

A MODEL FOR THE INTERPRETATION OF GROOMING PATTERNS APPLIED TO THE BELIZEAN BLACK HOWLING MONKEY (*Alouatta pigra*). BROCKETT, R.C., HORWICH, R.H. AND JONES, C.B.

Key Words: grooming, black howling monkeys, tactile communication, social competition, manipulation, deceit, ignoring, optimality

Abstract

We present preliminary findings of grooming in the Belizean black howling monkey (*Alouatta pigra*). Results are interpreted according to a general model derived from the evolutionary analysis of communication (BRADBURY & VEHCENCAMP, 1998). As reported for other species of *Alouatta*, grooming occurred infrequently. Adult males and juveniles were the most frequent groomers. Adult females were most frequently groomed. Contrary to expectation, adult females were never observed to groom one another, an observation that may be explained by stochastic population processes. Interpretation of our findings with the evolutionary model suggests that grooming in black howlers is best explained by manipulation or deceit to control resources, in particular, mates, group membership, and, food.

Grooming is one of the most frequently displayed behaviors among primates, although its expression varies within and between species, possibly in response to differential costs and benefits from grooming to both groomer (sender) and groomee (receiver) in varying social and physical regimes (SILK, 1986; HENZI & BARRETT, 1999; SANCHEZ-VILLAGRA et al., 1998; PEREZ & VEA, 1998). Primate grooming is especially characteristic of adult female kin and adult females of adjacent rank, though adult males and immatures may also groom (e.g., SILK, 1986). The purpose of this communication is to discuss grooming behavior in evolutionary terms, in particular the evolution of tactile communication within primate societies, exemplified by observations of grooming in the Belizean black howler monkey (*Alouatta pigra*).

The primary reason to touch a conspecific is to send or to receive information that benefits inclusive fitness. Information is employed to make behavioral and physiological decisions about which *ego* is uncertain (BRADBURY & VEHCENCAMP, 1998). Grooming entails the communication of information by signals which Bradbury and Vehrencamp define as any action or trait generated by the sender providing information used by the receiver to select a mutually advantageous response (p. 355). Primates may engage in reciprocal grooming, for instance, in a mutual exchange of information about their emotional or motivational states. If these behaviors do not change current events but reinforce them, pure signaling is said to have occurred (BRADBURY & VEHCENCAMP, 1998). If the contract between groomer and groomee is changed, however, grooming may represent tactical behavior (BRADBURY & VEHCENCAMP, 1998). Primate A may groom primate B in order to modify her response probabilities in the future, possibly explaining the failure to find a correlation between dominance rank and grooming patterns in some studies (e.g., BERNSTEIN & COOPER, 1999; TAKAHASI & FURUICHI, 1998).

Method, Study Site, and Animals

Monthly censuses and ad lib. behavioral observations were conducted of a population of marked black howler monkeys (*A. pigra*) at the Community Baboon Sanctuary (CBS), Belize District, Belize, C.A. (17°33' N, 88°35' W) from January 1995 until March 1997. A total of 1090 h were logged by one observer (RCB) censusing 17 groups. Opportunistic and systematic studies of this population have been conducted since the mid-1980's. Details of the study site can be found in HORWICH & LYON (1990) and SILVER (1998).

A. pigra are found in polygynous (single breeding male) or polygynandrous (multimale- multifemale) groups with an average of 1.6 males/group at the CBS (R.Horwich, unpublished data). SILVER (1998) found that black howlers spent < 10 % of their time-energy budget in activities other than traveling, feeding, and resting. Thus, similar to other species of *Alouatta*, grooming and other social responses occur infrequently (e.g., NEVILLE et al., 1988), making the study of social behavior challenging and time-consuming. In particular, sample sizes in studies of social behavior of *Alouatta* species are generally smaller than for more gregarious and tactile primate taxa. Nonetheless, howlers are highly communal and display a rich repertoire of stereotyped signals and displays, both visual and auditory. In addition, because howlers exhibit bisexual dispersal, groups are composed of unrelated individuals, enhancing their interest for the evolution of social behavior by mechanisms other than kin selection. Studies of black howler social organization and behavior are in the early stages (e.g., HORWICH, 1983; BROCKETT et al., 1999; HORWICH et al., in press), and the present report is the first attempt to analyze grooming patterns in *A. pigra*.

