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Vigilance in young baboons: effects of habitat, age, sex and maternal rank on glance rate

SUSAN C. ALBERTS*
Department of Ecology and Evolution, University of Chicago, Chicago, IL, 60637, U.S.A.
and
Institute for Primate Research, National Museums of Kenya

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Abstract. Glance rates, a measure of vigilance, were sampled in infant and young juvenile yellow baboons, *Papio cynocephalus*, in Amboseli, Kenya, to test ecological and social predictions about the ontogeny of vigilance. Glance rates of young baboons did not vary between closed and open habitats, but did vary with sex, maternal rank and age. Daughters of low-ranking mothers glanced significantly more often than daughters of high-ranking mothers, and the converse was true for males. Glance rates of females, but not males, decreased significantly between 6 and 24 months of age.

Vigilance in animals is considered to be an important means of facilitating predator detection (e.g. Kenward 1978) or of regulating social interactions (e.g. Keverne et al. 1978). In primates, some support exists for the suggestion that vigilance serves a mixed function. Vigilance, usually defined as scanning the environment or glancing up from the current activity, is strongly related to predator detection in some species (e.g. wedge-capped capuchin monkeys, *Cebus olivaceus*, de Ruiter 1986; red-bellied tamarins, *Saquinus labiatus*, Caine & Marra 1988), whereas glancing at conspecifics seems to comprise a large part of vigilance behaviour in other species (e.g. talapoin monkeys, *Miopithecus talapoin*, Keverne et al. 1978; squirrel monkeys, *Saimiri sciureus*, Caine & Marra 1988). The relative importance of each of these functions varies among species and across environmental conditions (Caine & Marra 1988; see Quenette 1990 for review).

Despite the emergence of a growing body of work on vigilance behaviour and its function in primates (Chance 1967; Keverne et al. 1978; Altmann 1980; van Schaik et al. 1983; Leighton-Shapiro 1986; de Ruiter 1986; Caine & Marra 1988), little information is available on the ontogeny of vigilance, particularly in primates (but see Seyfarth & Cheney 1980, 1986; Fragaszy 1990; Janson 1990). Because a primate infant is relatively altricial at birth, it is completely dependent on its mother nutritionally, and lacks the skills required to survive independently (Nicolson 1987). By the time it is weaned, a year or two later, the juvenile must have acquired a number of these skills, including the ability to monitor the social and ecological environment.

Here, I tested hypotheses concerning the pattern of vigilance behaviour in immature primates. I sampled infant and juvenile members of a well-studied population of wild baboons, *Papio cynocephalus*, in Amboseli, Kenya, for one measure of vigilance, glance rate, and tested the following hypotheses concerning glance rate.

Hypothesis 1

Social factors determine the pattern of vigilance behaviour in infants and juveniles

Prediction 1. Female immatures glance more frequently than male immatures. Among both baboons and macaques, young females suffer more aggression than do their male peers (Dittus 1977; Silk et al. 1981; Pereira 1988a); greater vigilance may be required of them to avoid still higher rates of aggression.

Prediction 2. Offspring of low-ranking mothers have higher glance rates than offspring of high-ranking mothers. Keverne et al. (1978) and Altmann (1980) reported higher glance rates for low-ranking

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*Present address: Department of Obstetrics and Gynecology, MC2050, University of Chicago, Chicago, IL 60637, U.S.A.

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animals than for high-ranking animals in two different species of primates, and in baboons these rank differences may emerge early in development, as do many other rank effects (Cheney 1977; Walters 1980; Altmann et al. 1988; Pereira 1989).

Prediction 3. Glance rates increase with age. As the infant spends increasing amounts of time away from its mother and is less able to depend on her for warning and protection, it should be increasingly vigilant. This pattern of increasing vigilance with age has been documented in wedge-capped capuchins (Fragaszy 1990).

Hypothesis 2

Risk of predation effects the pattern of vigilance in immature baboons

Prediction 1. Glance rates of immature baboons do not vary with sex. In the study population, overall mortality rates at this age do not differ between males and females (Altmann 1980; unpublished data). Moreover, predation risk is probably not sex-biased at this age; males and females do not differ significantly in size (Altmann & Alberts 1987), and both spend the same amount of time in proximity to other group members (Pereira 1988b). Therefore, males and females should be equally vigilant for predators.

Prediction 2. Glance rates of immature baboons do not vary with maternal dominance rank. Because there is no effect of maternal rank on time spent in proximity to other group members in this population (M. E. Pereira, unpublished data; J. Altmann, unpublished data), glance rates should not vary with maternal rank.

