause of mother-infant conflict.

Methods

Subjects and housing

Subjects of this study were members of a captive group of Japanese macaques (*Macaca fuscata*) living in Rome zoo. The group had been captured together in Takasakiyama, Japan, in 1977. During the study period, it numbered 53–87 monkeys and was housed in a 700-m^2 outdoor enclosure provided with smaller indoor compartments. Details of the group history and composition are given in Schino et al. (1995).

Data collection

Two different data sets were available. The larger data set consisted of 53 mother-infant dyads which were the

G. Schino (✉)
Centro Studi Etologici, Via Flaminia 109, I-00196 Rome, Italy
e-mail: glogab@rmnet.it

A. Troisi
Cattedra di Psichiatria, Università Tor Vergata, Rome, Italy

subjects of three 15-min observation sessions a week for the first 12 weeks of the infant's life. Data were collected using the one-zero method with 15-s intervals. Infants in the larger data set were born in the 1986, 1988, 1989, 1990, and 1992 birth seasons. Observations were carried out either in the morning or in the afternoon, avoiding the central hours of the day, but no formal attempt was made to sample the different hours evenly. For these reasons, the larger data set was not used to evaluate the effects of time of day. Temperature and relative humidity were not recorded at the time of the observations. Instead, mean daily temperatures for each week of each infant's life were obtained from the Ufficio Centrale di Ecologia Agraria of Rome, only a few kilometers from the zoo.

The smaller data set consisted of eight mother-infant dyads sampled during the 1991 birth season. Each dyad was the subject of seven 15-min observation sessions for each 3-week block for the first 27–33 weeks of the infant's life. Data were collected using the one-zero method with 15-s intervals. Observations were carried out between 1000 and 1700 hours and were balanced with respect to time of day. One session was carried out for each hour of the day for each infant for each 3-week block of its life. At the time of the observation, temperature and relative humidity were measured in the shade with a mercury thermometer and a hair hygrometer.

Summarizing, the first data set (which had not in fact been collected with this particular study in mind) was larger but based on a shorter infant life span and less accurate climatic data, whereas the second data set was smaller but based on a longer infant life span and more accurate and extensive climatic data.

A number of mother and infant behaviors were recorded during the study. Here we present data on time spent in ventroventral contact (the proportion of 15-s intervals during which the infant was recorded in ventroventral contact with its mother), on maternal rejection (the proportion of the infant's attempts to gain ventroventral contact that were rejected), and on the relative roles played by infants and mothers in maintaining ventroventral contact as evaluated through the index proposed by Hinde and Atkinson (1970). This index is calculated as the relative proportion of contacts initiated by the mother minus the relative proportion of contacts interrupted by the mother. Beside sampling mother-infant interactions, in 1990 and 1992, we collected data on mothers' general activity (the proportion of sampling points during which the mother was recorded resting or grooming) using the instantaneous sampling technique with 60-s intervals. Analysis of maternal activity is therefore based on a subsample of the larger data set (i.e., 27 out of 53 mother-infant pairs).

The method we chose for sampling mother-infant interactions (one-zero) provides slightly overestimated durations and slightly underestimated frequencies of behavior (Leger 1977; Rhine and Flanigon 1978). However, since interval duration was short (15 s), and since it seems unlikely that the above biases would affect our data differently in different climatic conditions, our results were unlikely to be significantly affected by our sampling technique.

Data analysis

Time of day

Since time spent in ventroventral contact is influenced by age of the infant (e.g., Schino et al. 1993) and since temperature and relative humidity vary during the day, these variables were inserted as covariates in the analysis of variance testing if time spent in ventroventral contact varied with time of day. Separate ANCOVAs were carried out for each mother-infant dyad in the small data set and the resulting probabilities were then combined using Fisher's technique. Such a technique is fully independent of sample size, being based directly on the *P* values (Sokal and Rohlf 1981). It was not possible to use this same procedure to test the effect of time of day on Hinde's index and maternal rejection because the data were insufficient to provide meaningful ratios for each hour of each 3-week block of each infant's life. Therefore, we averaged for each age block and each hour of day the different infants' scores, and carried out one-way repeated-measures ANOVAs on these averaged scores. Although not entirely satisfactory, this procedure allows a rough estimate of the effects of time of day on Hinde's index and maternal rejection.