Results and Discussion

Self-Grooming

Animals were observed to self-groom 8 times, once by an adult male and seven times by adult females. Self-grooming generally entailed manual manipulation of hairy body parts in an apparent attempt to remove objects, possibly debris, parasites, or insects. This low incidence of self-grooming suggests that grooming does not function hygienically in black howlers, a conclusion that can be generalized to other species of *Alouatta* since grooming is an infrequent activity, also, for *A. seniculus* (NEVILLE, 1972), *A. palliata* (JONES, 1979), *A. caraya* (JONES, 1983), and *A. fusca* (CHIARELLO, 1995; de OLIVEIRA & ADES, 1998).

Solicitations to Groom

Solicitations to groom (rear or side present) were observed nine times. In each instance an adult female received a solicitation from an adult female (n= 2), an adult male (n= 6), or a juvenile (n= 1), reinforcing the view that females are attractive socially. *A. pigra* may be intermediate to *A. palliata*, for whom solicitations to groom were not observed (JONES, 1979) and *A. caraya*, who were observed to solicit grooming with some frequency under captive conditions (JONES, 1983). Infrequent solicitations to groom suggest that the costs are high or the benefits low from grooming,

possibly resulting from low within- group relatedness due to bisexual dispersal (see CLARKE et al., 1998, pp. 463-464).

Grooming Matrix

Table 1 displays the distribution of grooming bouts in the present study. A total of 59 grooming bouts were observed. This contrasts with 118 grooming bouts recorded in 127 h observation for *A. seniculus* (SANCHEZ-VILLAGRA et al., 1998). Juveniles were most likely to groom ($X^2 = 19.19$, $P < .001$, $df = 3$) while adult females were the most likely recipients of grooming ($X^2 = 68.36$, $P < .001$, $df = 3$). Interestingly, contrary to the typical profile for primates, adult females were never observed to groom each other. This pattern may result from sampling error or may support WRANGHAM's (1980) idea that female-female reciprocity and "bonding" is expected to be minimal in species exhibiting female-transfer (also see HEMELRIJK & LUTEIJN, 1998). Additionally, our data suggest that population density and the rate of male takeovers are high at the CBS (BROCKETT et al., 1999; HORWICH et al., in press). These factors may impact the expression of tactile communication among females in a manner that decreases the benefits or increases the costs of grooming for them.

Table 1: Grooming matrix showing direction of grooming for adult males, adult females, juveniles, and infants. Groomer = Sender and Groomee = Receiver of the grooming act.

GROOMER	GROOMEE				
	Adult males	Adult females	Juveniles	Infants	Total
Adult males		17	1		18
Adult females	3		8		11
Juveniles	2	25		3	30
Infants					0
Total	5	42	9	3	59

Table 1 also shows that both adult males and juveniles concentrate their grooming on adult females but that adult females do not appear to reciprocate. If these results are confident, they suggest that adult female black howlers are not particularly gregarious when compared to females of other primate species. These results are contrary to reports of grooming patterns in *A. seniculus* (NEVILLE, 1972), *A. palliata* (JONES, 1979), *A. caraya* (JONES, 1983), and *A. fusca* (CHIARELLO, 1995; de OLIVEIRA & ADES, 1998), although the latter authors observed only four bouts of grooming between adult females out of a total of 49 bouts. As noted, we hypothesize that female-female social relations are suppressed by population processes at the CBS.

Similar to other studies (e.g., NEVILLE, 1972; JONES, 1979; de OLIVEIRA & ADES, 1998), infants were rarely groomed and were not observed to perform grooming, suggesting that social relations are temporally constrained. Infants, for example, may be too young, weak, and inexperienced to have benefits to offer a conspecific, or their mothers may be prepared to aggressively defend them, increasing the costs

associated with touching infants. Further, since age and reproductive value are negatively related, infants are expected to be selfish.

Proportion of Grooming by Age and Sex

Figure 1 presents the proportion and direction of grooming bouts expressed differentially by age-sex combinations in the present study ($X^2 = 100.45$, $P < .001$, $df = 6$). Grooming of adult females by juveniles accounted for 42 % of total grooming bouts while adult males groomed adult females 29 % of the time. Adult females, then, are very attractive to juveniles and adult males, possibly due to competition for and access to sex, food, infants, space, or group membership.

Figure 1 suggests that juveniles may be attractive grooming partners to adult females, possibly a result of appeasement by females of juveniles competing for access to resources. Adult males and infants are rarely groomed, suggesting that there is little to be gained or much to be lost from these interactions.

