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Crockett '84

Female Primates: Studies by Women Primatologists, pages 159-173
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Emigration by Female Red Howler Monkeys and the Case for Female Competition

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INTRODUCTION

In most polygynous primate species, males usually disperse, and this pattern is typical of other mammals [Greenwood, 1980]. As a consequence, the majority of polygynous primates dwell in matrilocal or "female-bonded" [Wrangham, 1980] groupings with daughters breeding in their natal troops and sons transferring to other troops. Wrangham [1980] contrasts "female-bonded" social systems with the few primate species in which females transfer between groups more frequently than do males; these "non-female-bonded" species include red colobus (*Colobus badius*), Hamadryas baboon (*Papio hamadryas*), mountain gorilla (*Gorilla gorilla beringei*), and chimpanzee (*Pan troglodytes*). Several other primate species categorized as "female-bonded" show female transfer [Wrangham, 1980]. Two of these species are howler monkeys, *Alouatta palliata* Gray [Jones, 1980] and *A seniculus* [Rudran, 1979]. During Jones' [1980] study of two mantled howler troops, eight females and one male emigrated, and three females and two males immigrated. Rudran [1979] reported that 22 immature males and eight immature females disappeared or emigrated from 20 red howler study troops, and 14 adult and subadult males but only two females nearing sexual maturity immigrated.

In this paper, I reserve the term "transfer" to refer to immigrations into established troops (ones that have produced offspring) in contrast to occasions when emigrating animals join other extratroop individuals [but see Harcourt, 1978]. By this definition, transfer by female red howlers is less common than male transfer [Rudran, 1979]. During my study of red howlers some females succeeded in breeding in their natal troops, but both sexes emigrated from their presumed natal troops with nearly equal frequency. Furthermore, some individuals of both sexes reproduced outside of their natal troops by forming new troops rather than by transferring into existing troops. Thus, whereas female "transfer" in red howlers is uncommon, female emigration and nonnatal breeding are not. I discuss the implications of these results for Wrangham's [1980] model. Female emigration in red howlers appears to be a consequence of competition among females for a limited number of breeding positions, complicated by uncertain benefits associated with colonization.

STUDY AREA AND METHODS

The data reported here were collected during October 1978, March 1979 to February 1981, and November to December 1981 at Hato Masaguaral, a private wildlife reserve and cattle ranch located approximately 8° 34′ N and 67° 35′ W in Guárico State, Venezuela. Regular census contacts were made with red howler (*Alouatta s seniculus*) troops in two habitat types following methods described by Rudran [1979]. The two study populations occupied quite different habitat types separated by approximately 4 km of shrubs, grassland, and occasional trees. One habitat type, studied by Neville [1972], Rudran [1979], and Sekulic [1982, 1983, and in press], is an open shrub woodland ("discrete mata bajío" and "shrub woodland bajío" [Troth, 1979] which I refer to in this paper as "Mata." According to M. Schön, personal communication, this habitat is more appropriately called "bosque calzada.") The second habitat, located to the east of the Mata area, extends from the banks of the Río Guárico, a part of the Orinoco drainage, and is categorized as "Gallery" forest [Troth, 1979]. The more or less continuous gallery forest along the banks of the Río Guárico provides an avenue for red howler dispersal. There were no effective barriers between the study areas and adjacent howler populations, and migration among them was possible.

After training with Rudran, we reached 100% agreement on identification of troops and nearly perfect agreement on age/sex classes. By December 1981 my census included 27 Mata troops and 25 Gallery troops for a total of 52 troops in two habitats (Table I). Other red howler troops were censused whenever they were encountered, both within and beyond the boundaries of Hato Masaguaral. All changes in troop composition between census contacts of the 52 troops could be ascertained through

TABLE I. Characteristics of Red Howler Study Population in Two Habitats

	Mata	Gallery	Overall
Total number of troops	27	25	52
Total troop-months	886	364	1,250
New troops formed during study	1	9	10
Number of established troops	26	12[a]	38
Troop-months, established troops (emigration and immigration rates)	861	260	1,121
February 1981, end of main study period:			
Number of established troops	26	17	43
Mean troop size	10.50	7.71	9.40
Range	6–16	4–12	4–16
Mean no. adult males per troop	1.58	1.18	1.42
Mean no. adult females per troop	2.89	2.47	2.72
Size of study area (km^2)	3.45	3.87	7.32
Population density (per km^2)[b]	112	36	—

[a] Four additional "established" Gallery troops were excluded from emigration and immigration calculations because of incomplete or insufficient census counts.

