Early Environment Shapes the Development of Gaze Aversion by Wild Bonnet Macaques (*Macaca radiata*)

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ABSTRACT. Among many species of primates, staring is perceived as a sign of aggression and averting the gaze usually serves to reduce such conflict. The current study conducted in southern India documented developmental differences among wild bonnet macaques (*Macaca radiata*) in their latency to gaze avert after establishing eye contact with other individuals. Feeding stations were used to gather macaques within a small area to facilitate the video recording of group dynamics and eye contact between subordinate and dominant individuals. Individuals were grouped into three age classes: juveniles, subadult males, and adult males. Comparisons were also made between urban and forest dwelling troops. In the forest, juveniles established eye contact with older males for significantly longer periods of time than did adults. A linear trend was observed in which the latency to gaze avert after establishing eye contact decreased with age. This trend was not evident in the urban troops, for which the latency to gaze avert did not change significantly with age. Urban juveniles were also more likely to be chased when they established eye contact with adults compared with their forest counterparts. These differences could be the result of increased predatory risk in the forest setting – the necessity for heightened predator vigilance in forests may reduce the frequency with which juveniles are monitored and chased or attacked as a result of their eye contact. Conversely, the rarity of predators in the city may engender more intense aggressive behavior between monkeys, accelerating the rate of learning to signal appeasement to dominant males.

Key Words: Bonnet macaque; *Macaca radiata*; Gaze aversion; Age differences.

INTRODUCTION

The tendency to avert the gaze from other individuals who are either foreign or more dominant, is common among many primate societies including humans (LARSEN & SHACKELFORD, 1996). A direct gaze can be disturbing and may suggest a threat or other ill intention on the part of the gazer (COSS, 1978; EMERY, 2000). Most macaque societies are based on dominant-subordinate relationships, making it beneficial for young monkeys to learn this social structure early on. At 1 week of age, rhesus macaques (*Macaca mulatta*) inspect the eye region of pictures of macaques, looking at them longer than any other portion of the face (MENDELSON et al., 1982). By 3 weeks of age, these infants begin to show distress to the fixed gaze of conspecifics, as evidenced by their looking for a much briefer period at pictures of faces appearing to stare at them than pictures of faces with eyes turned away (MENDELSON, 1982; MENDELSON et al., 1982).

A study by SUGIYAMA (1971) on provisioned troops of bonnet macaques (*M. radiata*) found that dominance hierarchies appeared to be linear, and about half of all dominance assertions were made by the alpha and beta males. This study also noted that most of the dominance assertions were unprovoked and made toward juveniles or other subordinate animals. The current study documents patterns of gaze aversion in relation to dominance and age of the individuals in troops of wild bonnet macaques in southern India. The study troops were provisioned so that group dynamics could be observed and video taped in a small area.

Table 1. Bonnet macaque troop sizes and locations.

Region	Troop identification	Adult males	Subadult	Juveniles	Troop size
Mundanthurai	Mundanthurai	8	5	7	34
Mundanthurai	Kariyar	7	3	3	31
Mundanthurai	Maylar	5	3	4	23
Mudumalai	Kargudi	5	2	6	26
Mudumalai	Theppakadu	6	4	3	28
Mudumalai	Kakkanala	7	4	3	31
Mudumalai	Bandipur	5	4	3	25
Bangalore	Bangalore 1	9	6	9	54
Bangalore	Bangalore 2	11	3	6	48

METHODS

This study documented the latency to gaze avert among three age classes (juveniles, subadult males, and adult males) and between urban and forest troops to determine if age or environmental factors influenced the development of gaze aversion. Two urban troops in Bangalore city and seven forest troops in the Mudumalai Wildlife Sanctuary and the Kalakad-Mudanthurai Tiger Reserve were included in this study. Information on troop sizes and location are listed in Table 1. The forest sites were rich in predators that could potentially prey on bonnet macaques (see Coss & Ramakrishnan, 2000; Ramakrishnan & Coss, 2000a). The urban troops selected for observation were free ranging and located in a University campus on the periphery of Bangalore city. Although the predators of bonnet macaques rarely enter Bangalore city, domestic dogs and humans pose occasional threats. The habitat at the urban site consisted of forest plantations interspersed with agricultural fields and buildings. To allow for multiple animals to aggregate within close proximity, feeding stations were set up and split peas were scattered in a 1-m radius. This also created a consistent motivational state for comparison of behavior among animals. All animals that came down to feed were video recorded for 3 min.