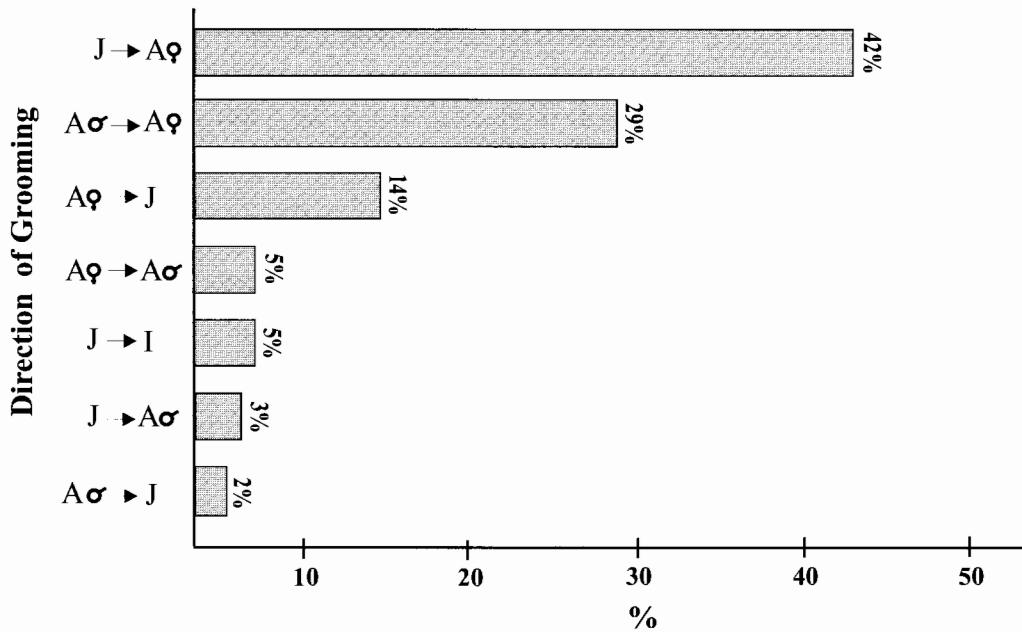


Fig. 2: Differential proportions of grooming and direction of grooming by age and sex (Sender→Receiver).

A Model to Interpret Grooming Patterns

Figure 2 displays the seven possible combinations of costs and benefits from information to groomers and gromees. When the value of information to both groomer and gromee is positive, true communication occurs. This state may characterize grooming between allies or coalition partners such as the mutual grooming observed among male chimpanzees by NISHIDA & HOSAKA (1996). SEYFARTH's (1977)

model of grooming among female primates is an example of true communication where females groom reciprocally for agonistic support and competitively for access to dominants. True communication may also facilitate conflict-resolution (AURELI & SMUCHNY, 1998; JONES, 1983) where groomer and groomee benefit from the interaction. While we did not measure benefits and costs directly in the present study, our results indicate that true communication cannot explain grooming in black howlers since most grooming bouts lasted <1 min and since grooming occurred infrequently. Supporting this view is the observation that the architecture of grooming does not appear to be reciprocal in black howlers (see Tab. 1). Rather, grooming appears to benefit one age-sex class over another. Further analyses of dyadic grooming with marked individuals is necessary to verify or refute these ideas.

		VALUE OF INFORMATION TO GROOME	
		Positive	Zero (or Negative)
VALUE OF INFORMATION TO GROOMER	Positive	True communication	Manipulation (deceit)
	Zero (or Negative)	Eavesdropping, cueing (exploitation)	Ignoring (spite)

Fig. 2: Possible combinations of value of information to Groomer (Sender) and Groomee (Receiver) and their descriptive terms (terms in parenthesis= negative values of information; after BRADBURY & VEHRNCAMP, 1998). See text for discussion.

When the value of grooming to the groomer is positive but the value to the groomee is zero, manipulation has occurred. For example, numerous studies show that males are more likely to groom females in estrus than females in other reproductive states (see WALTERS, 1987) Such behavior may benefit males but be of little or no value to females, particularly if the male is not her first “choice”. In one study of captive black and brown howler monkeys (*A. caraya*), for example, the pair most likely to copulate was the intersexual pair most likely to groom (JONES, 1983), suggesting that grooming may “test” a bond as well as serve as a sexual solicitation. The pattern of results in the present study is consistent with grooming as manipulation since grooming appears to be “one-sided”, benefitting only one age-sex class of the grooming pair (juveniles and adult males), since grooming bouts were generally

brief and since grooming appears not to be reciprocal (Tab. 1). We find no evidence in *A. pigra*, then, for a “service economy” based on grooming as reported by de WAAL (1997) for common chimpanzees.