[b] "Ecological density" [Eisenberg, 1979] estimate based on area of suitable howler habitat; individuals per km^2 includes extratroop monkeys and troop members.

individual recognition and some eartag markings [eg, Thorington et al, 1979]. To facilitate identification, I took photographs and made detailed notes and sketches, including such cues as scars, torn ears, stiff and missing digits, depigmentation on breasts, genital area, and soles of the feet, and patterns of hairline and crown hair. I could identify many animals shortly after they emigrated from troops, but younger animals generally had fewer unique characteristics; thus, the identities of many untagged juveniles were eventually lost after they emigrated from their natal troops.

I took ad libitum [Altmann, 1974] notes on behavior and spatial patterning of troop members during census contacts, and made additional observations during over 1,400 h of systematic data collection on two troops (M62 and G9; Crockett, in preparation). The 52 census troops were monitored for 1,250 troop-months (troop-months equal the number of months between the first and last observation, regardless of whether the troop was contacted every intervening month). Thirty-eight established troops from which emigration and immigration data were collected were monitored for 1,121 of the total troop-months. Average rates of events such as immigrations were calculated by dividing the appropriate number of troop-months by the number of times the event was observed. Dividing this quotient by 12 yields an estimate of troop-years per event.

Statistical tests were taken from Sokal and Rohlf [1969] and Imhof et al [1982].

RESULTS

Characteristics of the Study Population

In February 1981, both mean troop size and population density were larger in the Mata than in the Gallery (Table I). Between 1979 and 1981, the annual net rate of increase of animals in troops was 21% in the Gallery compared to 6% in the Mata. Furthermore, during the period that one new troop formed in the Mata, nine troops formed in the Gallery study area. Some individuals forming new troops apparently immigrated from outside the study area.

Sex Differences in Emigration From Natal Troops

Red howler males emigrated at an older average age than females, but both sexes emigrated at about the same rate. Table II presents the number of individuals I classified as immatures at the onset of my observations and which either left their presumed natal troops during the study period or remained in the troops where they were first observed ("left" includes known emigrations and possible deaths). Two males that left troops were

TABLE II. Fates of Individuals Recorded as Immature at Onset of Observations and Not Known to Have Immigrated[a]

Habitat	Males	Females	Total
Mata			
Remained	52	50	102
Left	29	25	54
Percent left	35.8	33.3	34.6
Gallery			
Remained	17	17	34
Left	4	4	8
Percent left	19.0	19.0	19.0
Total			
Remained	69	67	136
Left	33	29	62
Percent left	32.4	30.2	31.3

[a] Number of males and females that remained in presumed natal troops at end of study period compared with those that left (known emigrations and disappearances combined).

initially classified as subadults, and they possibly were not natal. The remaining animals were of size classes unlikely to have immigrated (see Table IV, below) and were almost certainly natal. Overall, of all "available" presumed natal animals, 32.4% of males left and 30.2% of females left. In Gallery troops there were fewer immatures and a smaller percentage left (19% of Gallery vs 34.6% of Mata immatures). A 2 × 2 × 2 G-test (habitat × sex × dispersal) confirmed that there was no sex difference in the number of immatures that left troops, but that there was a difference in dispersal by habitat (habitat × dispersal; $G = 3.996$, $P = 0.046$). Most individuals left their presumed natal troops singly, and only one pair of females and two pairs of males were known to have left the same troop during the same month.

