

Intragroup Social Relationships of Male *Alouatta palliata* on Barro Colorado Island, Republic of Panama

Elan Wang¹ and Katharine Milton^{2,3}

Received May 22, 2002; revision September 12, 2002; accepted May 20, 2003

We examined social and spatial relations of adult males in one group of mantled howling monkeys (*Alouatta palliata*) on Barro Colorado Island (BCI) in central Panama to document patterns of association. Beyond the existence of an alpha male, we could not distinguish any linear dominance hierarchy among the 6 study males. All males copulated with estrous females. Our findings contrast with reports of intragroup male behavior in Costa Rican howlers. Study males engaged in little or no affiliative or agonistic behavior with one another, but engaged in significantly more such interactions with females. The alpha male, the oldest male and a younger male were most frequently in association with females. Of group males, the oldest male associated significantly more with other males. Overall, male behavior in mantled howling monkeys on BCI generally followed the van Hooft and van Schaik (1994) model of male relationships. The low incidence of intragroup social interactions of any type in the focal males may reflect the energetic costs of social behavior. We suggest that intragroup social relationships among mantled howler males are structured by more subtle means than overt physical interactions, possibly including vocal communication, relationships with individual group females, and kinship.

KEY WORDS: *Alouatta*; mantled howlers; male social behavior; dominance; affiliation.

¹1725 Tennessee Street, Apt. 3, Lawrence, KS 66044; e-mail: elan.wang@yahoo.com

²Department of Environmental Science, Policy and Management, Division of Insect Biology, 201 Wellman Hall, University of California, Berkeley, California 94720-3112 USA.

³To whom correspondence should be addressed at Department of Environmental Science, Policy and Management, Division of Insect Biology, 201 Wellman Hall, University of California, Berkeley, California 94720-3112 USA ; e-mail: kmilton@socrates.berkeley.edu.

INTRODUCTION

Recently, researchers have given considerable attention to the role of adult males in primate social systems, with emphasis on male behavioral strategies (Kappeler, 2000; van Hooff, 2000; van Hooff and van Schaik, 1992, 1994). Early observational studies of primates focused primarily on intermale conflict and aggression (Zuckerman, 1932), with strong interest in topics such as dominance hierarchies, the role of the alpha male, and the proposed benefits accruing to high-ranking males (Hall and De Vore, 1965; Rowell, 1966; Washburn and Hamburg, 1968). As interest shifted to examination of female behavioral strategies in group life, studies of male relations continued to center around dominance and aggression. However, a few notable studies on male affiliation showed that in some species (red colobus: Struhsaker, 1975; Struhsaker and Leland, 1979; chimpanzees: de Waal, 1982; Simpson, 1973; bonnet macaques: Simonds, 1974; Sugiyama, 1971), male affiliative behaviors were as or more common than female affiliative behaviors. Studies of reconciliation behavior after agonistic encounters (de Waal, 1989) have also revealed a diversity of male social strategies beyond dominance and agonistic interactions.

Most recently, genetic analysis has shown that in some primate societies, kinship relations appear to influence male patterns of association or to contribute to intragroup stability (red howlers: Pope, 1990; chimpanzees: Morin *et al.*, 1994; contra Mitani *et al.*, 2000). Increasingly, data suggest that the social behavior of male primates is far more varied and complex than has previously been supposed (Hill and van Hooff, 1994; Kappeler, 2000). In view of a new appreciation of male social complexity, there is a need to document details of male relationships more fully and, as stressed by Strum (2002), move beyond the descriptive level of study.

Few models describing primate male social interactions exist. Van Hooff and van Schaik (1994) proposed a model in which male relationships are based on the structure of female social organization. Primate female social organization is influenced by primary socioecological factors such as food availability and predation risk, which determine the distribution pattern and nature of competition of group-living females. Female grouping and competition in turn establish patterns of female social relations, which then shape the structure of male social relationships. With consideration of dispersal patterns, the model then predicts the scope of male bonding. However, studies of the female relationships that form the basis for this model skew heavily towards Old World species (Perry, 1996; Strier, 1994). As male-female dispersal patterns are often reversed in the New World (Moore, 1992; Strier, 1994), it is of interest to examine the applicability of van Hooff and van Schaik's (1994) model to New World primate males.

INTRODUCTION

Recently, researchers have given considerable attention to the role of adult males in primate social systems, with emphasis on male behavioral strategies (Kappeler, 2000; van Hooff, 2000; van Hooff and van Schaik, 1992, 1994). Early observational studies of primates focused primarily on intermale conflict and aggression (Zuckerman, 1932), with strong interest in topics such as dominance hierarchies, the role of the alpha male, and the proposed benefits accruing to high-ranking males (Hall and De Vore, 1965; Rowell, 1966; Washburn and Hamburg, 1968). As interest shifted to examination of female behavioral strategies in group life, studies of male relations continued to center around dominance and aggression. However, a few notable studies on male affiliation showed that in some species (red colobus: Struhsaker, 1975; Struhsaker and Leland, 1979; chimpanzees: de Waal, 1982; Simpson, 1973; bonnet macaques: Simonds, 1974; Sugiyama, 1971), male affiliative behaviors were as or more common than female affiliative behaviors. Studies of reconciliation behavior after agonistic encounters (de Waal, 1989) have also revealed a diversity of male social strategies beyond dominance and agonistic interactions.

Most recently, genetic analysis has shown that in some primate societies, kinship relations appear to influence male patterns of association or to contribute to intragroup stability (red howlers: Pope, 1990; chimpanzees: Morin *et al.*, 1994; contra Mitani *et al.*, 2000). Increasingly, data suggest that the social behavior of male primates is far more varied and complex than has previously been supposed (Hill and van Hooff, 1994; Kappeler, 2000). In view of a new appreciation of male social complexity, there is a need to document details of male relationships more fully and, as stressed by Strum (2002), move beyond the descriptive level of study.

Few models describing primate male social interactions exist. Van Hooff and van Schaik (1994) proposed a model in which male relationships are based on the structure of female social organization. Primate female social organization is influenced by primary socioecological factors such as food availability and predation risk, which determine the distribution pattern and nature of competition of group-living females. Female grouping and competition in turn establish patterns of female social relations, which then shape the structure of male social relationships. With consideration of dispersal patterns, the model then predicts the scope of male bonding. However, studies of the female relationships that form the basis for this model skew heavily towards Old World species (Perry, 1996; Strier, 1994). As male-female dispersal patterns are often reversed in the New World (Moore, 1992; Strier, 1994), it is of interest to examine the applicability of van Hooff and van Schaik's (1994) model to New World primate males.

Mantled howling monkeys, *Alouatta palliata*, are unusually well suited for the study of male social relationships as they appear to be the only *Alouatta* sp. that consistently lives in relatively large, permanent, social groups with multiple (≥ 3) fully adult resident males (Treves, 2001). Other species typically live in smaller social units with only 1, 2, or occasionally more male members (Treves, 2001). The larger group size and presence of multiple males in mantled howler groups facilitates study of interindividual social interactions.

Early observers of mantled howlers on Barro Colorado Island (BCI), Panama described males as generally engaging in little interindividual aggression and rarely exhibiting intragroup agonism (Altmann, 1959; Carpenter, 1934; Southwick, 1963). More recently, studies at La Pacifica, Costa Rica, showed that mantled howlers of both sexes display a reverse age-graded dominance hierarchy, in which the youngest animal is dominant (Glander, 1980, 1992; Jones, 1980) and that dominant males exercise an apparent monopoly over available estrous females (Glander, 1980; Jones, 1985). Males at both sites are reported to engage in fights and chase each other before emigration from a natal group or during group takeover attempts (Young, 1981; Clarke, 1982, 1983, 1986; Clarke and Glander, 1984; Glander, 1992). However, before our study, social relationships between adult male howlers on BCI had never been systematically studied or quantified.