Intradyadic and interdyadic analyses

Effects of temperature and relative humidity on mother-infant interactions and maternal activity were evaluated both intradyadically and interdyadically. In the intradyadic analyses, separate correlation coefficients were calculated for each mother-infant dyad across the different infant ages. Their distribution between positives and negatives was obtained and the probability of obtaining a similar or more extreme distribution was calculated by means of the binomial test. This is the correlational equivalent of a paired sample or repeated-measures test in that each individual is compared only with itself. A similar method was used by Simpson (1973) and Schino et al. (1988, 1993). In the interdyadic analyses, separate correlation coefficients were calculated across the different dyads for each infant age block, and the probability of their distribution calculated as above. Thus, the intradyadic analyses evaluated whether mother-infant dyads changed their behavior in response to day-to-day climatic variations, whereas the interdyadic analyses evaluated whether the different climatic conditions experienced by infants born in different periods of the year accounted for the interindividual variation in mother-infant relationships.

Temperature

Effects of temperature were evaluated calculating partial correlation coefficients between ambient temperature and mother-infant behaviors and maternal general activity. In the intradyadic analyses carried out on the smaller data set, we partialled out the effects of infant age and relative humidity. In the larger data set, relative humidity data were not available, so only infant age was partialled out. In the interdyadic analyses, separate correlations were calculated for each infant age block. Therefore, only relative humidity was partialled out in the smaller data set, whereas no variable was partialled out in the larger data set.

Relative humidity

Effects of relative humidity were evaluated only in the smaller data set. The procedure was similar to that used to evaluate the effect of temperature. Infant age and ambient temperature effects were partialled out in the intradyadic analyses, whereas only temperature was partialled out in the interdyadic analyses.

Estimate of effect sizes

The analyses described above do not give information about effect sizes. To estimate effect sizes, for each data set we pooled data from all subjects and calculated partial correlation coefficients between climatic and behavioral variables while controlling for age effects. This procedure can neither discriminate between intradyadic and interdyadic effects, nor be used to test for significance due to large pseudoreplication, but gives nevertheless an estimate of effect size.

All variables were tested for normality. Ratio measures were subjected to arcsine transformation before being entered into analyses. Throughout the presentation of the results, N_{r+} indicates the number of positive *r*s and N_{r-}, the number of negative *r*s. All probabilities are two tailed.

Results

Mean temperatures experienced by our subjects were 22.4 ± 0.4 °C (mean and standard error) and 19.2 ± 0.6 °C in the larger and smaller data sets, respectively, while mean relative humidity was 65.6 ± 0.6% (small data set only). Infants in the larger data set spent on average 69.9 ± 1.6% of observation time in ventroventral contact. The score for maternal initiative in maintaining contact was 0.426 ± 0.029 and that for maternal rejection 0.074 ± 0.013. In the smaller data set, the equivalent figures were 42.7 ± 2.4%, 0.405 ± 0.026, and 0.170 ± 0.029, respectively. The differences between the two data sets are due to differences in the infant age span during which data were collected (the first 12 versus the first 27–33 weeks of infant life). More detailed data on the time course and interindividual variation of mother-infant relationships in these Japanese macaques can be found in Schino et al. (1993, 1995).

Effect of time of day

The effect of time of day on mother-infant interactions was evaluated only for the smaller data set (see Methods). No significant effects on ventroventral contact were observed for either time of day (Fisher's combined probability: $\chi^2 = 14.952$, $df = 16$, n.s.) or its interaction with temperature ($\chi^2 = 14.639$, $df = 16$, n.s.), relative humidity ($\chi^2 = 15.416$, $df = 16$, n.s.), or age of the infant ($\chi^2 = 14.445$, $df = 16$, n.s.). Similarly, time of day exerted no significant effect on either the relative roles played in maintaining contact ($F = 0.502$, $df = 6.36$, n.s.) or maternal rejection ($F = 0.629$, $df = 6.42$, n.s.).

Intradyadic analysis: effect of temperature

In the intradyadic analysis, ambient temperature exerted no significant effect on the time infants spent in ventroventral contact with their mothers either in the smaller data set ($N_{r+} = 3$, $N_{r-} = 5$, binomial test: n.s.), or in the larger data set ($N_{r+} = 22$, $N_{r-} = 31$, n.s.). Combining the probabilities from the two tests using Fisher's technique again yielded nonsignificant results ($\chi^2 = 3.25$, $df = 4$, n.s.).