Table III summarizes the size/age classes and subsequent sightings of individuals that left their presumed natal troops. At least 35.5% emigrated rather than died, and more males than females were positively identified as emigrants. This is partly due to the fact that emigrant males were on average older than females, and the number of identifying characteristics increases with age. Also, males tended to come and go from a troop for several months prior to emigration whereas females tended to leave abruptly. Some of the individuals that were never seen again presumably died, including one Gallery female who had a crippled leg for a year prior to her disappearance.

The sexes differed in modal size class at emigration (Table III). Females emigrated at approximately 2–4 years, whereas males emigrated

TABLE III. Size Classes of Individuals Leaving Presumed Natal Troops[a]

	Females					Males					
	S + J	MJ	LJ	SA	Tot	M + J	LJ	SA	SA+	A	Tot
Mata	3	9	10	3	25	1	7	12	6	3	29
Gallery	2	1	1	0	4	0	3	0	1	0	4
Total	5	10	11	3	29	1	10	12	7	3	33
Of total:											
Seen emig	1	1	5	2	9	0	3	5	4	1	13
Same size		2					2				
Prob died	1										

[a] Two males were subadult when first observed and might not have been natal. SJ: small juvenile; MJ: medium juvenile; LJ: large juvenile; SA: subadult; A: adult; "+" indicates transition between two size classes (S + J is "nearly medium"; SA+ is "nearly adult"). Seen emig: Individual seen in process of and/or after emigration. Same size: Emigrant not positively identified but individual of appropriate sex/size class seen in vicinity. Prob died: Cripple that disappeared probably died.

from their presumed natal troops at about 3–7 years of age. The modal size class for females was medium juvenile (about 2–3 years old). The modal size class of emigrating males was subadult, and most emigrating males were about 4–6 years of age.

Sex Differences in Immigration Into Established Troops

The sexes immigrated into established troops (those that had already produced offspring) at very different rates (Table IV). Twenty immature and adult males immigrated into troops during the same period that two females immigrated; female immigration occurred on average only once every 46.7 troop-years. In both cases, the females joined troops after the adult female composition had been reduced by death to one adult female. In one case, a natal female rejoined her troop 3 months after a troop adult female's death. In the other case, an unfamiliar female joined another troop between 4 and 13 months after an adult female's death. More males immigrated into troops than were positively known to have emigrated from the study troops during the same period (compare Tables III and IV), further suggesting that extratroop mortality is not particularly high.

Number of Adult Females and Troop Size

All of 65 red howler troops censused in Venezuela had four or fewer adult females (Table V), similar to Defler's [1981] study of Colombian *A seniculus*. Nearly half (49%) of the troops had only two adult females. These data support the notion that the number of breeding positions for females in red howler troops is limited.

The relationship between the number of individuals of the adult male, adult female, and immature age/sex classes and troop size was examined

TABLE IV. Immigrations Into 38 Established Troops[a] Monitored for 1,121 Troop-Months[b]

	Females		Males			
	L + J	SA + /Nulliparous	L + J	SA	SA+	A
Mata	1[c]	0	1	1	2	9
Gallery	0	1[d]	0	1	0	6
Total	1	1	1	2	2	15

[a] Same as those in Table III.
[b] Abbreviations as in Table III.
[c] Return to natal troop (see text).
[d] Unfamiliar female joins troop.

TABLE V. Number of Adult Females in Troops

	Number of adult females			
Location	2	3	4	Number of troops
Mata	8	15	4	27
Gallery	16	8	1	25
Other areas	8	3	2	13
Total troops	32	26	7	65
Percent	49%	40%	11%	

TABLE VI. Linear Regression of Troop Size as a Function of Age/Sex Classes—February 1981 Census Data[a]