Manipulation may also occur where subordinates “decide” to remain in a group rather than to emigrate, reflecting competition for group membership. Costs from appeasing dominants by grooming may be lower than costs from dispersal, possibly explaining the high proportion of grooming by juveniles (50%, Fig. 1) in the present study. Juveniles may have more to gain and less to lose than other group members, possibly because reproductive value is high during that period of development.

If the value of grooming to the groomer is positive while the value to the groomee is negative, deceit has occurred. It is deceitful, for example, to employ grooming as a “subterfuge” to obtain future benefits rather than as a “promise” to submit. This condition may obtain where younger animals with the potential to increase their rank groom dominants, as observed in the present study for juveniles who groom adult females. Since grooming may stress time budgets (JONES, 1983; ALTMANN, 1980), low rates of grooming observed in populations of some species or among some age-sex classes may indicate potential for deceit. The present results indicate that females do not groom frequently, a finding that we predict will be explained by the high costs or low benefits of grooming relations.

When the value of grooming to the groomer is zero and the groomee experiences a gain, eavesdropping or cueing characterizes the exchange. When grooming serves a hygienic function (e.g., BORRIES, 1992; PEREZ & VEA, 1998), groomers may inadvertently transmit cues correlated with the grooming interaction (e.g., about emotional state or reproductive condition). Since this tradeoff represents altruism, it is not expected to evolve unless its benefits to inclusive fitness, on average, outweigh its costs over the long term. As we suggested above, grooming in black howlers does not appear to serve a hygienic function. Furthermore, opportunities for eavesdropping or cueing are limited because grooming is infrequent and rarely solicited. Also, if grooming served a significant hygienic function, it would be expected that mothers would groom their infants and that autogrooming would occur with higher frequency. Neither was observed.

When grooming harms the groomer but benefits the groomee, exploitation has taken place. This state may occur when mothers groom their young and costs in time from grooming diminish a mother’s future reproductive success. In the present study, infants, juveniles, and adult males are rarely groomed, suggesting that black howlers behave selfishly towards each other, at least with respect to this action pattern. Exploitation may also occur where subordinates “decide” to remain in a group rather than to emigrate. Costs from appeasing other group members by grooming may be lower than costs from dispersal, possibly explaining the high proportion of grooming by juveniles (50%, Fig. 1) in the present study.

When neither the groomer nor the groomee gains from the interaction, ignoring is expected to occur and may explain cases for which grooming is rare or absent as for *A. palliata* (JONES, 1979) and *A. pigra* (present study). Gains may be low from a grooming exchange because probabilities of escalation are high or because time-energy budgets are severely constricted, possibly due to the limitations of folivorous diets (JONES, 1980; also see MILTON, 1980 and NEVILLE et al., 1988). ALTMANN (1980) has pointed out that grooming is usually assumed to be “beneficial” in the pri-

mate literature, but that grooming is a "time-consuming" behavior appearing to stress time budgets.

Theoretically, the value of grooming may be negative for both groomer and groomee (spite). For example, grooming may be a "waste of time". We are unable to locate studies demonstrating clear or apparent examples of spite, but research on black and brown howler monkeys (JONES, 1983) and baboons (ALTMANN, 1980) suggest that grooming may not always have a "relaxing" consequence and should be viewed within the context of social competition. At such times, grooming may increase levels of stress, likelihoods of escalation for the interactants, and interindividual distances, possibly inhibiting rather than facilitating social cohesion. The present study suggests that black howlers may avoid spiteful grooming by limiting their time spent engaging in the activity.

Conclusions

The present study suggests that grooming in black howlers functions socially, primarily as manipulation of adult females by adult males and juveniles for access to resources, in particular, sex and group membership, and, possibly, food and proximity to infants. Our results are also consistent with the view that grooming of adult females by adult males and juveniles represents deceit of females for access to resources. To distinguish between manipulation and deceit, it would be necessary to determine whether the costs of grooming to females in these bouts are, on average, zero or negative, respectively (Fig. 2). Our results, then, support a social rather than a hygienic or distensive function of grooming in black howler society, consistent with the conclusions for other *Alouatta* species (SANCHEZ-VILLAGRA et al., 1998).