Two teams of researchers decoded incidents of gaze aversion from videotapes. Gaze behavior was video recorded on different days with seven individuals typically in camera view. Although both males and females were video recorded at the feeding station, only males were included in the analysis because their dominance hierarchy was easy to establish. In this study, a gaze event is defined as a state in which the eyes and head are directed at another individual, and gaze aversion is defined as turning the head and/or body away from another individual following eye contact. Due to the limitation of video image resolution, only the change in an individual's head orientation was recorded when that individual looked up from feeding to face another individual. Latency to gaze avert was determined by counting the number of video fields (16.67 ms increments) between the onset of lifting or directing the head towards the other individual and the onset of the head being directed away from the other individual. Each gaze event was re-examined 2 – 5 times until team members agreed on head orientation changes. The units of analysis were the latencies to gaze avert by individuals in unique dyadic encounters with different dominant males.

Since early social learning might contribute to differences in gaze behavior, we also examined the frequency of specific circumstances that followed eye contact among only juveniles and adults. These circumstances were: (1) the adult chases the juvenile; (2) the juvenile runs away but is not chased by the adult; and (3) the juvenile gaze averts without running away or inciting the adult.

RESULTS

The number of individuals sampled in unique dyads was 105 (Urban: n = 56, of which juveniles: n = 13, subadults: n = 27, adults: n = 16; Forest: n = 49, of which juveniles: n = 10, subadults: n = 18, adults: n = 21). Some resampling of the gaze behavior of individuals occurred, especially among the urban troops; albeit, each bout of eye contact with a different male was unique. Latencies shorter than 200 ms were not included, because eye contact could not be established and averted in time frames this brief. Several latencies were unusually long and were identified as statistical outliers from the normal distribution of data. These outlying latencies (nine cases) were removed using the procedure of DIXON and MASSEY (1969).

Data were examined using a 2-factor (location and age) randomized groups analysis of variance coupled with tests of simple effects, planned comparisons of age classes, and analyses of linear and quadratic trends for behavioral changes with age. None of the main effects were statistically significant with α = 0.05. However, the interaction between age and location was approximately significant (F = 3.040, df = 2,99, p = 0.052). In the forested areas, there was a linear trend between increasing age and decreasing latency to gaze avert (F = 4.840, df = 1,99, p = 0.030, Fig. 1). Additionally, in the forested areas, juveniles exhibited a significantly longer latency to gaze avert than the combined average of adult and subadult males (F = 4.004, df = 1,99, p = 0.048). Latency to gaze avert did not differ significantly among subadults and adults. There was also a difference between the average latency to gaze avert observed in juvenile monkeys in the forest and those in the city, however, these differences were not statistically significant (F = 3.225, df = 1,99, p = 0.076). Finally, multinomial log-linear analysis with maxi-