Variables		Percent variation explained	Slope	Intercept	F	P
Independent	Dependent					
No. immatures[b]	Troop size[c]	92.3%	1.18	3.16	554.9	<0.01
No. adult females	Troop size	43.9%	3.00	0.81	36.1	<0.01
No. adult males	Troop size	17.6%	2.37	5.56	9.8	<0.01
No. adult females	No. adult males	5.8%	0.19	0.86	2.9	NS
No. adult females	Rest of troop[d]	25.8%	2.00	0.81	16.0	<0.01
No. adult males	Rest of troop	6.6%	1.37	5.56	3.3	NS
No. adult females	No. immatures	24.2%	1.80	−0.05	14.7	<0.01
No. adult males	No. immatures	5.4%	1.07	3.31	2.6	NS

[a] Degrees of freedom: regression = 1, residual = 46.

[b] No. immatures = troop size − No. adult males − No. adult females.

[c] Troop size = total number of individuals in troop.

[d] Rest of troop = troop size − No. adult females or males.

using linear regressions (Table VI). Troop size was primarily a function of the number of immature individuals. The number of adult females was a better predictor of troop size than was the number of adult males, mainly because of the significant relationship between number of adult females and immatures. The number of adult males was not significantly related to the number of adult females or to the number of immatures.

Location of Females' First Breeding

The relative availability of breeding options for females was examined by comparing the frequency of primiparous births during the study period in three locations: 1) the presumed natal troop; 2) an established troop into which a female had immigrated; and 3) a newly formed troop. The last was defined as a troop which was first observed as a bisexual association of extratroop individuals without infants, which later included infants.

In Mata troops, at least nine and possibly 13 primiparous females were considered natal. Two females that immigrated into established troops during Rudran's [1979] study period subsequently gave birth (using 191-day gestation [Crockett and Sekulic, 1982], both females conceived after immigration). Four females in two newly formed Mata troops, one formed during Rudran's study and one formed during mine, also had primiparous births. Thus during the 1979–1981 study period, natal breeding was 2–3 times more frequent for primiparous Mata females than was breeding in newly formed troops. The situation was reversed in the Gallery, where 84.2% of primiparous births ($n = 16$) were in new troops and 15.8% ($n = 3$) were in natal troops. The difference between the habitats in location of primiparous breeding (natal vs new troop) is statistically significant (chi-square with Yates's correction $= 7.26$, $df = 1$, $P < 0.01$, $n = 32$ primiparous births).

The Evidence for Female-Female Competition

The frequency of observed aggressive interactions among red howlers is quite low, and the outcomes of such encounters are often unclear. In over 1,500 h of direct observation, I saw only two fights in which blood was drawn, in both cases the result of canine slash wounds on a hind limb. One victim was a young male nearing subadulthood, and the other was a subadult female. Despite the low frequency of physical aggression, its intensity is often high. Many males have scars, primarily as a result of inferred or observed male-male fighting associated with reproductive competition [Crockett and Sekulic, in press; Sekulic, 1983]. In addition, many females also have permanent scars and injuries. Of 74 Mata adult females, at least 29 (39%) had scars or injuries; 13 (45%) of these 29 females received injuries during the study period. Four of these females almost certainly received the injuries as a result of female-female fighting, because these females were observed in intense agonistic interactions with other females while their injuries were still fresh. Both females that immigrated during Rudran's [1979] study period also received injuries, and Sekulic [in press] observed the other resident adult females to be aggressive toward one of them. Four more of the 13 adult female injuries occurred at the time a juvenile female approached sexual maturity; two of these cases involved two adult females and one large juvenile female that received injuries prior to the emigration of the juvenile. In another troop a presumed natal female received injuries the first time she gave birth. The link to female-female aggression was absent for only two of the 13 Mata females that received notable injuries, and in both cases juvenile females were present in their troops. At least eight (21%) of 37 Gallery females also had scars or injuries.

This is not to suggest that all injuries on females are the result of female-female aggression, but circumstantial evidence suggests that many of them are. However, some old scars may be the result of injuries received as infants surviving unsuccessful infanticide attempts, or as adults while attempting to defend infants from infanticide [Crockett and Sekulic, in press].

