

Differential Effects of Ambient Temperature and Humidity on Allogrooming, Self-Grooming, and Scratching in Wild Japanese Macaques

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ABSTRACT This study presents data on the effects of variations in ambient temperature and humidity on behaviors related to the care of the pelage (allogrooming, self-grooming, and scratching) in wild Japanese macaques (*Macaca fuscata yakui*). The amount of time monkeys spent allogrooming was essentially unaffected by variations in ambient temperature and relative humidity. Frequency of scratching and, to a lesser extent, time spent

self-grooming significantly increased when ambient temperature and/or relative humidity increased. These results are interpreted in relation to the differences in ultimate function that exist between allogrooming (with both hygienic and social functions) and self-grooming and scratching (with a solely hygienic function). *Am J Phys Anthropol* 126:453–457, 2005. © 2004 Wiley-Liss, Inc.

A number of studies investigated the effects of climatic variations on the behavior and time budget of primates (e.g., Iwamoto and Dunbar, 1983; Stelzner, 1988; Suchi and Rothe, 1999). Variations in temperature and humidity were shown to have the potential to force an animal to reallocate its time budgets and, ultimately, even give up time devoted to specific activities such as social time (Conradt et al., 2000). For example, because thermoregulation is affected by body contact between individuals, monkeys tend to engage in more interindividual contact under conditions of lower ambient temperatures (Dahl and Smith, 1985; Dahl et al., 1986; Schino and Troisi, 1990, 1998; Brent et al., 2003).

Allogrooming, the main behavior servicing primate social relationships, presents a more confused picture. Although earlier studies identified a possible relation between the amount of time monkeys spent allogrooming and variations in climatic conditions, they provided little or no statistical analyses and are therefore difficult to interpret (e.g., Bernstein and Mason, 1963; Bernstein, 1972, 1980). Quantitative assessments of the influence of ambient temperature and relative humidity on allogrooming were presented in only a couple of studies. Troisi et al. (1982), studying captive Japanese macaques (*Macaca fuscata*), reported that the occurrence of allogrooming was not affected by climatic variations (temperature range, 1–31°C; humidity range, 34–100%), while Troisi and Schino (1986, in captive long-tailed macaques, *M. fascicularis*) ob-

served more allogrooming under conditions of higher temperature and lower relative humidity (temperature range, 12–37°C; humidity range, 25–89%). In long-tailed macaques, allogrooming is not the only behavior that is influenced by climatic variations. Self-grooming and scratching show similar relations to environmental influences (Troisi and Schino, 1987; Pavani et al., 1991), suggesting that in this species, all behaviors related to the maintenance of the pelage may be similarly affected by variations in ambient temperature and humidity.

Based on the contrast observed in the effects of ambient temperature and humidity on the allogrooming behavior of Japanese and long-tailed macaques, Troisi and Schino (1986) speculated that the adaptation of *M. fuscata* to the temperate climate of Japan may have required its allogrooming to not be affected by variations in ambient temperature and

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humidity, in order not to jeopardize its social function under the harsher climatic conditions of Japan.

In this study, we provide quantitative data on the influence of ambient temperature and humidity on the occurrence of behaviors related to the maintenance of the pelage (allogrooming, self-grooming, and scratching) in wild Japanese macaques. We observed differential effects on the three behaviors, and interpreted them in light of the functional contrast that exists between allogrooming, which has both social and hygienic functions, and self-grooming and scratching, which have solely hygienic functions (Barton, 1985; Muroyama, 1991; Tanaka and Takefushi, 1993).

METHODS

Study area and subjects

We conducted this study on Yakushima, Japan. Yakushima is a volcanic island located 31°N and 131°E. The mean annual temperature is 21°C, and the annual rainfall is around 2,600 mm (Agetsuma, 1998). During the study period, temperatures were recorded ranged from 8–34°C, and relative humidity from 26–96%. The vegetation of the study site (0–200 m above sea level) is a warm temperate/subtropical broad-leaved forest.

The subjects were 7 adult males (age ≥ 7 years), 8 adult females (age ≥ 4 years), and 6 subadult males (age 4–6 years), and were members of a nonprovisioned troop (Nina A). At the beginning of the study, the group consisted of 25 individuals (the study subjects plus 3 yearlings and 1 infant).

Data collection

We collected data from June 2001–May 2002. Sampling consisted of 10-min focal animal sessions, during which we recorded allogrooming interactions, self-grooming, and scratching (defined as in Schino et al., 1988) of the subject on a continuous basis. Sampling sessions were distributed over the day from 7:00–18:00 hr. Data presented here come from a total of 336.5 hr of focal animal sampling, ranging from 5.9–26.9 hr per individual. During the course of the study, monkeys spent on average $18.1\% \pm 0.9\%$ (mean \pm SE) of their time allogrooming, and $3.5\% \pm 0.1\%$ (mean \pm SE) self-grooming. Overall frequency of scratching was 0.17 ± 0.01 (mean events per hr \pm SE).