Van Hooff and van Schaik's (1994) model, in combination with existing knowledge of mantled howlers, allowed us to make an initial prediction on male relationships on BCI. Female mantled howler behavior generally follows the pattern of scramble-type competition (Zucker and Clarke, 1998). Combining this with the apparent exclusive access of the dominant group male to estrous females (Glander, 1980; Jones, 1985), we expected howler males to display contest polygyny relationships and to compete overtly for status. To test this prediction and determine patterns of male association, we examined social and spatial relations of males in one group of BCI mantled howling monkeys.

METHODS

Study Site

Barro Colorado Island is a densely forested 1500-ha nature reserve in the Republic of Panama. (Hubbell and Foster, 1990; Leigh *et al.*, 1982). The island's climate is strongly seasonal, characterized by a 3-mo dry season (mid-January to mid-April) followed by a 7-mo wet season (May–November), and

a 4–6 week transition period (mid-December to mid-January). Heavy leaf loss in the dry season allows for good observational conditions; rain and denser vegetation hamper data collection in the wet season.

Study Subjects

From February to October, 2001, we focused on one group of howlers, composed (at the start of the study) of 6 adult males, 12 adult females, 1 subadult male, 4 juveniles, and 3 infants. During the course of the study, the subadult male emigrated (May 2001) and one adult male (possibly a former member) joined the group (June 2001). We presented only data on the original 6 males in analyses due to limited data on the immigrant male. Five of the 6 original males had been marked in June 2000 with color-coded ear beads, anklets with color-coded plastic markers, and distinctive patterns of hair dye, making them individually recognizable: The focal males were PK, YL, RD, PD, OR, and UM.

K. Glander estimated ages via examination of each captured individual's dentition. Accordingly, PK was ca. 10 yr old, YL 28 yr, RD 6 yr, PD 10 yr and OR 9 yr. UM's age was unknown, though he appeared to be a younger male (6–9 yr).

The group's home range encompassed roughly 34 ha of old second growth forest, interspersed with patches of primary forest. The forest was composed of both mid-canopy and canopy level trees, with some trees reaching heights of 30–40 m (Leigh *et al.*, 1982). The home range included the laboratory clearing on the northeast corner of the island. The monkeys frequently appeared at the edge of the clearing, facilitating location of the group. In addition, because the group had been exposed to humans regularly, the monkeys were well habituated and observation distances of 10–20 m were common.

Data Collection

We collected data from 18 February through 25 October 2001, encompassing portions of both the dry and wet seasons. We collected behavioral data in 3 forms—1-hr focal animal samples, 10-min instantaneous scan samples, and notes *ad libitum* (Altmann, 1974). During focal animal sampling, we recorded all activities, social interactions, and vocalizations involving the focal animal, along with the identity of any participants. Agonistic behaviors included displacements, pushes, chases, grabs, and fights. Affiliative behaviors included playing, greeting, and embracing. We recorded vocalizations using the following categories: howl, bark, glottal pop (corresponding to the

a 4–6 week transition period (mid-December to mid-January). Heavy leaf loss in the dry season allows for good observational conditions; rain and denser vegetation hamper data collection in the wet season.

Study Subjects

From February to October, 2001, we focused on one group of howlers, composed (at the start of the study) of 6 adult males, 12 adult females, 1 subadult male, 4 juveniles, and 3 infants. During the course of the study, the subadult male emigrated (May 2001) and one adult male (possibly a former member) joined the group (June 2001). We presented only data on the original 6 males in analyses due to limited data on the immigrant male. Five of the 6 original males had been marked in June 2000 with color-coded ear beads, anklets with color-coded plastic markers, and distinctive patterns of hair dye, making them individually recognizable: The focal males were PK, YL, RD, PD, OR, and UM.

K. Glander estimated ages via examination of each captured individual's dentition. Accordingly, PK was ca. 10 yr old, YL 28 yr, RD 6 yr, PD 10 yr and OR 9 yr. UM's age was unknown, though he appeared to be a younger male (6–9 yr).

The group's home range encompassed roughly 34 ha of old second growth forest, interspersed with patches of primary forest. The forest was composed of both mid-canopy and canopy level trees, with some trees reaching heights of 30–40 m (Leigh *et al.*, 1982). The home range included the laboratory clearing on the northeast corner of the island. The monkeys frequently appeared at the edge of the clearing, facilitating location of the group. In addition, because the group had been exposed to humans regularly, the monkeys were well habituated and observation distances of 10–20 m were common.

Data Collection

We collected data from 18 February through 25 October 2001, encompassing portions of both the dry and wet seasons. We collected behavioral data in 3 forms—1-hr focal animal samples, 10-min instantaneous scan samples, and notes *ad libitum* (Altmann, 1974). During focal animal sampling, we recorded all activities, social interactions, and vocalizations involving the focal animal, along with the identity of any participants. Agonistic behaviors included displacements, pushes, chases, grabs, and fights. Affiliative behaviors included playing, greeting, and embracing. We recorded vocalizations using the following categories: howl, bark, glottal pop (corresponding to the

Table I. Focal hours of observation

Monkey	Month								Total
	March	April	May	June	July	August	September	October	
OR	0.50	6.47	12.35	7.37	4.83	1.00	0.00	0.73	33.25
PD	1.00	11.35	12.70	6.53	2.00	0.00	0.00	0.55	34.13
PK	7.85	18.17	6.17	3.10	3.33	0.00	0.00	0.97	39.58
RD	0.93	7.33	10.08	6.63	3.57	3.00	1.00	1.00	33.55
UM	3.00	19.47	0.00	7.92	6.93	3.73	2.00	0.00	43.05
YL	5.50	16.73	10.38	4.50	2.90	2.77	0.00	1.00	43.78
Total	18.78	79.52	51.68	36.05	23.56	10.50	3.00	4.25	227.35

Only focal samples ≥ 30 min duration were used in analyses.

type 2 vocalization of Carpenter, 1934), throat rumble (oodle of Altmann, 1959 and Baldwin and Baldwin, 1976), cluck (type 3 vocalization of Carpenter, 1934) and other.

Observational conditions made it impossible to follow a predetermined focal animal sampling schedule. Thus, we chose focal animals opportunistically, but under the following conditions: no more than 2 full-length (1-h) samples on the same individual were taken within a 4-h period, and if 2 samples were taken of the same monkey within 4 h, they were spaced ≥ 1 h apart. We discarded any samples interrupted by temporary loss of visible contact with the focal animal if the monkey remained out of view for >15 min; we also discarded any sample that resulted in <30 min of contact time with the focal individual. Overall, we collected 227.35 focal h on the behavior of adult males (Table I).

At 10-min intervals during all contact hours, we took instantaneous scan samples to compile spatial pattern information for each visible adult male. In the scans, we recorded the identity or sex/age class of all monkeys (neighbors) within 3 spatial classes relative to each adult male—in contact, ≤ 1 m (proximity), and 1–5 m (neighborhood). As White and Chapman (1994) noted, individuals constantly make active decisions concerning the identities of their neighbors, and thus spatial placement of an individual within a group is a good indicator of social relationships. In all, we collected 3038 scan samples on neighbors of the 6 focal males.

Data Analysis

In order to examine male differences in behavioral patterns, we calculated hourly rates of affiliation, agonism, and different types of vocalization for each focal male, and compared variation in rates. We analyzed howls and clucks, which often occurred in bouts, somewhat differently. For them we

calculated number of bouts per h; all howls or clucks heard within a 5-min block were counted as 1 bout.