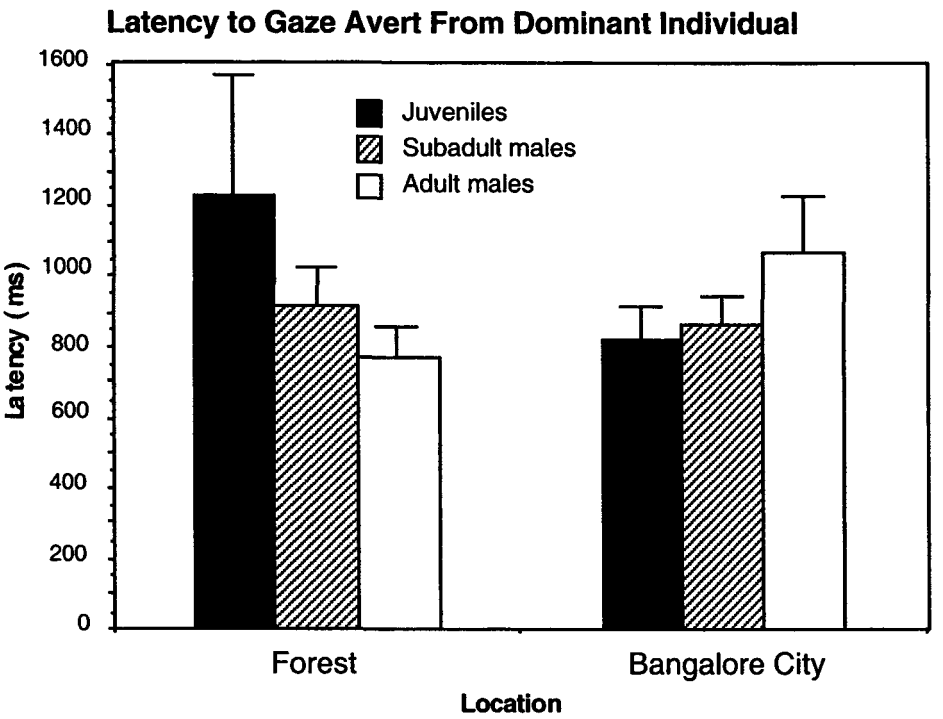

Fig. 1. Mean latencies and standard errors to gaze avert after the establishment of eye contact. Note the different developmental trends at forest and urban locations.

mum likelihood estimations examined the frequency in which, after establishing eye contact with an adult male, juveniles from the two locations simply averted their gaze, ran away, or were chased by males (Fig. 2). Analysis was restricted to the frequency of occurrence of unique juvenile-adult dyadic circumstances in which the same juvenile could contribute data for up to three distinct circumstances. One hundred six circumstances were examined (Urban: $n = 23$ chased by adult, $n = 8$ running but not chased, $n = 18$ gaze averting only; Forest: $n = 18$ chased by adult, $n = 4$ running but not chased, $n = 35$ gaze averting only). Analysis of this contingency table revealed a significant interaction between forest and urban locations, with the largest percentage of forest juveniles simply averting their gaze, contrasted by the largest percentage of urban juveniles experiencing chases (likelihood ratio, $\chi^2 = 6.917$, $df = 2$, $p < 0.05$).

DISCUSSION

The findings of this study suggest that early experience in bonnet macaques shapes their readiness to gaze avert in social situations. Such age differences in readiness to make eye contact have been reported for other primate species (THOMSEN, 1974), where the frequency of eye contact appears to decrease with age. Learning the aversive consequences of prolonged eye contact with dominant individuals thus appears to be accelerated in an urban setting relative to that of the forest.

The forest and urban troops differed in a number of other behaviors – forest macaques were generally slower to approach the feeding stations than urban troops. This difference has also been recorded in rhesus macaques (SINGH, 1966a), where urban rhesus macaques were more likely to approach humans for food compared with forest monkeys. Overall chasing, aggressive