Temperature and relative humidity were recorded by an electronic thermometer-hygrometer each time a focal session began, at about 1 m from the ground.

Data analysis

Allogrooming and self-grooming were expressed as the proportion of observation time spent grooming, and scratching as the rate of scratching per hour of observation. Data entered into analyses were individual scores for each observation session ($N = 2,115$). Since each subject was sampled repeatedly and since significant interindividual differences

in the overall frequency of the behaviors recorded during the study existed, the effects of ambient temperature and humidity could not be tested by simple regressions. Instead, we used analyses of covariance (ANCOVA), in which individual identity was inserted as a categorical factor and ambient temperature (or humidity) as a regressor. The main effect of temperature (or humidity) tests for the existence of a significant relation between temperature (or humidity) and behavior, while controlling for interindividual variation and avoiding pseudoreplication. The interaction effect between temperature (or humidity) and individual identity tests whether the effect of temperature (or humidity) is the same in all subjects (test of homogeneity of slopes). Although our data were not normally distributed, we used parametric ANCOVAs because they are relatively robust to violations of the assumption of normality, and no equivalent nonparametric test is currently available. The *P* values we report are therefore to be interpreted with caution. Note, however, that although we set significance at $P < 0.05$, all of our significant tests largely exceeded this threshold, so that minor inaccuracies in *P* estimation should not affect the biological significance of results. In order to confirm our results with a nonparametric technique, we split the data in two groups: those recorded under conditions of lower temperature (8–21°C), and those recorded under conditions of higher temperatures (22–34°C). Individual averages were calculated for the two conditions of temperatures, and compared using the Wilcoxon matched pairs test. Subjects that had been observed for less than 1 hr under either condition of temperature were discarded from analysis. The same procedure was used to confirm the effects of relative humidity (lower, 26–61%; higher, 62–96%).

Time of day is a potentially confounding variable, since marked variations in both activity patterns and temperature and humidity exist. Its effect on macaque behavior was assessed by one-way ANOVAs.

For allogrooming, we present only the results on the time each individual spent actively grooming a partner. Analyses run on the total time each individual spent grooming (i.e., time spent grooming plus time spent receiving grooming) gave the same results. Since too few data were recorded between 7:00–8:00 hr and between 17:00–18:00 hr, we collapsed sessions recorded between 7:00–9:00 hr, as well as those between 16:00–18:00 hr.

All tests are two-tailed.

RESULTS

Allogrooming

Japanese macaques spent similar amounts of time allogrooming in the different hours of the day ($F = 0.371$, d.f. = 8/2,016, n.s.).

Ambient temperature exerted no overall effect on time spent allogrooming ($F = 0.713$, d.f. = 1/2073,

n.s.), and this effect did not vary among different individuals (Temperature \times Individual interaction: $F = 1.210$, d.f. = 20/2,073, n.s.). The mating season is known to affect the allogrooming behavior of Japanese macaques as the overall proportion of time spent allogrooming decreases and females tend to groom adult males rather than females (D'Amato et al., 1982). Moreover, since ambient temperature also differs in different seasons, we analyzed separately the data collected in the mating and nonmating seasons. Effects of temperature were again nonsignificant (mating season: $F = 0.816$, d.f. = 1/975, n.s., and $F = 0.911$, d.f. = 20/975, n.s., for Temperature and for the Temperature \times Individual interaction, respectively; nonmating season: $F = 1.109$, d.f. = 1/1,056, n.s., and $F = 1.325$, d.f. = 20/1,056, n.s., for Temperature and for the Temperature \times Individual interaction, respectively). Finally, a Wilcoxon test comparing allogrooming under conditions of lower (8–21°C) and higher (22–34°C) temperatures confirmed the absence of a significant effect of ambient temperature on allogrooming ($t = 27$, $N = 15$, n.s.).

Similarly, ambient relative humidity did not influence time spent allogrooming (main effect of Humidity: $F = 0.383$, d.f. = 1/2,073, n.s.), and this effect did not vary among different individuals (Humidity \times Individual interaction: $F = 1.457$, d.f. = 20/2,073, n.s.). Again, separate analyses for the mating and nonmating seasons yielded similar results (mating season: $F = 1.590$, d.f. = 1/975, n.s., and $F = 0.641$, d.f. = 20/975, n.s., for Humidity and for the Humidity \times Individual interaction, respectively; nonmating season: $F = 0.000$, d.f. = 1/1,056, n.s., and $F = 1.491$, d.f. = 20/1,056, n.s., for Humidity and for the Humidity \times Individual interaction, respectively). Finally, allogrooming recorded under conditions of lower (26–61%) and higher (62–96%) humidity did not differ significantly ($t = 52$, $N = 14$, n.s.).

