

Red Howler Monkey Birth Data II: Interannual, Habitat, and Sex Comparisons

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Data presented in this paper are derived from the births and subsequent histories of red howler infants born in two habitats. Overall the sex ratio of infants at birth was about 1:1. Infant survivorship (at 1 yr) was about 80%, and 44% of infant mortality was attributed to infanticide by males. Survivorship curves indicated a dramatic sex difference, with far fewer females than males known to be alive at age 7 yr. However, this sex difference may be inflated because emigrant males are more easily identified than emigrant females, and females may be dispersing beyond the boundaries of the study area at a higher rate. Annual birthrate varied somewhat from year to year and was positively related to rainfall. Annual birthrate tended to be higher in the habitat with lower density and higher growth rate. Consistent with the trends in annual birthrate, variation in interbirth interval length (IBI) after births of surviving infants was related primarily to habitat differences and annual variation in rainfall. Season of birth and maternal age class had no effect on IBI. Infant sex had mostly nonsignificant effects on IBI. A small sample indicated that IBI's were significantly longer after the births of females who eventually became natal breeders than after the births of females who eventually emigrated. This difference might reflect differential parental (maternal) investment of some sort.

Key words: *Alouatta seniculus*, howler monkeys, interbirth intervals, birthrate, sex ratio, survivorship

INTRODUCTION

In a previous paper, Crockett and Rudran [1987, this issue] reported that red howler monkeys (*Alouatta seniculus*) living in two seasonal semideciduous habitats showed seasonal variation in births. That paper focused on the ecological factors affecting birth timing. In the present paper, the same set of birth data is used to examine other aspects of red howler reproduction. Year-to-year and habitat variation in infant sex ratio, birthrate, and interbirth interval length are described. The survival of known-aged howlers from the birth data set is analyzed in detail to determine sex and age differences in mortality.

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We also examined some sociobiological predictions about the timing of births derived from parental investment (PI) theory [Trivers, 1972; Clutton-Brock & Albon, 1982; Simpson et al, 1981; Simpson & Simpson, 1982; Simpson, 1983]. Most predictions about birth timing based on parental investment predict differential investment as a function of offspring sex and bodily condition of the nurturing parent, which in the case of mammals is usually the mother. Maternal investment in an offspring could affect birth spacing or interbirth interval [Altmann et al, 1978]. Especially in species that typically give birth to one offspring at a time and where parental investment is predominantly maternal investment, interbirth intervals can be viewed as inherently quantifiable, mutually exclusive pieces of "investment." Longer interbirth intervals are assumed to reflect greater investment in the offspring whose birth begins rather than ends the interval unless substantial variation in gestation length can be demonstrated. Thus, the timing of a particular birth could be affected by the sex of the sibling preceding it.

The general prediction for polygynous species with little paternal care is that mothers in good condition should invest more in sons than in daughters [Clutton-Brock & Albon, 1982; Fairbanks & McGuire, 1985; Maynard Smith, 1980; Meikle et al, 1984]. This difference is expected because mothers that help a son become a highly successful reproducer would have a higher genetic payoff (expressed in number of grandchildren) than if they diverted the energy to a daughter. This conclusion follows because the most successful females in polygynous species usually produce fewer offspring than the most successful males. Females in poor bodily condition should instead invest in the cheaper (that is, easier to raise) sex [Trivers & Willard, 1973]. They might abort or abandon the expensive sex, which they (while in a weakened condition) are unlikely to raise to become successful reproducers.

Silk [1983; see also Clark, 1978] proposed an alternative model to account for the differences seen between some primates and other polygynous species. This model is based on the assumption that under conditions of local resource competition, investment by mothers can influence the reproductive success (RS) of daughters, who tend not to disperse, more than the RS of sons, who usually disperse. Accordingly, when maternal rank is inherited and a female offspring's RS is positively related to her rank (and, thus, her mother's), higher ranking mothers should invest more in daughters; low ranking females should invest more in sons whose rank and thus RS is more independent of maternal rank.