Both of my main study troops provided evidence for aggression suggestive of female reproductive competition. In Gallery troop G9, the subadult daughter of female 922 engaged in numerous intense interactions, especially with 921 (the second adult female) and 921's juvenile son. Some of these interactions involved the subadult's grabbing the fingers, shoulders, and head of the recipient, similar to the "harassment" behavior often seen between juvenile males and by immature males toward adult males. The subadult harassed female 921 during the latter's estrus, but displayed no such behavior during her mother's estrus. Eventually, the subadult female became a reproducing adult in her natal troop, and the intense interactions declined in frequency.

Mata troop M62 provided further evidence for female-female aggression. One evening in July 1979, after observing M62 for 4 months, I found the troop split and sleeping in trees over 75 m apart, which is very unusual in the Mata habitat. Upon closer examination, I saw deep, fresh face and thigh wounds on adult female 6221 as she slept with her infant son and a subadult male. The troop's second adult female, 6222, slept with the rest of the troop and bore fresh wounds on her face and arm; her 20-month-old juvenile daughter, 6262, was missing. The next morning female 6221 appeared, extremely piloerected, and rapidly approached, grabbed, and harassed female 6222; the two females began to howl (howling can be a form of female-female aggression [Sekulic, 1982, and in press]). By afternoon there was nothing but the injuries to suggest that any aggression had taken place between them. Although the evidence is circumstantial, the severe injuries seem to have been inflicted by the adult females upon each other during a fight the previous day, coinciding with the disappearance of 6222's daughter.

In October 1980, less than 2 weeks after the birth of 6221's next infant, female 6222's 19-month-old daughter, 6282, disappeared; the two adult females had fresh wounds, and I observed an intense harassment bout between them. The fate of juvenile 6282 is unknown, but the fate of the previous daughter, 6262, is strong evidence that female-female competition influences the adult female composition of troops. Less than 3 months after emigration, female 6262 joined a newly formed association, but she left it in October 1980. Female 6221, who had fought with 6262's mother, died in January 1981. By February, 6262 was back in her natal range and rejoined her natal troop by April 1981 [Pope, personal communication]. Her reentry after 6221's death is consistent with the interpretation that her original emigration was not entirely "voluntary" and may have been precipitated by adult female 6221.

DISCUSSION

Why Do Females Emigrate?

In red howler monkeys, emigration by natal females is as common as emigration by natal males. Males may rapidly transfer to another troop, but females rarely do so. Emigrating female red howlers are more likely to end up in an extratroop assocation (which may become a new troop) than in a previously established troop.

Since male transfer is common, inbreeding avoidance is unlikely to be a major cause of female emigration in red howlers [cf Packer, 1979; Pusey, 1980]. During the 1979–1981 study period, natal recruitment occurred on average once every 5.8–7.8 troop-years (1,121 troop months divided by 12–16 natal primiparous births). Females are about 5 years old when they first give birth [Crockett and Rudran, in preparation]. In comparison, tenures of breeding males are estimated to average 5.1–6.7 years [Crockett and Sekulic, in press]. This suggests that regardless of whether natal females emigrate, they rarely have the opportunity to mate with their fathers. So far, there are no data available indicating that maturing females emigrate if their fathers are still resident as breeding males. However, females have emigrated from troops in which the resident male could not have been their father, and a few natal females have been recruited in troops whose current breeding male may have been their father. Thus, avoidance of inbreeding does not appear to be the main reason that female red howlers emigrate. More important factors favoring female emigration appear to be that 1) the number of breeding positions within a troop is limited, and 2) breeding opportunities can be found outside the natal troop.