In contrast, temperature was significantly and positively correlated with the role played by the mothers in maintaining ventroventral contact in the smaller data set ($N_{r+} = 8$, $N_{r-} = 0$, $P = 0.008$), whereas in the larger data set, the correlation approached significance ($N_{r+} = 27$, $N_{r-} = 15$, $P = 0.09$). The combined probability was also significant ($\chi^2 = 14.47$, $df = 4$, $P = 0.008$). In other words, decreasing temperatures were associated with an increasing role of the infants in maintaining contact with their mothers.

Temperature was also significantly and negatively correlated with maternal rejection in the larger data set ($N_{r+} = 11$, $N_{r-} = 25$, $P = 0.03$), but not in the smaller data set ($N_{r+} = 5$, $N_{r-} = 3$, n.s.). The combined probability was not significant ($\chi^2 = 7.65$, $df = 4$, n.s.). Thus, decreasing temperatures were associated with an increase in the proportion of the infant's attempts to establish contact that were rejected by the mother, at least in the larger data set.

Intradyadic analysis: effect of relative humidity

Relative humidity data were only available for the smaller data set. In the intradyadic analysis, relative

humidity had no effect on time spent in ventroventral contact ($N_{r+} = 2$, $N_{r-} = 6$, n.s.), on the relative roles played by mothers and infants in maintaining contact ($N_{r+} = 3$, $N_{r-} = 5$, n.s.), and on maternal rejection ($N_{r+} = 4$, $N_{r-} = 4$, n.s.).

Interdyadic analysis: effect of temperature

Results of the interdyadic analyses were similar to those of the intradyadic analyses. Ambient temperature was not significantly correlated with time spent in ventroventral contact (smaller data set: $N_{r+} = 5$, $N_{r-} = 4$, n.s.; larger data set: $N_{r+} = 7$, $N_{r-} = 5$, n.s.; combined probability: $\chi^2 = 0.51$, $df = 4$, n.s.). In contrast, temperature was significantly and positively correlated with the relative role played by the mothers in maintaining ventroventral contact (smaller data set: $N_{r+} = 8$, $N_{r-} = 1$, $P = 0.04$; larger data set: $N_{r+} = 10$, $N_{r-} = 2$, $P = 0.038$; combined probability: $\chi^2 = 12.98$, $df = 4$, $P = 0.012$). Unlike the intradyadic analysis, correlations between maternal rejection and temperature failed to reach significance (smaller data set: $N_{r+} = 3$, $N_{r-} = 5$, n.s.; larger data set: $N_{r+} = 3$, $N_{r-} = 8$, n.s.; combined probability: $\chi^2 = 3.61$, $df = 4$, n.s.).

Interdyadic analysis: effect of relative humidity

Similar to the intradyadic analyses, in the interdyadic analyses, ambient relative humidity had no effect on time spent in ventroventral contact ($N_{r+} = 5$, $N_{r-} = 4$, n.s.), on the relative roles played by mothers and infants in maintaining contact ($N_{r+} = 4$, $N_{r-} = 5$, n.s.), and on maternal rejection ($N_{r+} = 4$, $N_{r-} = 4$, n.s.).

Effect of temperature on mothers' general activity

To test whether the effects of ambient temperature on mother-infant interactions were mediated by its effects on maternal activity, we evaluated the relationship between temperature and the time mothers spent resting and grooming. This analysis was carried out on the larger data set only. In the intradyadic analysis, ambient temperature exerted no effect on time spent resting and grooming ($N_{r+} = 14$, $N_{r-} = 13$, n.s.). Similarly, the interdyadic analysis revealed no effect of temperature on resting and grooming ($N_{r+} = 9$, $N_{r-} = 3$, n.s.).

Estimate of effect sizes

Results of correlations based on pooled data are shown in Table 1. The analyses above had shown that the only consistently significant effect was that of temperature on the role played by the mother in maintaining contact. Variation in ambient temperature accounted for 1.4–15.8% of the variance in the role played by the mother in maintaining contact.