We analyzed the neighborhood information via several approaches. To determine similarities and differences among the males, we established 3 indices for comparison—one of number of adult neighbors of either sex, one of neighbor distribution across the 3 spatial classes, and one of female association. For the number of neighbors index, we calculated, for each sample scan, the total number of neighbors for each visible adult male. To determine neighbor spatial distribution, we then assigned each neighbor a different weight (in contact = 4 pts, proximity = 3 pts, neighborhood = 1 pt.). We assigned weights based on the social importance of the distances; we considered proximity and contact to have more social meaning than neighborhood so we assigned them arbitrarily higher weights. To determine degree of female association we calculated the following: $[(\# \text{ of female neighbors} - \# \text{ of male neighbors}) / \text{total number of adult neighbors}]$. We then compared the average scores for each male monkey in the 3 different indices via a one-way ANOVA and a two-sample t-test.

To test for differences among males in overall number and sex ratio of neighbors, we calculated an expected number of neighbors calibrated for either the total number of samples per monkey or the sociometric sex ratio of the group. To test for individual male association, we determined the distribution of individual male-male dyads in the 3 spatial classes. In both cases, we compared observations with expected values calculated on the premise that each male's data set was independent and that no preferential association existed between monkeys. We used a chi-square analysis to test deviations from the expected values.

We determined a male's degree of spatial centrality within the group by calculating the percentage of scan samples in which we recorded zero neighbors in all spatial classes.

RESULTS

Dominance Hierarchy

We could not discern an obvious linear dominance hierarchy beyond the existence of an alpha male (PK) because we almost never observed any pairwise supplantations or other dominance-related interactions. We identified PK as the alpha male based on his priority of access to food resources, his vocal coordination of group movement, and his high degree of spatial centrality within the group. We could roughly estimate the relative positions of some of the other males based on degree of spatial centrality, but not in strict linearity.

calculated number of bouts per h; all howls or clucks heard within a 5-min block were counted as 1 bout.

We analyzed the neighborhood information via several approaches. To determine similarities and differences among the males, we established 3 indices for comparison—one of number of adult neighbors of either sex, one of neighbor distribution across the 3 spatial classes, and one of female association. For the number of neighbors index, we calculated, for each sample scan, the total number of neighbors for each visible adult male. To determine neighbor spatial distribution, we then assigned each neighbor a different weight (in contact = 4 pts, proximity = 3 pts, neighborhood = 1 pt.). We assigned weights based on the social importance of the distances; we considered proximity and contact to have more social meaning than neighborhood so we assigned them arbitrarily higher weights. To determine degree of female association we calculated the following: [(# of female neighbors - # of male neighbors)/total number of adult neighbors]. We then compared the average scores for each male monkey in the 3 different indices via a one-way ANOVA and a two-sample t-test.

To test for differences among males in overall number and sex ratio of neighbors, we calculated an expected number of neighbors calibrated for either the total number of samples per monkey or the socionomic sex ratio of the group. To test for individual male association, we determined the distribution of individual male-male dyads in the 3 spatial classes. In both cases, we compared observations with expected values calculated on the premise that each male's data set was independent and that no preferential association existed between monkeys. We used a chi-square analysis to test deviations from the expected values.

We determined a male's degree of spatial centrality within the group by calculating the percentage of scan samples in which we recorded zero neighbors in all spatial classes.

RESULTS

Dominance Hierarchy

We could not discern an obvious linear dominance hierarchy beyond the existence of an alpha male (PK) because we almost never observed any pairwise supplantations or other dominance-related interactions. We identified PK as the alpha male based on his priority of access to food resources, his vocal coordination of group movement, and his high degree of spatial centrality within the group. We could roughly estimate the relative positions of some of the other males based on degree of spatial centrality, but not in strict linearity.

Table IIa. Rate per hour of agonistic interactions between adult males and females, adjusted for socionomic sex ratio

Monkeys	Male-Male Interactions		Male-Female Interactions		Adjusted Rate
	Observed	Rate	Observed	Rate	
OR	0	0.000	6	0.180	0.090
PD	1	0.029	3	0.088	0.044
PK	0	0.000	2	0.051	0.025
RD	1	0.030	3	0.089	0.045
UM	2	0.047	3	0.070	0.035
YL	0	0.000	5	0.114	0.057
Total/Mean	4	0.018	22	0.099	0.049
		SD = 0.020		SD = 0.045	SD = 0.023

Agonistic Interactions

Adult males rarely engaged in agonistic interactions of any type, and when they did, it was primarily with adult females (Table IIa). The overall mean rate of male-male agonistic interactions is 0.018/h ($SD = 0.020$). Hourly rates of male-male agonism ranged from 0.000/h (OR, PK, YL) to 0.047/h (UM), whereas the overall male-female rate, adjusted for the socionomic sex ratio of the group, is nearly 3 times as great (0.049/h, $SD = 0.023$). Interactions between males were never overtly violent; all took the form of spatial supplantations. Agonistic interactions with adult females generally occurred during feeding bouts. Males always won the interactions, either by displacing the female from her feeding site, or in rare instances, actually grabbing a food item from her.

Over the course of the study we observed 3 adult males with wounds; we could not determine their causes. In early March 2001, RD was licking a wound on his left elbow; in late March, UM had a large gash on the bottom of his left foot. In April 2001, YL had a wound mid-tail. The wounds appeared consistent with injuries sustained during falls or other accidents, though fighting, which we never observed, cannot be ruled out as a possible source for the injuries.

Affiliative Interactions

Males very rarely engaged in affiliative behaviors with each other; the overall male-male affiliative rate is only 0.018/h ($SD = 0.020$; Table IIb), the same as for agonism. Individual male-male affiliative rates ranged from 0.000/h (PD, PK, UM) to 0.046/h (YL). Males similarly did not interact much with females, with rates ranging only from 0.000/h (PK, RD, YL) to 0.044/h (PD).

Table IIb. Rate per hour of affiliative interactions between adult males and females, adjusted for socioeconomic sex ratio

Monkeys	Male-Male Interactions		Male-Female Interactions		Adjusted Rate
	Observed	Rate	Observed	Rate	
OR	1	0.030	1	0.030	0.015
PD	0	0.000	3	0.088	0.044
PK	0	0.000	0	0.000	0.000
RD	1	0.030	0	0.000	0.000
UM	0	0.000	1	0.023	0.012
YL	2	0.046	0	0.000	0.000
Total/Mean	4	0.018	5	0.024	0.012
		<i>SD</i> = 0.020		<i>SD</i> = 0.034	<i>SD</i> = 0.017

The most common affiliative interaction between males was a ritualized greeting, previously described by Glander (1975, 1980) and Young (1983), wherein 2 males approached and grasped each other in a deep embrace, both vocalizing (mostly throat rumbling and clucking), and often sniffing each other's genitals before or after the embrace. The greetings lasted 2–15 sec.

We observed 12 embrace greetings during combined focal and ad libitum observations, with a focal rate of 0.022/h. In most cases, one monkey clearly approached another and initiated the sequence. Of the 12 events, both participants could be accurately identified in 7 cases: YL-PK, OR-RD, RD-YL*, YL-RD, PK-YL, OR-PK*, RD-UM; the initiator is listed first except in cases marked by an asterisk where the approach was mutual. The oldest male (YL) was involved in the most greetings ($n = 4$). The alpha male (PK) and the youngest male (RD) each initiated one greeting, received one greeting, and mutually participated in a third. On occasion, a male would initiate a greeting, either by approaching another male and vocalizing or by sniffing him, without eliciting any response from the recipient. In these cases, the initiator would then continue his prior behavior without embracing the intended recipient. PK and UM each initiated one greeting without response; the non-responding recipients were not identified.