Troop members can influence troop size by limiting the number of females allowed to reproduce, and current theory suggests that the number of reproducing females should be limited by the females themselves. As elaborated by Wrangham [1979], the key resource that should determine the nature of female intrasexual competition is food, and females should be selected to maximize food intake. Two studies of *Alouatta palliata* on Barro Colorado have suggested a relationship between troop size and food. Gaulin et al [1980] found a positive correlation between troop size and the density of fig trees (howlers' most important food [Milton, 1980]). Leighton and Leighton [1982] showed that food patch size directly influences the size of "feeding aggregates," and suggested that patch density and dispersion could affect "foraging unit" (ie, troop) size. In 1981, the Mata and Gallery study areas showed differences in population density and mean troop size that were positively related to density of the fig *Ficus pertusa* [Crockett, 1982, unpublished]. However, since the Gallery population was experiencing a more rapid growth phase during the study period, I am reluctant to draw any conclusions about the relationship between food density and red howler troop size at the present time.

Red howler female emigration coincides with the time when young females approach breeding age. Births by these young females could potentially increase troop size beyond that consistent with an optimal foraging strategy for reproducing females. Some females may be actively excluded from reproducing in their natal troops and as a consequence, or in anticipation, emigrate. The implication is that other females, rather than males, should take a major role in "encouraging" female emigration.

It is also possible that females emigrate to find opportunities for breeding outside of the natal troop. Since immigration into established troops is rare (Table IV) and resisted by resident females [Sekulic, 1982], transfer is not a common option. Rather, under the present ecological regime, the formation of new troops is a viable alternative, especially in the gallery forest.

Costs of Emigration

The option of breeding in a newly formed troop does exist for red howlers in areas where population densities are below carrying capacity. However, emigration must be more costly than natal breeding. Although actual data are lacking, costs to emigrating females come from three possible sources: death, failure to breed, and delayed breeding.

1. Mortality rates are likely to be somewhat higher for extratroop immatures than for resident immatures. While some emigrants range only several hundred meters from their natal troops, others apparently leave the area. Some ear-tagged emigrants have disappeared entirely. However, certain extratroop individuals have been seen repeatedly for years, suggesting that many emigrants can survive in good health outside of a troop situation [Crockett, personal observation; Sekulic, 1982; Pope, in preparation].

2. Survival without reproducing does not increase fitness. Some females may be solitary or live in nonreproductive extratroop associations.

For example, a solitary adult female failed to enter a troop after repeated attempts [Sekulic, 1982]. Jones [1980] suggests that female mantled howlers cannot succeed in entering troops unless they are young adults.

3. The third potential cost to emigrants is a relative loss of fitness accrued by females that begin breeding at an older age. Females that begin reproducing earlier may achieve greater fitness than later-reproducing females in two ways: a) by producing more total offspring, because their expected reproductive life is longer (reproductive value is higher); or b) by shortening the generation length, since their first offspring will reach sexual maturity before those of later-reproducing females [Emlen, 1973].

Males have been known to transfer from one troop to another quite rapidly [Rudran, 1979; Sekulic, 1983], but this has not been observed for females. On the basis of size classes at emigration (Table III) and immigration (Table IV), both sexes, on average, experience a delay. Some females that mature in their natal troops, however, conceive as soon as they are physiologically able [Crockett and Rudran, in preparation]. Emigrants are less likely to breed at the earliest opportunity, as judged by the many months that some extratroop associations have persisted prior to births. Furthermore, newly formed troops may be more vulnerable to male replacement and, possibly, infanticide [Crockett, in preparation].

Female Competition and Conflicts of Interest

Assuming that it is more advantageous for females to breed in their natal troops than to emigrate, the limited number of breeding positions encourages competition. Because she shares half of her daughter's genes, a mother's fitness is affected by her daughter's reproductive success. If a maturing female's expected reproductive success is higher in her natal troop, then adult females might be expected to favor the retention of daughters, and daughters should always prefer to stay. However, other factors influence the fitness of mothers and daughters. For example, by staying in the natal troop, the maturing female will be rearing offspring that will compete with kin for food and other resources. Such competition might reduce the survivorship of relatives at the expense of one's inclusive fitness.