Prediction 3. Glance rates increase with age. Increasing time spent away from the mother should result in higher glance rates. This prediction is similar for both the predation risk hypothesis and the social factors hypothesis; danger from both predators and conspecifics should increase with decreased maternal contact.

Prediction 4. Glance rates in closed habitats (dense bushy areas and woodland) are higher than glance rates in open habitats (open grassland). In many primate populations, including baboons of Amboseli, immatures are preyed upon at a higher rate than adults (Cheney & Wrangham 1987). Because closed habitats in Amboseli provide cover for predators without providing protection for the baboons, glance rates in closed habitats should be higher than glance rates in open grassland (Quenette 1990).

METHODS

The subjects of this study were immature baboons living in two different social groups (Alto's Group and Hook's Group) in the Amboseli basin in southern Kenya. The Amboseli basin is a semi-arid savannah occupying a Pleistocene lake bed, with a full complement of vertebrate fauna, including many potential predators on baboons (for habitat descriptions see Western & van Praet 1973; Altmann & Altmann 1970; for predation rates on baboons see Cheney & Wrangham 1987). All members of the study groups were identified visually by individual physical characteristics, and have been part of longitudinal research projects on demography and behavioural ecology. The histories of all subjects of this study were known since birth, as a result of daily records of demographic events, reproductive cycles and social interactions.

The study subjects included all 24 infants and juveniles who, at the time of my study, were between 6 and 24 months of age, the period during which infants move from complete nutritional dependence to complete nutritional independence. The subjects were sampled over a period of 4 months between April and August 1985. Glance rates (number of glances/min) were collected during 10-min focal samples (Altmann 1974) by using a hand-held mechanical counter. A glance was defined as a head lift and brief inspection of the surrounding area that lasted for 5 s or less. It was not possible to determine the objects of glances, or to record glance durations. All samples were collected while the animal was feeding and/or moving. The 5-s cutoff time for glances was chosen as a means of making instantaneous decisions during sampling, and does not reflect any natural limit on the baboons' behaviour. Each subject was sampled one to four times during the study, yielding a total of 52 glance-rate samples for the 24 different subjects. Number of days between samples on a given individual was typically 30–60 days, with a minimum of one day (four cases) and a maximum of 120 days (seven cases). If an animal was sampled twice in 1 day and the samples were taken in different habitats (two cases), one of the samples was chosen at random and discarded because independence of same-day samples could not be assumed. If an animal was sampled twice in 1 day in the same habitat, samples were pooled to yield one glance rate for the animal for that day (seven cases). For each sample, habitat type was recorded (grassland

Table I. General linear model of mean glance rate (glances/min)

Source	R^2	*df*	Mean square	*F*	*P*
Overall model					
Model	0·71	5	0·555	8·74	0·002
Error		18	0·063		
Total		23			
Independent variables					
Mean age (months)		1	0·038	0·60	0·45
Maternal rank		1	0·040	0·63	0·44
Sex		1	0·075	1·18	0·29
Mean age by sex		1	0·438	6·89	0·017
Maternal rank by sex		1	1·608	25·30	0·0001

or bush/woodland). The agonistic dominance rank of the mother at the infant's conception was established from longitudinal records of agonistic behaviour (J. Altmann, unpublished data).

Analyses were carried out using GLM (general linear models) and linear regression procedures in SAS® (SAS Institute 1988). The dependent variable was log-transformed in each case to conform to the assumptions of general linear models. Glance rates did not differ significantly between social groups; consequently, samples from both social groups were pooled and treated as a single data set.

Analysis proceeded in two stages. First, in order to investigate effects of habitat on glance rate, I constructed a model treating all 52 samples as independent samples. In this case, some individuals were represented by glance-rate samples at several different ages. I treated age in months, sex, mother's dominance rank at offspring's conception, and habitat as independent variables predicting glance rate. Second, because individuals contributed different numbers of samples to the data set, compromising independence assumptions and yet precluding a repeated measures analysis, I also analysed the data using each individual's mean glance rate as the dependent variable. I did not include habitat in this model using mean glance rates, because it was not possible to designate an average habitat effect for the set of samples on an individual. Each individual was represented by one value for mean glance rate. The independent variables included mean age in months at which samples on that individual were collected, mother's dominance rank at offspring's conception, infant sex, a maternal rank by offspring sex interaction term, and a mean age by sex interaction term (previous studies on this population have documented sex-specific effects of maternal rank and age on a number of developmental variables, e.g. Altmann et al. 1988; Pereira 1988b). This initial model revealed strong interactive effects of sex with maternal rank and age, and so I subsequently analysed data for males and females separately using a multiple regression of the natural log of mean glance rate on maternal rank and mean age.