Red howler monkeys are sexually dimorphic, and adult females are about 69% as heavy as adult males [Thorington et al, 1979]. Troops are polygynous, with an adult sex ratio averaging one and one-half to two adult females per adult male [Rudran, 1979; Crockett & Eisenberg, 1987]. In red howlers, most males disperse and so do many females [Rudran, 1979; Crockett, 1984]. Reproductive success of females is suspected to be higher in those who breed natively, since emigrants are likely to suffer higher mortality and have some difficulty finding or establishing a troop in which to breed [Crockett, 1984]. Thus, mothers are more likely to affect the reproductive success of daughters by somehow increasing their chances of breeding natively, than the RS of offspring of either sex who emigrate.

We used interbirth interval length as a measure of maternal investment in offspring. Since data on maternal rank or bodily condition were unavailable, we used maternal age class as a possible correlate. Bodily condition is likely to decrease with age. Also, age is inversely correlated with rank in mantled howlers (*Alouatta palliata*) [Jones, 1980], so the possibility also exists for red howlers.

A complicating consideration is that theory predicts total parental investment in the two sexes to be equalized in the long run, and facultative adjustment of the sex ratio could achieve equal investment when one sex is more expensive to raise [Fisher, 1958; Clutton-Brock & Albon, 1982; Williams, 1979; Maynard Smith, 1980]. The ability of a mother to alter the sex ratio of her progeny could influence whether differential investment might be reflected in interbirth interval length.

METHODS

The study area, study population, and most data collection and analysis procedures are described in Crockett and Rudran [1987, this issue]. Data were collected in two habitats, a woodland-type savanna (W) and a gallery forest (GF). The following summarizes additional aspects of analysis pertinent to the present paper.

Infant's Sex

Red howler infants can be sexed at birth since the male's scrotum is already pendulous. Under field conditions, however, determining an infant's gender is considerably easier after about 3 wk of age, when the males' testes descend. Once the testes have descended, they freely dangle in the scrotum and the penis is rarely seen. In contrast, the clitoris of an infant female is conspicuous, whereas the spherical labia are firmly attached to the body. Sex differences in genitalia persist throughout a red howler's life.

Survival

Troop timelines summarized each individual's presence [see Crockett & Rudran, 1987, this issue]. For each howler in the birth data set, the month that it was last seen and its fate were recorded (eg, seen alive in natal troop during last census; disappeared, fate unknown; emigrated, month and location when last seen; etc.). Infant mortality refers to deaths occurring during the first year of life. Individuals that were 18 mo or younger when they disappeared from troops were assumed to have died since howlers of this age class have not been found outside of troops. Individuals that were older than 18 mo could have emigrated. The youngest female positively known to emigrate was 20 mo old whereas the youngest documented male emigrant was 43 mo old. Survival analysis is described in more detail in the Results and Appendix.

Annual Birthrate

The annual birthrate was estimated by summing births per female-month (BFM) for 12 mo periods to yield births per female year (BFY) [see Appendix and Crockett & Rudran, 1987, this issue].

Interbirth Interval Length

When successive births to the same female could be estimated to within 1 mo, an interbirth interval (IBI) length was calculated. In the cases when the IBI was known more accurately, eg, to the nearest 0.5 mo, the data set included the most precise measurement. The analyses in this paper only include IBIs after births of surviving infants. For this purpose only, "surviving" is defined as living at least until the mother's subsequent infant was conceived. Since gestation length in red howler monkeys is known to average 191 days [Crockett & Sekulic, 1982], the survival status of the infant can be determined by backdating 6.3 mo from the

TABLE I. Sex Ratio of 403 Infants Born Into 26 W and 17 GF Troops

Period	Woodland				Gallery Forest			
	M	F	UN	Prop. M	M	F	UN	Prop. M
6/76-1/77	11	4	2	.73				
2/77-1/78	8	16	3	.33				
2/78-1/79	14	20	0	.41				
2/79-1/80	19	24	2	.44	9	6	0	.60
2/80-1/81	27	35	1	.44	16	13	1	.55
2/81-1/82	21	22	0	.49	10	12	1	.45
2/82-1/83	17	21	0	.45	18	16	2	.53
2/83-2/84	18	13	5	.58	8	5	7	.62
Totals			P*				P*	
Overall	135	155	.26	.47	61	52	.44	.54
Habitats Combined					196	207	.62	.49

*Two-tailed probability, binomial test; M, males; F, females; UN, unsexed; Prop. M, Proportion of sexed births that were male.

subsequent sibling's birth. In other analyses in the Results, "infant survival" refers to surviving the first year of life, the period of infancy.