If colonization of new habitats were easy, reproductive success in newly formed troops could potentially equal or exceed that in established troops, and offspring would not be competing with as many relatives. However, the potential benefits of colonization must be devalued by the probability of not breeding at all, through death or failure to find a troop situation, and the possibility of delayed age of first reproduction. Given these potential costs associated with emigration, individual daughters that emigrate generally have more to lose than do their mothers. Unless the mother can replace the daughter with two or more siblings, any fitness decrement to the daughter by emigration will affect her fitness more than her mother's. This conflict of interest could be modified by differences in reproductive success associated with natal versus new-troop breeding, but in general mothers' and daughters' fitness interests may differ with respect to potential benefits associated with emigration.

When maturing females are recruited, however, resident females should favor the retention of their own daughters over another female's daughters. The fact that co-resident females are not necessarily related potentially intensifies competition among them over allowing daughters to stay. First-generation troops, those that formed from nonnatal associations, are unlikely to be composed of adult females that came from the same natal troop. Female composition of extratroop associations is unstable, and various females may join and leave prior to the establishment of a permanent troop.

Since the number of female breeding positions in red howler troops is limited and female relatedness is variable, we should expect to see female-female competition, involving both immatures and adults, as individuals attempt to resolve conflicts of interest over the emigration of juveniles. I have summarized preliminary evidence for female-female aggression suggestive of reproductive competition. However, the relative importance of mother-daughter conflicts versus competition between adult females and other adult females (and/or their daughters) has yet to be evaluated.

CONCLUSIONS

Female emigration in red howlers may be the result of female reproductive competition. This competition appears to be a product of limitations on troop size and female foraging strategies. Under ecological conditions where population growth and new troop formation are possible, dispersing howlers of both sexes may have high reproductive success. In fact, female emigration in red howlers may have been favored because colonization is often possible in the successional habitats where red howlers are sometimes the only primate species. The possibility of increased fitness associated with colonization also produces potential conflicts of interest between mothers and daughters.

The red howler data illustrate some of the limitations of Wrangham's [1980] female-bonded primate model. For example, first-generation red howler troops (ones formed from nonnatal associations) should show many characteristics of non-female-bonded primates, whereas multiple-generation "old" troops should be "female-bonded." Grooming, which is largely directed by mothers toward offspring, and close interindividual distances should be more common between adult females in "old" troops (which may contain mother-daughter pairs) than in first-generation troops. I suspect that quantitative data will bear out these predictions. More importantly, the *resource base* and *foraging strategy* of first- vs multiple-generation red howler troops are unlikely to differ in any significant, consistent way, complicating the application of Wrangham's [1980] model.

An aspect yet to be integrated into any predictive model of primate social organization is the source of new social units. Primate species that typically fission along matrilines (eg, macaques [Kurland, 1977]) are more likely to be female-bonded than those in which new social units arise from the association of individuals dispersing separately (eg, gorillas [Harcourt, 1978]; red howlers [this study]). However, to the extent that multiple-generation troops arise from first-generation ones, through the recruitment of natal females, female-bonded characteristics may emerge.

ACKNOWLEDGMENTS

This research was funded by a Smithsonian Institution International Environmental Science Program Grant to J. F. Eisenberg, and by Smithsonian and Friends of the National Zoo Fellowships to the author. I thank D. Fragaszy, D. Mack, T. Pope, J. Robinson, R. Rudran, and R. Sekulic for additional information on troop histories and individual identification. This manuscript was greatly improved by comments from M. Small, R. Brooks, R. Sekulic, C. Janson, and R. Reineke. I especially thank Bob Brooks for field assistance, statistical advice, and companionship. I thank J. Eisenberg for having confidence in my ability to carry out this field project. I am most grateful to T. and C. Blohm for their hospitality and permission to conduct this research at Hato Masaguaral.

REFERENCES

Altmann J (1974): Observational study of behavior: Sampling methods. Behaviour 49:227–267.

Crockett CM (1982): Behavioral ecology of red howlers in two deciduous habitats. In "Biological Adaptations of *Alouatta* in the Northern Neotropics," Symposium at IX Congress of the International Primatological Society, Atlanta, Georgia, August 1982 (unpublished).