Self-grooming

Time of day had a significant influence on self-grooming ($F = 2.873$, d.f. = 8/2,106, $P < 0.005$). Most self-grooming occurred in the early morning, with a second minor peak between 15:00–16:00 hr.

Temperature did not affect self-grooming when data collected at different hours of day were lumped (main effect of Temperature: $F = 0.018$, d.f. = 1/2,073, n.s.; Temperature \times Individual interaction: $F = 1.432$, d.f. = 20/2,073, n.s.). Considering that ambient temperature presents obvious diurnal variations, and that self-grooming was clearly influenced by time of day (see above), we decided to add time of day as a categorical variable in the ANCOVA. The main effect of Temperature remained nonsignificant ($F = 0.000$, d.f. = 1/1,527, n.s.), but significant two- and three-way interactions emerged (Individual \times Temperature: $F = 2.451$, d.f. = 14/1,527, $P < 0.005$; Individual \times Time of Day \times Temperature: $F = 2.424$, d.f. = 112/1,527, $P < 0.0001$). These interactions are not easy to interpret, as they

seem to indicate that the effects of temperature on self-grooming differed in different individuals and at different hours of the day. Overall, however, self-grooming did not seem completely independent from the influences of ambient temperature. Indeed, a Wilcoxon test comparing self-grooming recorded under conditions of lower and higher temperatures revealed significantly more self-grooming under conditions of higher temperatures ($t = 6$, $N = 15$, $P < 0.005$).

Similarly, relative humidity did not affect self-grooming when data collected at different hours of the day were lumped (main effect of Humidity: $F = 2.096$, d.f. = 1/2,073, n.s.; Humidity \times Individual interaction: $F = 0.690$, d.f. = 20/2,073, n.s.). Again, when Time of Day was added to the ANCOVA, significant two- and three-way interactions emerged (Time of Day \times Humidity: $F = 5.765$, d.f. = 8/1,527, $P < 0.0001$; Individual \times Time of Day \times Humidity: $F = 1.998$, d.f. = 112/1,527, $P < 0.0001$). Self-grooming was thus also influenced in complex ways by relative humidity. Again, comparing self-grooming recorded under conditions of higher and lower relative humidity revealed a significant difference ($t = 9$, $N = 14$, $P < 0.01$).

Scratching

Time of day had no significant influence on rate of scratching ($F = 0.377$, d.f. = 8/2,106, n.s.).

Increasing ambient temperatures were associated with increasing rates of scratching (main effect of Temperature: $F = 60.844$, d.f. = 1/2,073, $P < 0.0001$), and this effect did not vary among different individuals (Temperature \times Individual interaction: $F = 1.240$, d.f. = 20/2,073, n.s.). Confirming the above result, significantly more scratching was recorded under conditions of higher than lower temperatures ($t = 0$, $N = 15$, $P < 0.001$).

Similarly, increasing relative humidity was associated with increasing rates of scratching (main effect of Humidity: $F = 38.358$, d.f. = 1/2,073, $P < 0.0001$), and once again this effect did not vary among different individuals (Humidity \times Individual interaction: $F = 1.268$, d.f. = 20/2,073, n.s.). Finally, more scratching was recorded under conditions of higher than lower humidity ($t = 0$, $N = 14$, $P < 0.005$).

Since in our sample ambient temperature and relative humidity were positively correlated ($r = 0.56$, d.f. = 2,113, $P < 0.001$), we tried to disentangle their independent contributions to the observed variations in scratching rates. We therefore ran a multiple regression including both temperature and relative humidity as independent variables. The overall regression was highly significant ($r = 0.297$, $P < 0.0001$), and both temperature and relative humidity had significant independent effects ($t = 8.057$, $P < 0.0001$, and $t = 5.301$, $P < 0.0001$, respectively). Note, however, that such an analysis cannot control for the influence of interindividual variations.

DISCUSSION

The results of this study show that in wild Japanese macaques, weather variations exerted differential effects on the various behaviors involved in the maintenance of the pelage. Scratching and (although less consistently) self-grooming were considerably affected by variations in ambient temperature and humidity, while allogrooming proved to be essentially independent of these environmental factors. The significant two- and three-way interactions observed between self-grooming, temperature/humidity, time of day, and individual identity are difficult to interpret, but may be affected by the different amounts of allogrooming exchanged by different monkeys. Animals who receive less allogrooming may require a greater amount of self-grooming for the maintenance of the pelage. However, we are unable to provide a convincing account for the observed statistical interactions.