Discussion

The results reported in this paper show that mother-infant contact is influenced neither by time of day (within the 10.00–17.00 hours time window) nor by relative humidity. Temperature did not influence the amount of mother-infant contact, but did influence the relative roles played by mothers and infants in maintaining such contact. Decreasing temperatures were associated with an increasing role played by the infants in maintaining contact with their mothers and (at least in the larger sample of the intradyadic analysis) with more frequent maternal rejection. Not only was temperature associated with day-to-day variations in mother-infant interactions, but it also explained part of the interindividual variability. In other words, each infant had to play a greater role in maintaining contact on those days on which temperature was lower, *and* those infants that were born when average temperatures were lower had to play a greater role in maintaining contact with their mothers than those infants born when average temperatures were higher. Thus, temperature effects extended from single mother-infant interactions to whole mother-infant relationships (Hinde 1976).

One could hypothesize that the effects of temperature on mother-infant interactions were secondary to the effect of temperature on maternal time budgets since, when temperatures are higher, monkeys often tend to rest and groom more and thus (possibly) reject their infant less (see the Introduction for a discussion of context-dependent maternal rejection). This hypothesis is, however, unlikely to explain our results, since in our

Table 1 Estimate of effect sizes: partial correlations between climatic and behavioral variables based on pooled data

	Temperature		Relative humidity
	Larger sample	Smaller sample	Smaller sample
Ventroventral contact	0.031	0.030	−0.087
Maternal role in maintaining contact	0.118	0.398	−0.103
Maternal rejection	−0.076	0.076	−0.069
Maternal resting and grooming	0.173	–	–

sample, temperature did not affect mothers' general activity (see also Troisi et al. 1982 for more detailed data on the absence of an effect of temperature on grooming in this Japanese macaque group).

It is worth noting that the Japanese macaque subjects of our study were exposed to climatic conditions similar to those typical of their natural environment. Italy and Japan share a similar temperate climate: for example, annual mean temperatures in Rome and Oita (the weather station closest to Takasakiyama, where our macaques originated) are 15.7 °C and 15.6 °C, respectively, while seasonal variations are also similar, although in Japan they are slightly more extreme [Rome data were provided by the Istituto Nazionale di Statistica, Japanese data are taken from the Japan Statistical Yearbook (Statistics Bureau Management and Coordination Agency 1984), see also Arakawa and Taga 1969]. The results we obtained are therefore likely to apply to wild Japanese macaques as well.

Unlike mother-infant contact, huddling between adult macaques has been reported to increase with decreasing temperatures (Dahl and Smith 1985; Dahl et al. 1986; Schino and Troisi 1990). Interindividual contact requires the coordination of the behavior of both partners. The absence of an increase in mother-infant contact with lower ambient temperatures could be explained by the different thermoregulatory needs of adults and infants. Being smaller, infants have a higher surface-to-volume ratio and therefore lose heat more rapidly than adults. They are expected to be more sensitive to low ambient temperatures than adults and, as a consequence, to attempt to establish thermoregulatory contact when the mother does not have the same need. Furthermore, their smaller size may make them less profitable as thermoregulatory huddling partners. This interpretation is supported by the observation that the relative role played by infants in maintaining contact increased with decreasing ambient temperatures. In addition, when temperatures were lower, mothers tended to reject a higher proportion of infants' attempts to establish contact, further supporting the hypothesis that under such conditions, the thermoregulatory needs of mothers and infants may clash. Thus, climatic variations and the different thermoregulatory needs of mothers and infants may constitute a (further) cause for mother-infant conflict.

Several studies have demonstrated that, in nonhuman primates, early interactions with the mother can have long-lasting effects on the development of social behavior. In vervet monkeys, male and female infants born to restrictive mothers were less enterprising as juveniles, and female infants were more restrictive towards their own infants as adults (Faibanks and McGuire 1988; Fairbanks 1989). Furthermore, infant macaques who had to play a greater role in maintaining proximity to their mothers were more likely to show depressive reactions as a consequence of maternal separation (Hinde and Spencer-Booth 1970). These findings may be relevant for a better understanding of the implications of our results.