Spatial Class Patterns

Males differed from one another in total number of neighbors recorded in all 3 spatial classes, though the overall difference is not significant (Table IIIa). However, males significantly favored female neighbors over male neighbors (neighborhood: $\chi^2 = 84.290$, $p < 0.001$; proximity: $\chi^2 = 185.73$, $p < 0.001$; contact: $\chi^2 = 21.000$, $p < 0.05$; Table IIIb). PK, UM, and

Table IIb. Rate per hour of affiliative interactions between adult males and females, adjusted for socioeconomic sex ratio

Monkeys	Male-Male Interactions		Male-Female Interactions		Adjusted Rate
	Observed	Rate	Observed	Rate	
OR	1	0.030	1	0.030	0.015
PD	0	0.000	3	0.088	0.044
PK	0	0.000	0	0.000	0.000
RD	1	0.030	0	0.000	0.000
UM	0	0.000	1	0.023	0.012
YL	2	0.046	0	0.000	0.000
Total/Mean	4	0.018	5	0.024	0.012
		SD = 0.020		SD = 0.034	SD = 0.017

The most common affiliative interaction between males was a ritualized greeting, previously described by Glander (1975, 1980) and Young (1983), wherein 2 males approached and grasped each other in a deep embrace, both vocalizing (mostly throat rumbling and clucking), and often sniffing each other's genitals before or after the embrace. The greetings lasted 2–15 sec.

We observed 12 embrace greetings during combined focal and ad libitum observations, with a focal rate of 0.022/h. In most cases, one monkey clearly approached another and initiated the sequence. Of the 12 events, both participants could be accurately identified in 7 cases: YL-PK, OR-RD, RD-YL*, YL-RD, PK-YL, OR-PK*, RD-UM; the initiator is listed first except in cases marked by an asterisk where the approach was mutual. The oldest male (YL) was involved in the most greetings (n = 4). The alpha male (PK) and the youngest male (RD) each initiated one greeting, received one greeting, and mutually participated in a third. On occasion, a male would initiate a greeting, either by approaching another male and vocalizing or by sniffing him, without eliciting any response from the recipient. In these cases, the initiator would then continue his prior behavior without embracing the intended recipient. PK and UM each initiated one greeting without response; the non-responding recipients were not identified.

Spatial Class Patterns

Males differed from one another in total number of neighbors recorded in all 3 spatial classes, though the overall difference is not significant (Table IIIa). However, males, significantly favored female neighbors over male neighbors (neighborhood: $\chi^2 = 84.290$, $p < 0.001$; proximity: $\chi^2 = 185.73$, $p < 0.001$; contact: $\chi^2 = 21.000$, $p < 0.05$; Table IIIb). PK, UM, and

Table IIIa. Total number of adult neighbors observed during scan samples per adult male in neighborhood, proximity, and contact spatial classes^a

	Neighborhood			Proximity			Contact		
	Observed	Expected	χ^2	Observed	Expected	χ^2	Observed	Expected	χ^2
OR	88	94.316	0.423	43	38.947	0.422	5	2.737	1.871
PD	264	248.273	0.996	89	102.522	1.783	5	7.205	0.675
PK	314	319.704	0.101	138	132.018	0.271	9	9.278	0.008
RD	139	148.409	0.597	69	61.284	0.972	6	4.307	0.666
UM	254	260.765	0.175	110	107.676	0.050	12	7.567	2.597
YL	359	328.026	2.925	109	135.455	5.167	5	9.519	2.146
Total χ^2 Statistic ^d			5.220			8.660			7.960

YL in particular contributed the majority of non-randomness in the female-skewed results. The data show an inverse relationship between female and male association—i.e. the males (PK, UM, and YL) that associate with females the most associate with males the least.

Table IIIb. Total number of adult female and male neighbors per adult male, adjusted for socioeconomic sex ratio

	Females			Males			Total χ^2 Statistic ^d
	Observed	Expected	χ^2	Observed	Expected	χ^2	
Neighborhood							
OR	67	58.670	1.180	21	29.333	2.370	84.290 ^b
PD	208	176.000	5.820	56	88.000	11.640	
PK	260	209.330	12.260	54	104.670	24.530	
RD	101	92.670	0.750	38	46.330	1.500	
UM	205	169.330	7.510	49	84.670	15.020	
YL	251	239.330	0.570	108	119.670	1.140	
Proximity							
OR	40	28.670	4.480	3	14.330	8.960	185.730 ^b
PD	82	59.330	8.660	7	29.670	17.320	
PK	135	92.000	20.100	3	46.000	40.200	
RD	62	46.000	5.570	7	23.000	11.130	
UM	104	73.330	12.820	6	36.670	25.650	
YL	100	72.670	10.280	9	36.330	20.560	
Contact							
OR	5	3.330	0.830	0	1.670	1.670	21.000 ^c
PD	5	3.330	0.830	0	1.670	1.670	
PK	9	6.000	1.500	0	3.000	3.000	
RD	6	4.000	1.000	0	2.000	2.000	
UM	12	8.000	2.000	0	4.000	4.000	
YL	5	3.330	0.830	0	1.670	1.670	

^aNo statistic achieved significance.

^b $p < 0.001$.

^c $p < 0.05$.

^ddf = 5.

Table IV. Individual male dyadic associations observed during scan sampling

Dyads	Neighborhood			Proximity		
	Observed	Expected	χ^2	Observed	Expected	χ^2
OR-PD	7	9	0.444	0	1.2	1.200
OR-PK	1	9	7.111	0	1.2	1.200
OR-RD	1	9	7.111	0	1.2	1.200
OR-UM	4	9	2.778	0	1.2	1.200
OR-YL	5	9	1.778	3	1.2	2.700
PD-PK	4	9	2.778	0	1.2	1.200
PD-RD	1	9	7.111	2	1.2	0.533
PD-UM	11	9	0.444	5	1.2	12.033 ^b
PD-YL	28	9	40.111 ^b	1	1.2	0.033
PK-RD	1	9	7.111	0	1.2	1.200
PK-UM	5	9	1.778	0	1.2	1.200
PK-YL	18	9	9.000	1	1.2	0.033
RD-UM	2	9	5.444	0	1.2	1.200
RD-YL	25	9	28.444 ^b	5	1.2	12.033 ^b
UM-YL	22	9	18.778 ^b	1	1.2	0.033
Total	135		140.222 ^{a,c}	18		37.000 ^{a,c}

^a $p < 0.001$.^bDyad contributing large proportion of non-randomness.^cdf = 13.

Although, overall, males associated little with one another, some males exhibited a significant preference for certain male neighbors over others (Table IV). Notably the oldest male (YL) was a member of 4 of 5 special male-male dyads, across both neighborhood and proximity spatial classes. We never observed males in contact during sampling.

The alpha male (PK) had the smallest percentage of samples with zero neighbors (38.6%; Fig. 1), while OR had the highest (67.3%). Analysis of the 3 spatial pattern indices revealed significant (two-sample t-test, $p < 0.001$) similarities and differences between certain males. For example, PD and YL were similar in having more monkeys, especially females, in closer proximity than other males did. OR and RD differed from the other males in having fewer neighbors of both sexes and across all spatial classes. OR and RD's spatially peripheral status in the group suggests that they were low-ranking males. Using the same logic, we inferred PD, UM and YL to be higher-ranking group males.