RESULTS

Mean (±SE) glance rate for the entire set of samples ($N=52$) was 3·27±0·21 glances/min, with a range of 0·9–7·6 glances/min.

Glance rates did not differ by habitat, either when habitat was included in the general model or in a simple bivariate comparison (*t*-test, variances equal, $P=0{\cdot}88$). I also performed a matched pairs *t*-test on subjects for which I had samples in both habitats; again, no effect of habitat on glance rate was detected (matched pairs *t*-test, $P=0{\cdot}92$). Consequently, I dropped habitat from the model and used a single mean glance-rate value for each individual in subsequent analyses.

The initial model using mean values accounted for 70% of the variance in mean glance rate (Table I). The interactions of sex with maternal rank and with mean age were the only independent terms contributing significantly to the model.

Table II. Multiple regressions of mean glance rate (glances/min) on maternal rank and mean age

	Adj R^2	N	F or partial F	P
Females	0·41	14	5·45	0·023
Mean age			−2·33	0·039
Maternal rank			2·97	0·013
Males	0·63	10	8·68	0·013
Mean age			1·36	0·22
Maternal rank			−4·17	0·004

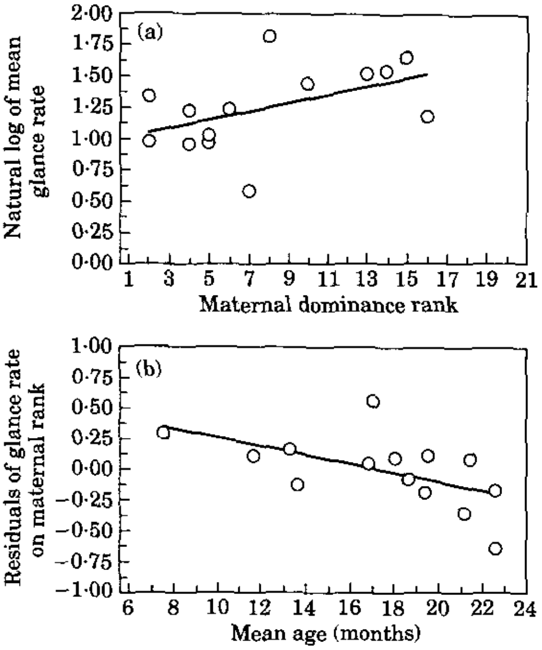

Figure 1. Glance rates of juvenile females: effects of age and maternal dominance rank. (a) Linear regression of the natural log of mean glance rate on maternal rank. Each symbol on the plot represents the natural log of one individual's mean glance rate, plotted against maternal dominance rank. (b) Linear regression of the residuals of the first regression (i.e. of the variance in glance rate unexplained by maternal rank) on mean age. Each symbol on the plot represents one individual's residual value, plotted against the mean age at which samples on that animal were collected. See also Table II.

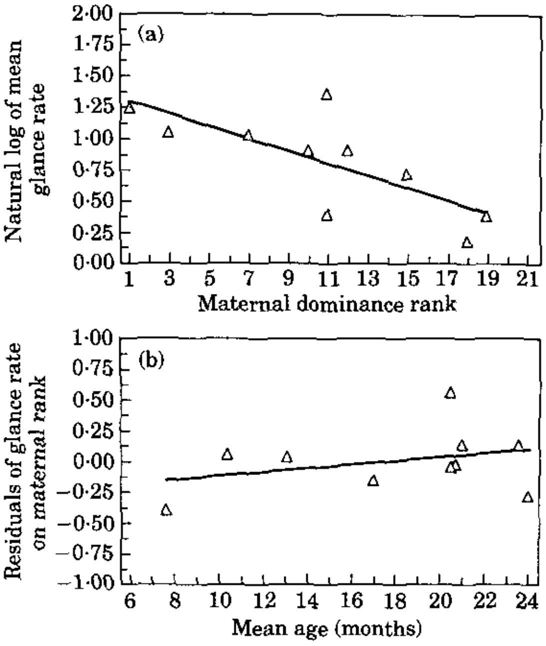

Figure 2. Glance rates of juvenile males: effects of age and maternal dominance rank. (a) Linear regression of the natural log of mean glance rate on maternal rank. (b) Linear regression of the residuals of the first regression (i.e. of the variance in glance rate unexplained by maternal rank) on mean age. Conventions as in Fig. 1. See also Table II.

Separate analyses for males and females revealed the following patterns. For females, a multiple regression of the natural log of mean glance rate on maternal rank and mean age revealed that both variables predicted mean glance rate (Table II). Daughters of high-ranking mothers glanced significantly less often than daughters of low-ranking mothers (Table II, Fig. 1a) and glance rates for young females decreased with age (Table II, Fig. 1b).