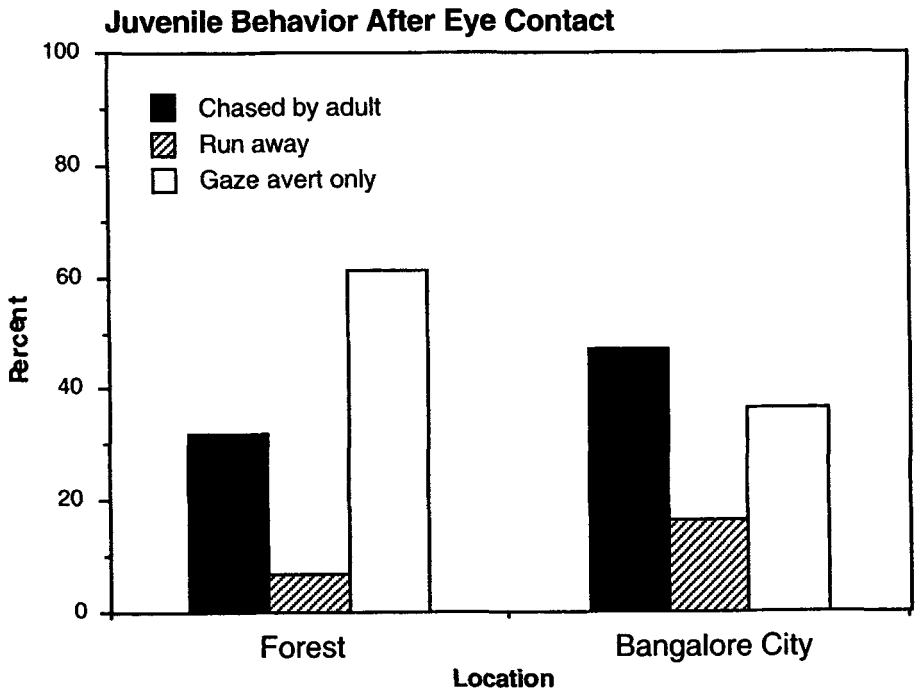

Fig. 2. Frequency of juvenile behavior between locations following eye contact with adults.

encounters, and fighting episodes were fewer in the forest. When responding to a threat or an attentive gaze, animals were frequently approached quickly or chased for a short distance, but this rarely erupted into a full-fledged attack or violent contest; both animals were usually observed to resume their feeding now at a greater distance from one another. Fights that occurred in the city tended to be longer and more violent, with screeching vocalizations and biting. Urban juvenile monkeys were significantly more likely to be chased following eye contact with an adult male; forest-dwelling individuals were more likely to simply avert their gaze without running away or being chased (Fig. 2).

Increased aggressiveness among urban monkeys compared with forest individuals has also been reported in rhesus macaques. SINGH (1966b) attributed the hyperaggressive nature of urban macaques to increased competition in the urban setting. Staring is perceived by adult monkeys as a sign of aggression (COSS, 1978; EMERY, 2000; MENDELSON et al., 1982) while gaze aversion, evident in turning the head and body away from the gaze of another animal, complements other subordination gestures such as moving away (MENDELSON et al., 1982; SILK, 1994; SIMONDS, 1965). Based on our findings, it seems reasonable to assume that young monkeys have not yet determined their gazing boundaries, and may stare longer at an adult than would be expected for an older monkey.

We observed a significant linear trend in the latency to gaze avert as a function of age in the forest troops (Fig. 1), with the latency to gaze avert decreasing as age increased. Such a trend was not apparent among urban macaques. The reason for this difference is unclear, and merits further investigation. One possible explanation could be the presence of predators. Differences in the presence of predators in the two regions could affect the amount of time and energy spent by the animals in each area on vigilance. Juveniles in the forest troops spent more time watching and/or gazing at older monkeys, especially adults. The information that these young animals may gain from more experienced animals may be critical for their survival in this predator-rich area; we found that, among bonnet macaques, the recognition of appropriate threats improves with age (RAMAKRISHNAN & COSS, 2000a). The tendency to establish shorter episodes of eye contact with dominant males in the urban setting might reflect the reduction of predatory threats in this environment. In the forest where predators are common, animals usually remain alert, with adults spending a large proportion of their time watching for predators. We also found for forest troops that, compared to adults, juveniles spent significantly more time scanning following exposure to unfamiliar sounds (RAMAKRISHNAN & COSS, 2000b), a property of gaze behavior that also appears to be affected by predation risk.