Crockett CM, Sekulic R (1982): Gestation length in red howler monkeys. Am J Primatol 3:291–294.

Crockett CM, Sekulic R (in press): Infanticide in red howler monkeys (*Alouatta seniculus*). In Hausfater G, Hrdy SB (eds): "Infanticide: Comparative and Evolutionary Perspectives." New York: Aldine.

Defler TR (1981): The density of *Alouatta seniculus* in the eastern llanos of Colombia. Primates 22:564–569.

Eisenberg JF (1979): Habitat, economy, and society: Some correlations and hypotheses for the neotropical primates. In Bernstein IS, Smith EO (eds): "Primate Ecology and Human Origins." New York: Garland STPM, pp 215–262.

Emlen JM (1973): Ecology: An Evolutionary Approach." Reading, Massachusetts: Addison-Wesley.

Gaulin SJC, Knight DH, Gaulin CK (1980): Local variance in *Alouatta* group size and food availability on Barro Colorado Island. Biotropica 12:137–143.

Greenwood PJ (1980): Mating systems, philopatry and dispersal in birds and mammals. Anim Behav 28:1140–1162.

Harcourt AH (1978): Strategies of emigration and transfer by primates with particular reference to gorillas. Z Tierpsychol 48:401–420.

Imhof MA, Hewett SW, Imhof KM (1982): "Statmod Users Manual for Statpro Statistics and Graphics Database Package." Madison, Wisconsin: Blue Lakes Software Ltd.

Jones CB (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.

Kurland JA (1977): Kin selection in the Japanese monkey. In "Contributions to Primatology," Vol 12. Basel: S. Karger.

Leighton M, Leighton DR (1982): The relationship of size of feeding aggregate to size of food patch: Howler monkeys (*Alouatta palliata*) feeding in *Trichilia cipo* fruit trees on Barro Colorado Island. Biotropica 14:81–90.

Milton K (1980): "The Foraging Strategy of Howler Monkeys." New York: Columbia University Press.

Neville MK (1972): The population structure of red howler monkeys (*Alouatta seniculus*) in Trinidad and Venezuela. Folia Primatol 17:56–86.

Packer C (1979): Inter–troop transfer and inbreeding avoidance in *Papio anubis*. Anim Behav 27:1–36.

Pusey AE (1980): Inbreeding avoidance in chimpanzees. Anim Behav 28:543–552.

Rudran R (1979): The demography and social mobility of a red howler (*Alouatta seniculus*) population in Venezuela. In Eisenberg JF (ed): "Vertebrate Ecology in the Northern Neotropics," Washington: Smithsonian Institution Press, pp 107–126.

Sekulic R (1982): Behavior and ranging patterns of a solitary female red howler (*Alouatta seniculus*). Folia Primatol 38:217–232.

Sekulic R (1983): Male relationships and infant deaths in red howler monkeys (*Alouatta seniculus*). Z Tierpsychol 61:185–202.

Sekulic R (in press): The effect of female call on male howling in the red howler monkeys (*Alouatta seniculus*). Int J Primatol.

Sokal RR, Rohlf FJ (1969): "Biometry," San Francisco: Freeman.

Thorington RW Jr, Rudran R, Mack D (1979): Sexual dimorphism of *Alouatta seniculus* and observations on capture techniques. In Eisenberg JF (ed): "Vertebrate Ecology in the Northern Neotropics." Washington: Smithsonian Institution Press, pp 97–106.

Troth RG (1979): Vegetational types on a ranch in the central llanos of Venezuela. In Eisenberg JF (ed): "Vertebrate Ecology in the Northern Neotropics." Washington: Smithsonian Institution Press, pp 17–30.

Wrangham RW (1979): On the evolution of ape social systems. Soc Sci Inform 18(3):335–368.

Wrangham RW (1980): An ecological model of female-bonded primate groups. Behaviour 75:262–300.