Seasonal variations in allogrooming, self-grooming, and scratching might be explained by trade-offs between pelage care and other activities such as feeding and traveling. For example, time devoted to pelage care could increase when animals spend less time feeding (e.g., in periods of high food availability). Our results, however, contrast with this explanation. In fact, if time-budget trade-offs were at the basis of our results, then stronger effects should have been observed on allogrooming (the most time-consuming of the behaviors we observed), while no effect would be expected on scratching (an essentially instantaneous behavior with no time-budget constraints). The pattern of results we observed is the opposite of what was predicted by time-budget trade-offs, and therefore we conclude that direct influences on pelage-care needs constitute a more likely explanation. Previous studies on long-tailed macaques were conducted in captivity, and their results were therefore unlikely to be affected by time-budget trade-offs.

Earlier research demonstrated that in long-tailed macaques, a species confined to tropical Southeast Asia, allogrooming is as sensitive to weather variations as the other behaviors related to maintenance of the pelage (Troisi and Schino, 1986, 1987; Pavani et al., 1991). Troisi and Schino (1986) speculated that, given the social function of allogrooming, adaptation of macaques to temperate climates may have required the emancipation of allogrooming from the proximate influence of variations in ambient temperature and humidity. Our results suggest that self-grooming and scratching (that share with allogrooming its hygienic but not its social function) may have, in contrast, retained their original sensitivity to environmental influences.

In other words, we suggest that the differences in ultimate function that exist between allogrooming and self-grooming/scratching may translate into differences in their proximate causation, i.e., into a differential sensitivity to environmental influences.

Thus, while variations in the need for pelage care are presumably associated with changes in ambient temperature and humidity, these seem only to affect self-grooming and scratching. Allogrooming, although still having an important hygienic function (Tanaka and Takefushi, 1993; Zamma, 2002), is primarily a social behavior whose dependence on ambient temperature and humidity would interfere with its role in mediating interindividual relationships. Adaptation of Japanese macaques to the temperate/subtropical climate of their present range may thus have required a readjustment of the proximate causation of some behaviors. Self-grooming and scratching, with a primarily hygienic function, retained their sensitivity to the stimuli provided by the pelage (e.g., sweating or presence of ectoparasites), and thus remained influenced by environmental conditions. Conversely, allogrooming, which has both hygienic and social functions, became independent of the influence of climatic variations, in order not to jeopardize its social function. For example, a reduction of allogrooming during the cold winter months would conflict with its critical role in regulating interindividual relationships during the mating season. Interestingly, among wild impalas (*Aepyceros melampus*), where allogrooming plays no social function, allogrooming, self-grooming, and scratching show similar seasonal variations correlated with the intensity of tick challenge (Mooring, 1995).

In macaques, whether the influence of ambient temperature and humidity on pelage care is mediated through variations in piloerection, sweating, abundance of ectoparasites, or other mechanisms is presently unknown and warrants further investigation. Seasonal variations in the presence of ticks in the environment and in the degree of infestation of monkeys were reported by Rajagopalan and Anderson (1971, in *M. radiata* and *Presbytis entellus*) and Saunders and Hausfater (1988, in *Papio cynocephalus*). The latter also reported that frequency of baboon allogrooming was not correlated with tick challenge, but did not report data on self-grooming or scratching. Japanese macaques are mainly infested with the lice *Pedicinus obtusus* and *P. eurygaster* (Kaneko, 1971, as cited in Tanaka and Takefushi, 1993). Zamma (2002) estimated that an adult Japanese macaque harbors an average of 500 louse eggs and reported that both autogrooming and allogrooming were primarily directed at those sites of the body that were more heavily infested. Given that lice, in contrast to ticks, complete their life cycle on the body of their host, it is possible that seasonal variations in their degree of infestation are comparatively smaller. Moreover, the observations conducted in captive parasite-free environments suggest that variations in ambient temperature/humidity may also affect pelage care independently of the presence of parasites (Troisi and Schino, 1986, 1987; Pavani et al., 1991). To summarize, the scant available data do not seem to support the notion that variations in

pelage care associated with ambient temperature/humidity are mediated by variations in ectoparasite challenge. The role of piloerection and sweating remains to be investigated.

Studies of evolutionary ecology have traditionally neglected issues related to the proximate causation of behavior to concentrate on ultimate function. Adaptation, however, often involves a restructuring of the causal relations underlying behavior so as to modify responsiveness to environmental/ecological stimuli (e.g., Gould, 1982). Adding information on the proximate determinants of behavior will thus contribute to enhancing our understanding of the ecology and adaptation of primates to their environment.

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