Statistical Tests

All probabilities are two tailed with 0.05 as the selected level of significance.

RESULTS

Sex Ratio at Birth

A total of 403 sexed infants were born into the 43 study troops between August 1976 and February 1984 (Table I). The combined population progeny sex ratio was 0.49 males, not significantly different than unity. In W between 2/77-1/81, the sex ratio was 0.42 males, $P = 0.04$, binomial test; however, there seems to be no valid reason for testing this subset separately. There was a trend for the sex ratio to be female-biased in the woodland and male-biased in the gallery forest, but the difference was not significant (Mann-Whitney $U = 9$, $n_1 = 5$ years, $n_2 = 8$ years, $P = 0.12$).

The progeny sex ratio for each female with 3-7 sexed offspring was calculated individually and then averaged so that each female contributed equally [see Williams, 1979]. For this sample, the overall mean of individual female's progeny sex ratios was 0.44 ± 0.29 SD ($N = 68$), 0.43 ± 0.24 SD for W females ($N = 49$), and 0.46 ± 0.39 SD for GF females ($N = 19$). The central tendency of the sex ratios did not differ significantly between habitats (Mann-Whitney $U = 439.5$, $n_1 = 49$, $n_2 = 19$, $P = 0.72$). W females were twice as likely to have more daughters than sons whereas GF females were about equally likely to have more sons or more daughters, but this difference was not significant ($\chi^2 = 0.87$, $df = 1$, $P = 0.35$, $N = 62$, excluding 6 W females with 0.50 progeny sex ratio).

In summary, there was a tendency toward a female-biased progeny sex ratio in the woodland, but on the whole it was not statistically significant. In general, the progeny sex ratio of individual females was highly variable.

Infant Survival

A previous analysis compared infant mortality in the two habitats during the time that both were studied [Crockett & Sekulic, 1984]. Woodland infant mortality was 16%, and gallery forest infant mortality was 19%; the difference was not

TABLE II. Fates of Red Howler Infants Born Through February 1981*

Fate	Males	Females	Unsexed	Total	Percent
Survived at least 1st yr	90	96	0	186	78.8
Disappeared age < 18 mo ^a	7	2	0	9	3.8
Died, infanticide ^b	6	12	4	22	9.3
Died, other cause suspected ^c	2	1	2	5	2.1
Disappeared, < 1 yr ^d	2	8	4	14	5.9
Died, ear-tagging related ^e	1	1	0	2	
Total	108	120	10	238	

*All disappearances < 1 yr considered deaths.

^aPresumed dead; disappeared between ages < 1 yr and 18 mo during gaps in observation; some may actually have survived to 1 yr.

^bObserved and suspected [Rudran, 1979; Crockett & Sekulic, 1984].

^cThree mothers disappeared along with their infants (presumed dead); one infant had botfly on throat; one twin disappeared.

^dIncludes "questionable" infanticides [Crockett & Sekulic, 1984].

^eSubtotal used to calculate percentages excludes these deaths.

statistically significant. Crockett and Rudran [1987, this issue] reported that infant mortality was unrelated to season of birth and that deaths did not appear to occur more frequently during particular months of the year.

In this section we examine sex and age differences in mortality. Undetected births and deaths were more likely to have occurred during the times when censuses were intermittent [see Crockett & Rudran, 1987, this issue, for details of study periods]. Thus, survival analysis was restricted to infants born through the end of the main study period (June 1976–February 1981). The fates of 238 infants are presented in Table II. About 80% of the infants survived their first year of life. At least 44% of infant mortality involved observed or probable infanticide.