Vocalizations

All 6 males engaged in howl, bark, glottal pop, throat rumble, and cluck vocalizations, but some males engaged in certain vocalizations more than others. The alpha male (PK) vocalized more via glottal pop and throat rumble

Table IV. Individual male dyadic associations observed during scan sampling

Dyads	Neighborhood			Proximity		
	Observed	Expected	χ^2	Observed	Expected	χ^2
OR-PD	7	9	0.444	0	1.2	1.200
OR-PK	1	9	7.111	0	1.2	1.200
OR-RD	1	9	7.111	0	1.2	1.200
OR-UM	4	9	2.778	0	1.2	1.200
OR-YL	5	9	1.778	3	1.2	2.700
PD-PK	4	9	2.778	0	1.2	1.200
PD-RD	1	9	7.111	2	1.2	0.533
PD-UM	11	9	0.444	5	1.2	12.033 ^b
PD-YL	28	9	40.111 ^b	1	1.2	0.033
PK-RD	1	9	7.111	0	1.2	1.200
PK-UM	5	9	1.778	0	1.2	1.200
PK-YL	18	9	9.000	1	1.2	0.033
RD-UM	2	9	5.444	0	1.2	1.200
RD-YL	25	9	28.444 ^b	5	1.2	12.033 ^b
UM-YL	22	9	18.778 ^b	1	1.2	0.033
Total	135		140.222 ^{a,c}	18		37.000 ^{a,c}

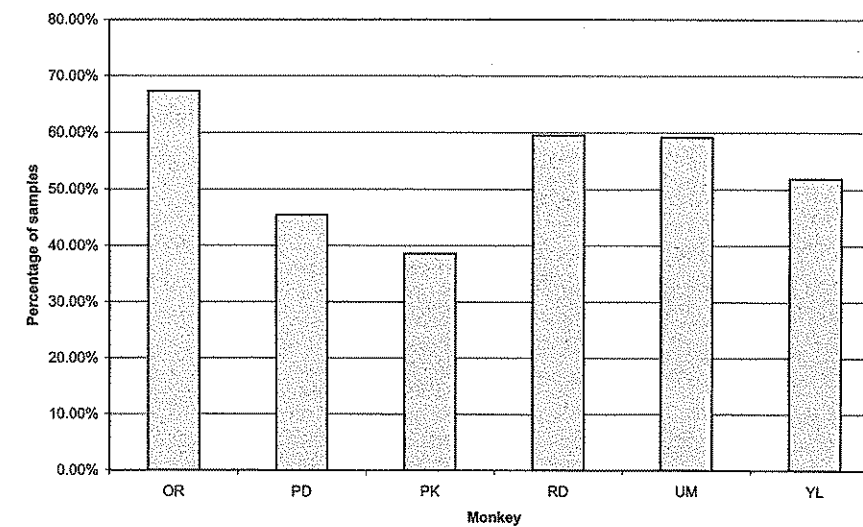
^a $p < 0.001$.^bDyad contributing large proportion of non-randomness.^cdf = 13.

Although, overall, males associated little with one another, some males exhibited a significant preference for certain male neighbors over others (Table IV). Notably the oldest male (YL) was a member of 4 of 5 special male-male dyads, across both neighborhood and proximity spatial classes. We never observed males in contact during sampling.

The alpha male (PK) had the smallest percentage of samples with zero neighbors (38.6%; Fig. 1), while OR had the highest (67.3%). Analysis of the 3 spatial pattern indices revealed significant (two-sample t-test, $p < 0.001$) similarities and differences between certain males. For example, PD and YL were similar in having more monkeys, especially females, in closer proximity than other males did. OR and RD differed from the other males in having fewer neighbors of both sexes and across all spatial classes. OR and RD's spatially peripheral status in the group suggests that they were low-ranking males. Using the same logic, we inferred PD, UM and YL to be higher-ranking group males.

Vocalizations

All 6 males engaged in howl, bark, glottal pop, throat rumble, and cluck vocalizations, but some males engaged in certain vocalizations more than others. The alpha male (PK) vocalized more via glottal pop and throat rumble

**Fig. 1.** Percentage of scan samples with zero neighbors for each adult male.

than the other males did (Table V). His hourly rates of glottal pop and throat rumble are almost 2 and 4 times, respectively, those of the other males. The youngest male (RD) engaged in the most clucks, a vocalization usually characteristic of tension or anxiety (Carpenter, 1934).

Copulations

We observed 27 copulations (Table VI). Different males copulated with the same female during the same estrous period, sometimes even within minutes of each other. No male moved away from the group with an estrous female to form a consort pair. Instead, copulations often occurred in full view of other group members, including other adult males, and there was

Table V. Vocalization rates per hour (unless noted otherwise)

Monkeys	Glottal Pop	Throat Rumble	Howl ^a	Cluck ^a	Other
OR	0.602	0.120	0.049	0.027	0.632
PD	0.117	0.117	0.066	0.034	0.410
PK	2.072	0.455	0.059	0.017	0.606
RD	0.298	0.149	0.034	0.058	0.537
UM	1.370	0.046	0.048	0.022	0.627
YL	1.188	0.000	0.032	0.006	0.434

^aRate per 5-min block

Table VI. Copulation dates and initiators

Monkey	Date	Initiator
YL	18/02/2001	—
PK	1/03/2001	—
OR	8/03/2001	—
YL	9/03/2001	—
UM	20/03/2001	—
PK ^a	21/03/2001	—
PK	22/03/2001	—
UM ^a	22/03/2001	M
YL ^a	22/03/2001	—
UM	28/03/2001	—
PK	29/03/2001	F
UM	29/03/2001	—
UM	9/04/2001	M
YL ^a	12/04/2001	F
UM ^a	13/04/2001	—
UM	13/04/2001	M
UM	14/04/2001	F
YL	18/04/2001	M
PD	20/04/2001	F
UM	14/05/2001	—
UM	1/06/2001	—
RD	2/06/2001	F
YL	2/06/2001	F
YL	13/06/2001	—
RD	20/06/2001	M
RD	20/06/2001	M
RD	20/06/2001	M
OR	25/10/2001	M

^aSame female copulation partner

no obvious attempts to hide copulations, nor did any male attempt to interfere with or to interrupt copulation of other males. Both males and females initiated copulations.

DISCUSSION

Results revealed the presence of an alpha male (PK) but no linear hierarchy could be discerned among the other males in the study group. This finding contrasts with the reverse age-graded linear hierarchy reported for male Costa Rican howlers at La Pacifica (Glander, 1980, 1992; Jones, 1980) as PK was not the youngest male in our group. Instead, at 10 yr, PK was older than 3, and likely 4 of the other males. Our males also differed from those in Costa Rica in their low agonistic rates. While Zucker and Clarke (1986) described agonistic interactions as infrequent among 4 focal males, their agonism rate of 0.200/h is >13 times the rate in our group.

Table VI. Copulation dates and initiators

Monkey	Date	Initiator
YL	18/02/2001	—
PK	1/03/2001	—
OR	8/03/2001	—
YL	9/03/2001	—
UM	20/03/2001	—
PK ^a	21/03/2001	—
PK	22/03/2001	—
UM ^a	22/03/2001	M
YL ^a	22/03/2001	—
UM	28/03/2001	—
PK	29/03/2001	F
UM	29/03/2001	—
UM	9/04/2001	M
YL ^a	12/04/2001	F
UM ^a	13/04/2001	—
UM	13/04/2001	M
UM	14/04/2001	F
YL	18/04/2001	M
PD	20/04/2001	F
UM	14/05/2001	—
UM	1/06/2001	—
RD	2/06/2001	F
YL	2/06/2001	F
YL	13/06/2001	—
RD	20/06/2001	M
RD	20/06/2001	M
RD	20/06/2001	M
OR	25/10/2001	M

^aSame female copulation partner

no obvious attempts to hide copulations, nor did any male attempt to interfere with or to interrupt copulation of other males. Both males and females initiated copulations.