Grooming has important consequences for the phenotypes of individuals because of its influences upon the time-energy budgets of groomer and groomee and the contexts in which grooming is displayed. The functions of grooming may be simple (e.g., hygienic) or complex (e.g., reproductive effort) and grooming bouts brief or protracted. Grooming, thus, is best viewed as an alternative social tactic (short-term) or strategy (long-term), and the grooming game will depend upon who is playing it in which conditions at a given time. In some primate species (e.g., the black howling monkey), partners are infrequently sought or found.

Acknowledgements

We are grateful to Dr. K.E. Glander for his assistance in marking the animals. These studies were carried out with the support of the National Geographic Society (Grants #5352-94 and #5653-96).

References

ALTMANN, J.: Baboon Mothers and Infants. Cambridge, MA: Harvard University Press (1980).

- JONES, C.B.: Grooming in the mantled howler monkey, *Alouatta palliata* Gray. *Primates* (1979) 23: 130-134.
- JONES, C.B.: The functions of status in the mantled howler monkey, *Alouatta palliata* Gray: intraspecific competition for group membership in a folivorous neotropical primate. *Primates* (1980) 21: 389-405.
- JONES, C.B.: Social organization of captive black howler monkeys (*Alouatta caraya*): "social competition" and the use of non-damaging behavior. *Primates* (1983) 24: 25-39.
- MILTON, K.: The Foraging Strategy of Howler Monkeys: A Study in Primate Economics. New York: Columbia University Press (1980).
- NEVILLE, M.K.: Social relations within troops of red howler monkeys (*Alouatta seniculus*). *Folia Primatol.* (1972) 18: 47-77.
- NEVILLE, M.K., GLANDER, K.E., BRAZA, F. and RYLANDS, A.B. The howling monkeys, genus *Alouatta*. In: MITTERMEIER, R.A., RYLANDS, A.B., COIMBRA-FILHO, A. and FONSECA, G.A.B. (eds.): *Ecology and Behavior of Neotropical Primates*, Vol. 2. Washington, D.C.: World Wildlife Fund (1988): 349-453.
- NISHIDA, T. and HOSAKA, K.: Coalition strategies among adult male chimpanzees of the Mahale Mountains, Tanzania. In: MCGREW, W.C., MARCHANT, L.F. and NISHIDA, T. (eds.): *Great Ape Societies*, Cambridge, U.K.: Cambridge University Press (1996): 114-134.
- PEREZ, A. and VEA, J.J.: Cost-benefit analysis of allogrooming behaviour in primates II. *Primate Report* (1998) 50: 15-37.
- SANCHEZ-VILLAGRA, M.R., POPE, T.R. and SALAS, V.: Relation of intergroup variation in allogrooming to group social structure and ectoparasite loads in red howlers (*Alouatta seniculus*). *International Journal of Primatology* (1998) 19: 473-491.
- SEYFARTH, R.M.: A model of social grooming among adult female monkeys. *J. Theor. Biol.* (1977) 65: 671-698.
- SILK, J.B.: Social behavior in evolutionary perspective. In: SMUTS, B.B., CHENEY, D.L., SEYFARTH, R.M., WRANGHAM, R.W. and STRUHSAKER, T.T. (eds.): *Primate Societies*, Chicago: University of Chicago Press (1986): 318-329.
- SILVER, S.C.: The feeding ecology of translocated howler monkeys, *Alouatta pigra*, in Belize. Unpublished Ph.D. Dissertation, Fordham University, New York (1998).
- TAKAHASHI, H. and FURUICHI, T.: Comparative study of grooming relationships among wild Japanese macaques in Kinkazan A Troop and Yakushima M Troop. *Primates* (1998) 39: 365-374.

WALTERS, J.R.: Transition to adulthood. In: SMUTS, B.B., CHENEY, D.L., SEYFARTH, R.M., WRANGHAM, R.W. and STRUHSAKER, T.T. (eds.): *Primate Societies*. Chicago: University of Chicago Press (1986): 358-369.

WRANGHAM, R.W.: An ecological model of female-bonded primate groups. *Behaviour* (1980) 75: 262-296.

Correspondence to:

Clara B. Jones, Livingstone College, Division of Social Sciences, 701 W. Monroe Street, Salisbury, North Carolina 28144, U.S.A.

E-mail: cjones@livingstone.edu or howler425@cs.com