Based on data in Table II, infant male mortality was about 16% compared to about 19% for females; however, about 4% of the infants died before their gender could be identified. To determine the existence of age and sex differences in mortality, survivorship curves were calculated using SPSS program SURVIVAL [Hull & Nie, 1981; see Appendix]. Figure 1 presents survivorship curves by sex based on the survival histories of 234 infants. Nine of the infants were unsexed and died before reaching 5 mo of age. If they were omitted from the analysis, infant mortality would be underestimated. Thus, these infants were randomly assigned a gender. However, statistical tests comparing sex differences in mortality were based on sexed infants only.

The most vulnerable stage of a red howler's infancy was during the first 4 mo, when about 58% of infant mortality occurred. The lowest infant mortality occurred at 5 through 8 mo of age for males and 9 through 12 mo for females. Using randomly assigned sex for unsexed infants, survivorship at 12 mo was 0.83 for males (17% mortality), 0.79 for females (21% mortality), and 0.81 (19%) overall. These values are similar to those calculated from Table II in a different way. The sex difference in survivorship curves through 84 mo of age is highly significant, with males showing much higher survivorship (Lee-Desu statistic = 22.6, $df = 1$, $P < 0.0001$). The sex difference through 18 mo of age, the oldest age when disappearances can be attributed to deaths with certainty, also indicates higher male survival (Lee-Desu statistic = 22.6, $df = 1$, $P < 0.0001$).

This sex difference in mortality is partly due to the fact that twice as many females were considered to be victims of infanticide (all known and suspected infanticide victims have been under 10 mo of age). This appeared to be a chance

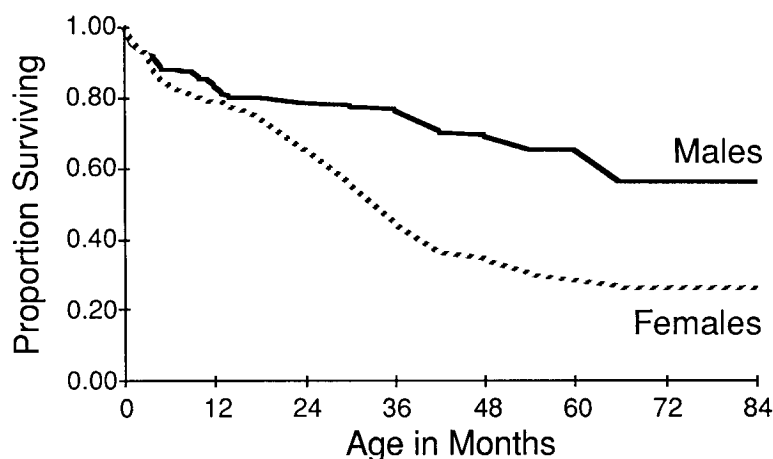


Fig. 1. Survivorship of 234 known-aged red howlers.

result of female-bias in infants available to be victims. However, between the ages of 13 and 18 mo, only one male disappeared compared to six females, suggesting a sex difference in small juvenile mortality.

Mortality was not markedly linked to significant developmental stages [see Mack, 1979]. Low mortality occurred during the transition to independent locomotion (5–7 mo). Slightly increased mortality occurred at 8–9 mo and 11–13 mo and might reflect stresses imposed by increasing reliance on a vegetarian diet and eventual weaning.

Survivorship curves beyond 18 mo of age must be regarded as approximations. Some proportion of both sexes emigrated from their natal troops, and most of these could not be followed after emigration because they were untagged or left the study area. Owing to the inherent risks of dispersal, their deaths are likely to occur at a higher rate compared to peers remaining in natal troops, but the precise rate is unknown. However, some animals that “disappeared” from troops and were classified as “dead” (see Appendix) may have actually emigrated undetected or unrecognized. These two sources of “error” somewhat compensate for one another.