DISCUSSION

Results revealed the presence of an alpha male (PK) but no linear hierarchy could be discerned among the other males in the study group. This finding contrasts with the reverse age-graded linear hierarchy reported for male Costa Rican howlers at La Pacifica (Glander, 1980, 1992; Jones, 1980) as PK was not the youngest male in our group. Instead, at 10 yr, PK was older than 3, and likely 4 of the other males. Our males also differed from those in Costa Rica in their low agonistic rates. While Zucker and Clarke (1986) described agonistic interactions as infrequent among 4 focal males, their agonism rate of 0.200/h is >13 times the rate in our group.

Furthermore, PK tied with one other male for the lowest agonistic rate among group males, which indicates that dominance rank in BCI howlers is not maintained via consistent or obvious overt aggressive tactics, a result which supports previous observations of howlers on BCI (Altmann, 1959; Carpenter, 1934; Chivers, 1969).

The low agonism rate may relate to the fact that all group males had access to estrous females. In contrast to Costa Rican howlers (Jones, 1985), PK did not have exclusive access to sexually receptive females and did not copulate more frequently than other group males did. He may have copulated exclusively with each female at peak estrus (Jones, 1985), the time when the female would be most likely to conceive, but observational conditions made it impossible to determine the exact estrous stage of his partners. In one instance, PK, YL, and UM all copulated with the same female within a 24-h period, suggesting that subordinate males also have access to females at peak estrus. (This assumes that the alpha male only copulates with females at peak estrus). K. Milton has observed similar copulation activities in howler males from other groups on BCI.

Shared reproductive access by males on BCI could imply that the alpha male may be allowing other males to copulate in exchange for some type of benefit. For example, Vehrencamp (1983), suggested that dominant individuals in animal societies might concede some percentage of reproduction to a subordinate as an incentive to stay in the group and help to rear the dominant's offspring. Accordingly, PK may tolerate shared access to estrous females in exchange for male aid in group defense. This aid could directly benefit the well being of his offspring as successful defense generally permits favored access of group members to desired food sources and deters potential predators (K. Milton, 1980). In addition, the benefits subordinate males provide to the alpha male purely in terms of deterring extragroup male rivals may exceed the costs associated with some degree of shared reproductive access (van Hooff, 2000).

If, as in our focal group, a dominant male does not monopolize group females, van Hooff and van Schaik's 1994 model predicts scramble polygynandry and egalitarian relationships among males instead of contest polygyny. Combined with a pattern of male philopatry, the model also predicts male cooperation in intergroup contests. Mantled howler males are well known for cooperative howling during intergroup encounters (Carpenter, 1934, 1965; Chivers, 1969; Milton, 1980). However, data from Costa Rica show that mantled howlers of both sexes typically disperse before sexual maturity (Glander, 1980, 1992; Clarke, 1982; Clarke et al. 1998). Therefore, philopatry (and its associated kinship and inclusive fitness consequences) does not appear necessary for male tolerance and cooperation in mantled howlers. However, genetic analyses to determine the degree of

relatedness characteristic of males in howler groups on BCI are required before we can dismiss the role of kinship in shaping their social relations.

Ritual embracing is another factor that may mediate social relations in mantled howlers. Ritualized greetings may help negotiate status relationships in savanna baboons (Colmenares, 1991; Smuts and Watanabe, 1990) and white-faced capuchin monkeys (Perry, 1998). In addition, the mutual genital inspection (and attendant vulnerability) frequently included in the embrace exchange, may enhance the efficacy of the act as social mediation (Smuts and Watanabe, 1990). This appears to be the case in Costa Rica, where the alpha male initiated the majority of howler male embrace greetings (Zucker and Clarke, 1986). However, on BCI, no dominance-correlated pattern of initiator and recipient in the greeting was apparent, suggesting that the ritual embrace may, as in males of *Cebus apella* (Matheson *et al.* 1996), indicate social affiliation, which could explain why YL, the oldest male in the group, participated in the most embrace greetings. Due to his advanced age, he is likely the least-threatening and best-tolerated male of the group. YL's probable long group tenure, given an average male immigration age of 5 yr and no report of secondary male dispersal (Glander, 1992), suggests both a degree of familiarity with and a lack of threat to younger males. The persistent stereotyped vocal attribute of the embrace greeting may also serve to reaffirm social relations. As these and other vocalizations are by far the most common behaviors with social significance exhibited by howler males, it would be useful to study their structure and function to gain a better understanding of male communication and affiliation.

YL's advanced age may also explain why he was the only male to participate in multiple special male-male dyads. Younger males may practice aggressive restraint in actively avoiding one other (Jones, 1983), knowing that agonistic interactions can be energetically costly and that each male is capable of inflicting lethal wounds. Howlers are restricted in energy expenditure due to their low-energy, folivorous diet (Milton, 1980), and postmortem analysis shows that adult male howlers can suffer cranial trauma inflicted by conspecifics (DeGusta and Milton, 1998).

In contrast to their rare association with one other, group males were more often in the neighborhood of group females, and males that appeared to be of higher status especially favored female neighbors over male ones. This raises the possibility that, like mountain gorillas (Robbins, 1996), each howler male may be trying to develop long-term relationships with females rather than with one another. In turn, male-female relationships may play an important role in structuring male-male association patterns.

Though mantled howler males rarely engage in overt social interactions, this does not mean that their social system is simple. Rather, their unique social structure may be regulated by more subtle means than overt physical

relatedness characteristic of males in howler groups on BCI are required before we can dismiss the role of kinship in shaping their social relations.

Ritual embracing is another factor that may mediate social relations in mantled howlers. Ritualized greetings may help negotiate status relationships in savanna baboons (Colmenares, 1991; Smuts and Watanabe, 1990) and white-faced capuchin monkeys (Perry, 1998). In addition, the mutual genital inspection (and attendant vulnerability) frequently included in the embrace exchange, may enhance the efficacy of the act as social mediation (Smuts and Watanabe, 1990). This appears to be the case in Costa Rica, where the alpha male initiated the majority of howler male embrace greetings (Zucker and Clarke, 1986). However, on BCI, no dominance-correlated pattern of initiator and recipient in the greeting was apparent, suggesting that the ritual embrace may, as in males of *Cebus apella* (Matheson *et al.* 1996), indicate social affiliation, which could explain why YL, the oldest male in the group, participated in the most embrace greetings. Due to his advanced age, he is likely the least-threatening and best-tolerated male of the group. YL's probable long group tenure, given an average male immigration age of 5 yr and no report of secondary male dispersal (Glander, 1992), suggests both a degree of familiarity with and a lack of threat to younger males. The persistent stereotyped vocal attribute of the embrace greeting may also serve to reaffirm social relations. As these and other vocalizations are by far the most common behaviors with social significance exhibited by howler males, it would be useful to study their structure and function to gain a better understanding of male communication and affiliation.

YL's advanced age may also explain why he was the only male to participate in multiple special male-male dyads. Younger males may practice aggressive restraint in actively avoiding one other (Jones, 1983), knowing that agonistic interactions can be energetically costly and that each male is capable of inflicting lethal wounds. Howlers are restricted in energy expenditure due to their low-energy, folivorous diet (Milton, 1980), and postmortem analysis shows that adult male howlers can suffer cranial trauma inflicted by conspecifics (DeGusta and Milton, 1998).

In contrast to their rare association with one other, group males were more often in the neighborhood of group females, and males that appeared to be of higher status especially favored female neighbors over male ones. This raises the possibility that, like mountain gorillas (Robbins, 1996), each howler male may be trying to develop long-term relationships with females rather than with one another. In turn, male-female relationships may play an important role in structuring male-male association patterns.

Though mantled howler males rarely engage in overt social interactions, this does not mean that their social system is simple. Rather, their unique social structure may be regulated by more subtle means than overt physical

interactions, including vocal communication, individual relationships with group females, or kinship relations.