For males, a multiple regression of the natural log of mean glance rate on maternal rank and mean age revealed that maternal rank, but not mean age, predicted mean glance rate (Table II). In contrast to daughters, sons of high-ranking mothers glanced significantly more often than sons of low-ranking mothers (Table II, Fig. 2a) and glance rates for young males did not change significantly with age (Table II, Fig. 2b).

Although females in the study glanced at higher rates overall than did males (females, $\bar{X}=3{\cdot}7$ glances/min, $N=14$; males, $\bar{X}=2{\cdot}4$ glances/min, $N=10$; t-test, variances equal, $P<0{\cdot}001$), the fact that sex did not significantly contribute to the general linear model suggests that this was a non-significant trend, due in part to an unequal distribution of male and female offspring between mothers of different ranks.

DISCUSSION

The strong interactive effects of sex, age and maternal rank on glance rates of immatures suggest that, for these infants and juveniles, patterns of vigilance were strongly determined by social factors. The absence of an effect of habitat on glance rates is inconclusive with respect to the possible effect of predation risk on glance rates. Some of the predictions of each hypothesis were supported, although key predictions of each remained unsupported by the current data set.

I expected that glance rates in closed habitats would be higher than glance rates in open habitats. The absence of any effect of habitat on glance rates may be attributable to a real absence of effect of habitat on risk of predation (for which adequate data were not available), or to the fact that the subjects monitored the non-social environment at a level so much below the level of social monitoring that environmental considerations had no detectable effect on patterns of vigilance. Glance-rate data collected on adult females in this population (Altmann 1980) are similarly inconclusive with respect to these two possibilities: an analysis of glance rates by habitat revealed no significant difference in glance rate between closed and open habitats (Altmann 1980, page 133; t-test, variances equal, $P=0{\cdot}33$). Furthermore, while open habitats are associated with lower levels of vigilance than closed habitats for some ungulates, this is not always the case (Quenette 1990). Based on these results, it was not possible to exclude the possibility that predation risk affects glance rates.

Daughters of low-ranking females glanced more frequently than daughters of high-ranking females, and the converse was true for males. This was not predicted by the predation risk hypothesis, but is consistent with the idea that social factors affect vigilance. The interactive effects of maternal rank and offspring sex on glance rates of immatures are related to several patterns of life history and maternal investment that are well documented in this population. High-ranking mothers tend to produce a disproportionate number of daughters, while low-ranking mothers are more likely to produce sons (Altmann 1980; Altmann et al. 1988). Similarly, high-ranking mothers spend more time carrying daughters than sons during group travel (Altmann & Samuels 1992). Furthermore, although overall offspring survival does not vary significantly with maternal rank, among high-ranking mothers, survival is highest for daughters, and among low-ranking mothers, survival is highest for sons (Altmann et al. 1988).

The effects of maternal rank on glance rate may relate strongly to these differing survival probabilities and investment patterns. The increased vigilance among daughters of low-ranking mothers and sons of high-ranking mothers may be related to many of the same factors that lower their survival relative to their opposite-sexed siblings. These may include a number of forms of differential investment, such as carrying during group travel (Altmann & Samuels 1992) and less frequent or less effective maternal support during agonistic encounters (Walters 1980; Pereira 1989).

Glance rate decreased with age for females, and did not change with age for males. This was not predicted by either hypothesis, although the lack of sex-biased predation risks in this age group make it unlikely that this sex difference can be explained by the predation risk hypothesis. It is likely that, during the transition to independence, juveniles engage in several different monitoring activities simultaneously: vigilance for predators, vigilance for dangers or benefits likely to come from other group members, and specific monitoring of the mother. A decrease in glance rates of females might result if young females decrease their monitoring of the position and activity of their mothers as they gain independence, even if other kinds of monitoring increase. Without data on objects of juvenile glancing, i.e. what juveniles are glancing at, it is not possible to resolve this issue. Such data might also help to explain the observed sex difference in the extent to which glance rate changes with age.

Finally, under the social factors hypothesis, I expected that females would glance more frequently than males because of their greater vulnerability to aggression from conspecifics. The fact that a sex difference in glance rates was not detected in the linear model is perhaps the strongest support this study offers for the predation risk hypothesis. Again, since juveniles probably engage in several different monitoring activities simultaneously, it is difficult to resolve this issue further without data on objects of juvenile glancing.

In summary, it was not possible to exclude either the social factors hypothesis or the predation risk hypothesis as explanations for glance rate patterns observed in this study. However, there was conclusive evidence that social factors play an important role in determining glance rate patterns of immature yellow baboons, as well as some evidence that predation risk may also affect vigilance.

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