Currently it is difficult to assess whether the sex difference in survivorship through 7 yr of age is actually as great as suggested by Figure 1, although the issue may be clarified through additional analyses beyond the scope of the present paper. Males tend to be older than females when they emigrate, and they are easier to identify after emigration [Crockett, 1984]. Female emigrants also appear to disperse farther than males. Of the oldest individuals in the birth sample who were no longer in their natal troops, 11 males and only 5 females were located in February 1984.

Interannual and Habitat Comparisons in Birthrate

Crockett and Rudran [1987, this issue] reported that the two habitats showed similar patterns in monthly birthrate even though the seasonal distribution of births varied somewhat from year to year. Mean monthly birthrate (BFM) was significantly higher in GF than in W during the year period 3/79–2/80, but the habitats did not differ during the period 3/80–2/81. In this section we examine interannual variation in annual rainfall and its relationship to birthrate and other variables reflecting female reproductive success in the two habitats. Between 1976 and 1983, annual

TABLE III. Pearson's Correlations Between Annual Rainfall and Parous Female Parameters

Year	Rain (mm)	Af dis ^a		Dis/trp-yr ^a		Af/troop ^b		Inf/af ^b		Births/f-yr ^c	
		W	GF	W	GF	W	GF	W	GF	W	GF
1976	1,743	1	—	.15		2.47		.49			
1977	1,163	4	—	.20		2.24		.53		.55	
1978	1,552	3	—	.13		2.41		.66		.68	
1979	1,892	0	0	.00	.00	2.65	2.44	.59	.91	.73	1.17 ^d
1980	2,135	1	2	.04	.15	2.85	2.36	.64	.64	.88	1.05 ^d
1981	1,753	2	1	.08	.06	2.73	2.24	.58	.61	.61 ^e	.63 ^e
1982	1,347	6	1	.24	.06	2.63	2.65	.64	.78	.63 ^e	.83 ^e
1983	1,958	3	7	.13	.41	2.65	2.29	.56	.51		
		20	11								
Mean	1,693			.12	.16	2.58	2.40	.59	.69	.68 ^f	.83 ^f
	r			-.79	+.38	+.78	-.70	+.10	-.33	+.87	+.51
	df			6	3	6	3	6	3	4	2
	P			< 0.02	NS	0.02	NS	NS	NS	< 0.025	NS

^aNumber of adult females that disappeared (presumed dead) divided by troop-months (see Appendix) for each year, divided by 12 mo. Mean rate is total disappearances divided by total troop years. W troop-months, 2,078; GF troop-months, 811.

^bMean number of parous females per troop and mean number of infants per parous female estimated for February of year following rainfall total, except 12/81 for 1981.

^cBirths per female-year calculated by summing monthly totals from February through January of following year.

^dBirthrate elevated because of high proportion of primiparous females entering population (see Appendix).

^eMay be low estimates due to undetected infant mortalities between census contacts.

^fMedian of births per female-year estimates for years Feb–Jan (presented above) and years Aug–July (not shown).

rainfall at Hato Masaguaral averaged about 1,700 mm, but year-to-year variation is notable. Table III presents correlations between annual rainfall and four parameters of parous females that give some index of reproductive success. Annual rainfall was significantly related to three of four W measures (adult female disappearances per troop-year, mean number of adult females per troop, and annual birthrate), but to none of the GF measures. Adult female mortality was greater in the woodland during drier years. Reflecting both adult female survivorship and recruitment of new breeding females, the average number of parous females per W troop was positively correlated with rainfall. For these two measures, the GF correlation was in the opposite direction (but not statistically significant).

In both habitats, the annual birthrate (natality or births per female-year, BFY) was positively correlated with annual rainfall, but not significantly so in GF. The lowest W birthrate occurred in 1977, the year of lowest rainfall. The annual birthrate tended to be higher in GF than in W (Table III; Appendix). A similar measure is the number of infants per parous female. However, this measure did not correlate significantly with rainfall in either habitat, perhaps because it reflects both birthrate and infant survival (Table III).