ACKNOWLEDGEMENTS

The research was supported in part by funds to K. Milton from the California Agricultural Experiment Station. We thank the Smithsonian Tropical Research Institute for use of the BCI facilities. Steven Paton, Seth Roberts, and especially Steven Selvin provided many useful suggestions and aided greatly with data analysis. Our thanks also to Ken Glander for his assistance in aging and marking the study subjects and to anonymous reviewers for providing helpful comments on the manuscript.

REFERENCES

- Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour* 49: 227-267.
- Altmann, S. (1959). Field observations on a howling monkey society. *J. Mammal.* 40: 317-331.
- Baldwin, J. D., and Baldwin, I. I. (1976). Vocalizations of howler monkeys (*Alouatta palliata*) in Southwestern Panama. *Folia Primatol.* 26: 81-108.
- Carpenter, C. R. (1934). A field study of the behavior and social relations of howling monkeys. *Comp. Psychol. Monogr.* 10: 1-168.
- Carpenter, C. R. (1965). The howlers of Barro Colorado Island. In DeVore, I., (ed.), *Primate Behavior: Field Studies of Monkeys and Apes*. Holt, Rinehart and Winston, New York, pp. 250-291.
- Chivers, D. (1969). On the daily behavior and spacing of howling monkey groups. *Folia Primatol.* 10: 48-102.
- Clarke, M. R. (1982). *Socialization, Infant Mortality and Infant-Nonmother Interactions in Howling Monkeys (Alouatta palliata) in Costa Rica*, PhD Thesis, University of California, Davis.
- Clarke, M. R. (1983). Infant-killing and infant disappearance following male takeovers in a group of free-ranging howling monkeys (*Alouatta palliata*) in Costa Rica. *Am. J. Primatol.* 5: 241-247.
- Clarke, M. R. (1986). Interactions of adult male howling monkeys (*Alouatta palliata*) with immatures in a free-ranging social group. *Am. J. Phys. Anthropol.* 69: 188.
- Clarke, M. R., and Glander, K. E. (1984). Female reproductive success in a group of free-ranging howling monkeys (*Alouatta palliata*) in Costa Rica. In Small, M. (ed.), *Female Primates: Studies by Women Primatologists*, Alan R. Liss, New York, pp. 111-126.
- Clarke, M. R., Glander, K. E., and Zucker, E. L. (1998). Infant-nonmother interactions of free-ranging mantled howlers (*Alouatta palliata*) in Costa Rica. *Int. J. Primatol.* 19: 451-472.
- Colmenares, F. (1991). Greeting, aggression, and coalitions between male baboons: Demographic correlates. *Primates* 32: 453-463.
- de Waal, F. B. M. (1982). *Chimpanzee Politics*, Jonathan Cape, London.
- de Waal, F. B. M. (1989). *Peacemaking Among Primates*, Harvard University Press, Cambridge, MA.
- DeGusta, D., and Milton, K. (1998). Skeletal pathologies in a population of *Alouatta palliata*: Behavioral, ecological, and evolutionary implications. *Int. J. Primatol.* 19: 615-650.
- Glander, K. E. (1975). *Habitat and Resource Utilization: An Ecological View of Social Organization in Mantled Howling Monkeys*, PhD Thesis, University of Chicago, Chicago.

- Glander, K. E. (1980). Reproduction and population growth in free-ranging mantled howling monkeys. *Am. J. Phys. Anthropol.* 53: 25–36.
- Glander, K. E. (1992). Dispersal patterns in Costa Rican mantled howling monkeys. *Int. J. Primatol.* 13: 415–436.
- Hall, K. R. L., and De Vore, I. (1965). Baboon social behavior. In De Vore, I. (ed.), *Primate Behavior*, Holt, Rinehart and Winston, New York, pp. 53–110.
- Hill, D. A., and van Hooff, J. A. R. A. M. (1994). Affiliative relationships between males in groups of nonhuman primates: A summary. *Behaviour* 130: 143–149.
- Hubbell, S. P., and Foster, R. B. (1990). Structure, dynamics and equilibrium status of old-growth forest on Barro Colorado Island. In Gentry, A. H. (ed.), *Four Neotropical Rain Forests*, Yale University Press, New Haven, CT, pp. 522–541.
- Jones, C. B. (1980). The functions of status in the mantled howler monkey, *Alouatta palliata* Gray: Intraspecific competition for group membership in a folivorous neotropical primate. *Primates* 21: 389–405.
- Jones, C. B. (1983). Social organization of captive black howler monkeys (*Alouatta caraya*): “Social competition” and the use of non-damaging behavior. *Primates* 24: 25–39.
- Jones, C. B. (1985). Reproductive patterns in mantled howler monkeys: Estrus, mate choice and copulation. *Primates* 26: 130–142.
- Kappeler, P. M. (2000). Primate males: History and theory. In Kappeler, P. M. (ed.), *Primate Males: Causes and Consequences of Variation in Group Composition*, Cambridge University Press, Cambridge, UK, pp. 3–7.
- Leigh, E. G., Rand, A. S., and Windsor, D. M. (1982). *The Ecology of a Tropical Forest*. Smithsonian Press, Washington, DC.
- Matheson, M. D., Johnson, J. S., and Feuerstein, J. (1996). Male reunion displays in tufted capuchin monkeys (*Cebus apella*). *Am. J. Primatol.* 40: 183–188.
- Milton, K. (1980). *The Foraging Strategy of Howler Monkeys*, Columbia University Press, New York.
- Mitani, J. C., Merriweather, D. A., and Zhang, C. (2000). Male affiliation, cooperation and kinship in wild chimpanzees. *Anim. Behav.* 59: 885–893.
- Moore, J. (1992). Dispersal, nepotism, and primate social behavior. *Int. J. Primatol.* 13: 361–378.
- Morin, P. A., Moore, J. J., Chakraborty, R., Jin, L., Goodall, J., and Woodruff, D. S. (1994). Kin selection, social structure, gene flow, and the evolution of chimpanzees. *Science* 265: 1193–1201.
- Perry, S. (1996). Female–female social relationships in wild white-faced capuchin monkeys, *Cebus capucinus*. *Am. J. Primatol.* 40: 167–182.
- Perry, S. (1998). Male–male social relationships in wild white-faced capuchins, *Cebus capucinus*. *Behaviour* 135: 139–172.
- Pope, T. R. (1990). The reproductive consequences of male cooperation in the red howler monkey: Paternity exclusion in multi-male and single-male troops using genetic markers. *Behav. Ecol. Sociobiol.* 27: 439–446.
- Robbins, M. M. (1996). Male–male interactions in heterosexual and all-male wild mountain gorilla groups. *Ethology* 102: 942–965.
- Rowell, T. E. (1966). Forest-living baboons in Uganda. *J. Zool. Soc. Lond.* 147: 344–364.
- Simonds, P. E. (1974). Sex differences in bonnet macaque networks and social structure. *Arch. Sex. Behav.* 3: 151–166.
- Simpson, M. J. A. (1973). The social grooming of male chimpanzees. In Michael, R. P., and Crook, J. H. (eds.), *Comparative Ecology and Behaviour of Primates*, Academic Press, London, pp. 411–506.
- Smuts, B. B., and Watanabe, J. M. (1990). Social relationships and ritualized greetings in adult male baboons (*Papio cynocephalus anubis*). *Int. J. Primatol.* 11: 147–172.
- Southwick, C. H. (1963). Challenging aspects of the behavioral ecology of howling monkeys. In Southwick, C. H. (ed.), *Primate Social Behavior*, D. Van Nostrand, Princeton, NJ, pp. 185–191.
- Strier, K. B. (1994). Myth of the typical primate. *Yrbk. Phys. Anthropol.* 37: 233–271.
- Struhsaker, T. T. (1975). *The Red Colobus Monkey*, University of Chicago Press, Chicago.