As discussed above, developmental differences in the gaze behavior of forest and urban troops may be due to the greater likelihood in the urban setting of being attacked after establishing eye contact. The aversive circumstances of frequent chases would likely act as unconditioned Pavlovian stimuli, prompting the developmental modulation of the duration of eye contact coupled with learning which individuals pose a threat. Although gaze aversion is thought to function as a cut-off act to reduce unpleasant arousal (COSS, 1978), it simultaneously signals appeasement which might mitigate subsequent attacks. From this perspective, gaze aversion by bonnet macaques appears to have a learned component mediating the expression of social skills not unlike the way humans use eye contact in social discourse (see ARGYLE & COOK, 1976, p. 122).

Although all troops included in this study were habituated to humans, allowing close-up video recording, the general caution of forest troops relative to that of urban troops is analogous to that of rhesus macaques reported by SINGH (1966a). Such caution by members of forest troops of both species might be a developmental by-product of frequent flight behavior after hearing alarm calls, beginning in infancy when mothers flee with clinging infants

(RAMAKRISHNAN & COSS, 2000a). Consistent with this argument, but difficult to quantify in terms of targets of visual fixation, we noticed that adults in the forest looked around at their surroundings for longer periods than adults in the city. To provide a greater understanding of site-specific differences in gaze-avoidance behavior, future research should incorporate other socially relevant behaviors, such as attending to conspecific interactions and monitoring their antipredator vigilance.

REFERENCES

ARGYLE, M.; COOK, M. 1976. *Gaze and Mutual Gaze.* Cambridge Univ. Press, Cambridge.

COSS, R. G. 1978. Perceptual determinants of gaze aversion by the lesser mouse lemur (*Microcebus murinus*), the role of two facing eyes. *Behaviour*, 64: 248 – 270.

COSS, R. G.; RAMAKRISHNAN, U. 2000. Perceptual aspects of leopard recognition by wild bonnet macaques (*Macaca radiata*). *Behaviour*, 137: 315 – 335.

DIXON, W. J.; MASSEY, F. J. JR. 1969. *Introduction to Statistical Analysis.* McGraw-Hill, New York.

EMERY, N. J. 2000. The eyes have it: the neuroethology, function and evolution of social gaze. *Neurosci. Biobehav. Reviews*, 24: 581 – 604.

LARSEN, R. J.; SHACKELFORD, T. K. 1996. Gaze avoidance: personality and social judgments of people who avoid direct face-to-face contact. *Personality & Individual Differences*, 21: 907 – 917.

MENDELSON, M. J. 1982. Visual and social responses in infant rhesus monkeys. *Amer. J. Primatol.*, 3: 333 – 340.

MENDELSON, M. J.; HAITH, M. M.; GOLDMAN-RAKIC, P. S. 1982. Face scanning and responsiveness to social cues in infant rhesus monkeys. *Develop. Psychol.*, 18: 222 – 228.

RAMAKRISHNAN, U.; COSS, R. G. 2000a. Age differences in the responses to adult and juvenile alarm calls by bonnet macaques (*Macaca radiata*). *Ethology*, 106: 131 – 144.

RAMAKRISHNAN, U.; COSS, R. G. 2000b. Recognition of heterospecific alarm vocalizations by bonnet macaques (*Macaca radiata*). *J. Comp. Psychol.*, 114: 3 – 12.

SILK, J. B. 1994. Social relationships of male bonnet macaques: male bonding in a matrilineal society. *Behaviour*, 130: 271 – 291.

SIMONDS, P. E. 1965. The bonnet macaque in South India. In: *Primate Behavior*, DEVORE, I. (ed.), Holt, Rinehart & Winston, New York, pp. 175 – 196.

SINGH, S. D. 1966a. The effects of human environment upon the reactions to novel situations in the rhesus. *Behaviour*, 26: 243 – 250.

SINGH, S. D. 1966b. The effects of human environment on the social behavior of rhesus monkeys. *Primates*, 7: 33 – 39.

SUGIYAMA, Y. 1971. Characteristics of the social life of bonnet macaques (*Macaca radiata*). *Primates*, 12: 247 – 266.

THOMSEN, C. E. 1974. Eye contact by non-human primates toward a human observer. *Anim. Behav.*, 22: 144 – 149.

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