Interbirth Intervals After Surviving Infants

Birthrate is inversely related to interbirth interval (IBI) length (see Appendix for equation). In order to gain a more complete understanding of the factors affecting birthrate, IBI data were analyzed in detail. IBIs are significantly shorter after infant death, and they are excluded from the present analysis. (IBI's after infants that died before conception of the next sibling averaged 10.5 mo [Crockett & Sekulic, 1984].)

The distribution of 135 interbirth interval lengths (IBI's) recorded during the study is presented in Figure 2. The overall mean was 17.4 mo \pm 4.5 SD. The four longest recorded IBI's were well beyond two SD's above the mean and probably

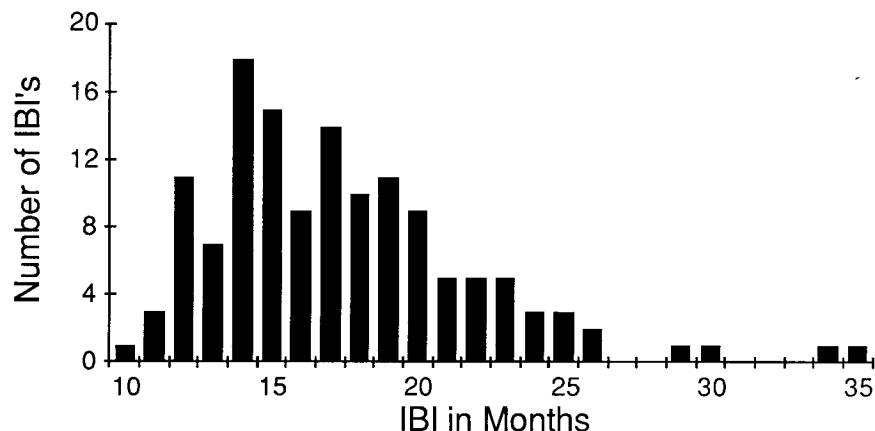


Fig. 2. Distribution of 135 interbirth interval lengths after surviving infants.

represent cases in which an unrecorded infant died during the interval between recorded births to the females. These four IBI's were excluded from subsequent analyses. The overall mean IBI excluding them is 17 mo (range 10.5 to 26 mo). For females with three IBI's in the sample, between-female differences were not significant ($F = 1.09$, $df = 9$, $P > 0.42$).

Analyses of variance (SPSS ANOVA, regression model [Nie et al, 1975]) were performed to assess the source of variation in IBI length. The IBIs were classified according to six factors. Three factors selected to assess the effects of environmental variation were HABITAT (Woodland versus Gallery Forest), SEASON when IBI began (early wet, late wet, early dry, late dry; see Crockett and Rudran [1987, this issue]), and PHASE of study when IBI began. The phases of the study were 1) IBIs beginning during the first year of the study (6/76–7/77), since low rainfall in 1977 was associated with a depressed birthrate; 2) IBI's beginning 8/77–1/79, prior to the main study of the gallery forest; 3) IBI's beginning 2/79 and thereafter, the phase when both habitats were studied (2 of 28 GF IBI's began in phase 2).

Factors to assess sex differences were sex of infant beginning the IBI (BEG.SEX) and ending it (END.SEX). Since mothers might show different birthrates depending on physical condition or other factors that might vary with age, the effects of maternal age class (MOM AGE) was the sixth factor (no data on maternal rank were available). Also, parental investment theory would predict a MOM AGE \times BEG.SEX interaction (see Appendix for details).

Table IV summarizes the results of the ANOVA analyses. HABITAT was the only significant main effect, with W averaging longer IBI's than GF. However, for W, PHASE was a highly significant effect, and the IBI's beginning during phase 1 averaged 3 mo longer than W IBIs beginning during phases 2 and 3. When phase 1 was excluded, the habitat effect was reduced and only approached significance.

SEASON, the third environmental factor, was not significant in any analysis. Maternal age class (MOM AGE) had no significant effect on IBI length; the overall mean IBI's differed by less than 0.2 mo across the three age classes.