Infants of primate species inhabiting temperate areas can experience different ambient temperatures depending on their date of birth, even if births are restricted to the warmest months of the year. For example, in our sample, mean temperatures experienced by infants during their first 12 weeks of life varied between 13.4 and 25.7 °C. If temperature can affect early mother-infant interactions, and if these interactions can in turn influence adult behavior, then early "climatic experiences" may be a factor that should be taken into account when trying to explain variability in adult interindividual behavior. It is hoped that this study will stimulate more detailed investigations of both short- and long-term influences of climatic factors on primate behavior.

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References

Altman J (1980) Baboon mothers and infants. Harvard University Press, Cambridge, Mass

Arakawa H, Taga S (1969) Climate of Japan. In: Arakawa H (ed) Climates of northern and eastern Asia. Elsevier, Amsterdam, pp 119–133

Barrett L, Dunbar RIM, Dunbar P (1995) Mother-infant contact as contingent behaviour in gelada baboons. Anim Behav 49:805–810

Bernstein IS (1975) Activity patterns in a gelada monkey group. Folia Primatol 23:50–71

Bernstein IS (1976) Activity patterns in a sooty mangabey group Folia Primatol 26:185–206

Bernstein IS (1980) Activity patterns in a stumptail macaque group (*Macaca arctoides*). Folia Primatol 33:20–45

Dahl JF, Smith EO (1985) Assessing variation in the social behavior of stumptail macaques using thermal criteria. Am J Phys Anthropol 68:467–477

Dahl JF, Bernstein IS, Williams LE (1986) Thermoregulation and social structure of a captive group of rhesus macaques. In: Taub DM, King FA (eds) Current perspectives in primate social dynamics. Van Nostrand Reinhold, New York, pp 243–251

Fairbanks LA (1989) Early experience and cross-generational continuity of mother-infant contact in vervet monkeys. Dev Psychobiol 22:669–681

Fairbanks LA, McGuire MT (1988) Long-term effects of early mothering behavior on responsiveness to the environment in vervet monkeys. Dev Psychobiol 21:711–724

Hinde RA (1976) Interactions, relationships, and social structure. Man 11:1–17

Hinde RA, Atkinson S (1970) Assessing the roles of social partners in maintaining mutual proximity, as exemplified by mother-infant relations in monkeys. Anim Behav 18:169–176

Hinde RA, Spencer-Booth Y (1970) Individual differences in the responses of rhesus monkeys to a period of separation from their mothers. J Child Psychol Psychiatry 11:159–176

Leger D (1977) An empirical evaluation of instantaneous and one-zero sampling of chimpanzee behavior. Primates 18:387–393

Rhine RJ, Flanigon M (1978) An empirical comparison of one-zero, focal animal, and instantaneous methods of sampling spontaneous primate social behavior. Primates 19:353–361

Schino G, Troisi A (1990) Behavioral thermoregulation in long-tailed macaques: effect on social preference. Physiol Behav 47: 1125–1128

Schino G, Scucchi S, Maestripieri D, Turillazzi PG (1988) Allogrooming as a tension-reduction mechanism: a behavioral approach. Am J Primatol 16:43–50

Schino G, D'Amato FR, De Angelis N, Mari N, Troisi A (1993) Development of mother-infant relationships in Japanese macaques (*Macaca fuscata*). Boll Zool 60:301–306

Schino G, D'Amato FR, Troisi A (1995) Mother-infant relationships in Japanese macaques: sources of interindividual variation. Anim Behav 49:151–158

Simpson MJA (1973) The social grooming of male chimpanzees. In: Michael R, Crook J (eds) Comparative ecology and behaviour of primates. Academic Press, London, pp 411–505

Sokal RR, Rohlf FJ (1981) Biometry, 2nd edn. Freeman, New York

Statistics Bureau Management and Coordination Agency (ed) (1984) Japan statistical yearbook. Japan Statistical Association, Tokyo

Trivers RL (1974) Parent-offspring conflict. Am Zool 14:249–264

Troisi A, Schino G (1987) Environmental and social influences on autogrooming behaviour in a captive group of Java monkeys. Behaviour 100:292–303

Troisi A, D'Amato FR, Fuccillo R, Scucchi S (1982) Diurnal pattern of allogrooming in a group of Japanese macaques (*Macaca fuscata fuscata* Blyth). Monit Zool Ital 16:149–160

Troisi A, Schino G (1986) Diurnal and climatic influences on allogrooming behaviour in a captive group of Java monkeys. Anim Behav 34:1420–1426

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