- Glander, K. E. (1980). Reproduction and population growth in free-ranging mantled howling monkeys. *Am. J. Phys. Anthropol.* 53: 25–36.
- Glander, K. E. (1992). Dispersal patterns in Costa Rican mantled howling monkeys. *Int. J. Primatol.* 13: 415–436.
- Hall, K. R. L., and De Vore, I. (1965). Baboon social behavior. In De Vore, I. (ed.), *Primate Behavior*, Holt, Rinehart and Winston, New York, pp. 53–110.
- Hill, D. A., and van Hooff, J. A. R. A. M. (1994). Affiliative relationships between males in groups of nonhuman primates: A summary. *Behaviour* 130: 143–149.
- Hubbell, S. P., and Foster, R. B. (1990). Structure, dynamics and equilibrium status of old-growth forest on Barro Colorado Island. In Gentry, A. H. (ed.), *Four Neotropical Rain Forests*, Yale University Press, New Haven, CT, pp. 522–541.
- Jones, C. B. (1980). The functions of status in the mantled howler monkey, *Alouatta palliata* Gray: Intraspecific competition for group membership in a folivorous neotropical primate. *Primates* 21: 389–405.
- Jones, C. B. (1983). Social organization of captive black howler monkeys (*Alouatta caraya*): "Social competition" and the use of non-damaging behavior. *Primates* 24: 25–39.
- Jones, C. B. (1985). Reproductive patterns in mantled howler monkeys: Estrus, mate choice and copulation. *Primates* 26: 130–142.
- Kappeler, P. M. (2000). Primate males: History and theory. In Kappeler, P. M. (ed.), *Primate Males: Causes and Consequences of Variation in Group Composition*, Cambridge University Press, Cambridge, UK, pp. 3–7.
- Leigh, E. G., Rand, A. S., and Windsor, D. M. (1982). *The Ecology of a Tropical Forest*. Smithsonian Press, Washington, DC.
- Matheson, M. D., Johnson, J. S., and Feuerstein, J. (1996). Male reunion displays in tufted capuchin monkeys (*Cebus apella*). *Am. J. Primatol.* 40: 183–188.
- Milton, K. (1980). *The Foraging Strategy of Howler Monkeys*, Columbia University Press, New York.
- Mitani, J. C., Merriweather, D. A., and Zhang, C. (2000). Male affiliation, cooperation and kinship in wild chimpanzees. *Anim. Behav.* 59: 885–893.
- Moore, J. (1992). Dispersal, nepotism, and primate social behavior. *Int. J. Primatol.* 13: 361–378.
- Morin, P. A., Moore, J. J., Chakraborty, R., Jin, L., Goodall, J., and Woodruff, D. S. (1994). Kin selection, social structure, gene flow, and the evolution of chimpanzees. *Science* 265: 1193–1201.
- Perry, S. (1996). Female–female social relationships in wild white-faced capuchin monkeys, *Cebus capucinus*. *Am. J. Primatol.* 40: 167–182.
- Perry, S. (1998). Male–male social relationships in wild white-faced capuchins, *Cebus capucinus*. *Behaviour* 135: 139–172.
- Pope, T. R. (1990). The reproductive consequences of male cooperation in the red howler monkey: Paternity exclusion in multi-male and single-male troops using genetic markers. *Behav. Ecol. Sociobiol.* 27: 439–446.
- Robbins, M. M. (1996). Male–male interactions in heterosexual and all-male wild mountain gorilla groups. *Ethology* 102: 942–965.
- Rowell, T. E. (1966). Forest-living baboons in Uganda. *J. Zool. Soc. Lond.* 147: 344–364.
- Simonds, P. E. (1974). Sex differences in bonnet macaque networks and social structure. *Arch. Sex. Behav.* 3: 151–166.
- Simpson, M. J. A. (1973). The social grooming of male chimpanzees. In Michael, R. P., and Crook, J. H. (eds.), *Comparative Ecology and Behaviour of Primates*, Academic Press, London, pp. 411–506.
- Smuts, B. B., and Watanabe, J. M. (1990). Social relationships and ritualized greetings in adult male baboons (*Papio cynocephalus anubis*). *Int. J. Primatol.* 11: 147–172.
- Southwick, C. H. (1963). Challenging aspects of the behavioral ecology of howling monkeys. In Southwick, C. H. (ed.), *Primate Social Behavior*, D. Van Nostrand, Princeton, NJ, pp. 185–191.
- Strier, K. B. (1994). Myth of the typical primate. *Yrbk. Phys. Anthropol.* 37: 233–271.
- Struhsaker, T. T. (1975). *The Red Colobus Monkey*, University of Chicago Press, Chicago.

- Struhsaker, T. T., and Leland, L. (1979). Socioecology of five sympatric monkey species in the Kibale Forest, Uganda. In Rosenblatt, J. S., Hinde, R. A., Beer, C., and Busnel, M. C. (eds.), *Advances in the Study of Behavior*, Vol. 9, Academic Press, New York, pp. 159–228.
- Strum, S. C. (2002). Book review: Primate Males. *Int. J. Primatol.* 23: 223–225.
- Sugiyama, Y. (1971). Characteristics of the social life of bonnet macaques (*Macaca radiata*). *Primates* 12: 247–266.
- Treves, A. (2001). Reproductive consequences of variation in the composition of howler monkey (*Alouatta* spp.) groups. *Behav. Ecol. Sociobiol.* 50: 61–71.
- van Hooff, J. A. R. A. M. (2000). Relationships among non-human primate males: A deductive framework. In Kappeler, P. M. (ed.), *Primate Males: Causes and Consequences of Variation in Group Composition*, Cambridge University Press, Cambridge, UK, pp. 183–191.
- van Hooff, J. A. R. A. M., and van Schaik, C. P. (1992). Cooperation in competition: The ecology of primate bonds. In Harcourt, S., and de Waal, F. B. M. (eds.), *Coalitions and Alliances in Humans and Other Animals*, Oxford University Press, Oxford, pp. 356–390.
- van Hooff, J. A. R. A. M., and van Schaik, C. P. (1994). Male bonds: Affiliative relationships among nonhuman primate males. *Behaviour* 130: 309–337.
- Vehrencamp, S. L. (1983). A model for the evolution of despotic versus egalitarian societies. *Anim. Behav.* 31: 667–682.
- Washburn, S. L., and Hamburg, D. A. (1968). Aggressive behavior in Old World monkeys and apes. In Jay, P. C. (ed.), *Primates*, Holt, Rinehart and Winston, New York, pp. 458–478.
- White, F. J., and Chapman, C. A. (1994). Contrasting chimpanzees and bonobos: nearest neighbor distances and choices. *Folia Primatol.* 63: 181–191.
- Young, O. P. (1981). Chasing behavior between males within a howler monkey troop. *Primates* 22: 424–426.
- Young, O. P. (1983). An example of "apparent" dominance–submission behavior between adult male howler monkeys (*Alouatta palliata*). *Primates* 24: 283–287.
- Zucker, E. L., and Clarke, M. R. (1986). Male–male interactions in a group of mantled howling monkeys (*Alouatta palliata*) in Costa Rica. *Am. J. Primatol.* 10: 443.
- Zucker, E. L., and Clarke, M. R. (1998). Agonistic and affiliative relationships of adult female howlers (*Alouatta palliata*) in Costa Rica over a 4-year period. *Int. J. Primatol.* 19: 433–449.
- Zuckerman, S. (1932). *The Social Life of Monkeys and Apes*, Harcourt, Brace, New York.