BEG.SEX was not significant in the overall analysis, and the IBI lengths after males and females showed similar distributions. However, mean IBI's averaged consistently shorter after males than females in W but were slightly shorter after females than males in GF. BEG.SEX did approach significance in W when phase 1

TABLE IV. Summary of Interbirth Interval ANOVA's (see Appendix)

Factor	F	df,df	P	Pattern of IBI	Mean IBI
Phase (Woodland only)	5.23	2,89	0.007	1 > 2 & 3	20.3 > 17.1
Habitat (Overall)	4.16	1,120	0.04	W > GF	17.5 > 15.3
Habitat (phases 2-3)	2.96	1,108	0.09	W > GF (trend)	17.1 > 15.3
Season	1.15	3,120	0.33	NS	—
Maternal Age Class	0.50	2,74	0.61	NS	—
Beginning Sex					
Phases 1-3	2.22	1,120	0.14	NS	—
Phases 2-3 (W only)	3.72	1,81	0.057	M < F (trend)	16.3 < 17.7
MOM AGE set (W and GF)	5.71	2,74	0.019	M < F	15.8 < 17.7
Ending Sex (phases 1-3)	1.06	1,120	0.31	NS	—

was excluded. BEG.SEX was significant for the MOM AGE sample (habitats combined), but there were no significant interactions. END.SEX was not a significant main factor.

Overall, the differences among mean IBI lengths was small, usually less than 2 mo. The main pattern was for IBIs to be longest after W females, whereas IBIs after W males and GF infants of both sexes were shorter and of similar length.

The male-biased survivorship curves (Fig. 1) suggested a further IBI analysis. Females that remain in their natal troops are practically assured of reproducing there, whereas the reproductive success of emigrant females is suspected to be considerably lower [Crockett, 1984]. Therefore, mothers might increase their own reproductive success by investing in female offspring to reduce their daughters' probability of emigrating. IBI lengths after eight female infants who became natal breeders and eight females who were known to emigrate were available for analysis (due to the shorter period that GF had been studied and the fewer animals tagged there, this data set included only one GF female). The mean IBI after 1 GF and 5 W nately breeding females was $19.9 \text{ mo} \pm 2.06 \text{ SD}$, significantly longer than the mean IBI after seven emigrant females (all W), which was $16.6 \text{ mo} \pm 2.9$ ($t = 2.32$, $df = 11$, $P < 0.05$, two tailed) (two natal and one emigrant females were excluded because their births occurred during phase 1, which was associated with longer IBIs; their inclusion produced a one-tailed but not two-tailed level of significance). The omega squared measure of association [Runyon and Haber, 1980] for these data (est $\omega^2 = 0.25$) indicates that 25% of the variation in IBI length is explained by whether or not the females in the sample emigrated. Interestingly, all eight natal breeders had sisters for their next (younger) sibling, whereas six of the eight emigrant females were followed by brothers and only two by sisters (Fisher exact probability test, $P < 0.01$).

DISCUSSION

Birthrate and Interbirth Interval Length

For this population of red howler monkeys, variation in interbirth interval length is related primarily to environmental variation. The phase of low rainfall was associated with the longest IBIs and lowest birthrate. However, the season that the IBI began was unrelated to IBI length. IBIs averaged somewhat shorter and median birthrate was higher in GF than in W. These habitat differences are unrelated to age structure of the populations since maternal age class had no significant effect on IBI length. However, they are consistent with habitat differences in popu-

lation growth: GF is characterized by low density and high growth rate, whereas W is moderate density with a low (but positive) growth rate [Crockett, 1984, 1985]. Birthrate in GF was also higher because there were more primiparous females giving birth for the first time, which was associated with the more frequent formation of new troops [Crockett, 1984]. The nonsignificant correlations between annual rainfall and GF female parameters are probably due in part to a combination of small sample size and the lack of data during the driest year. However, the fact that GF female disappearances and female group size are in the opposite direction than in W suggests that other factors such as differences in population growth phase are involved.

The overall red howler mean IBI length of 17 mo is the same as Milton's [1982] tentative estimate for *A. palliata* on Barro Colorado Island, and both are shorter than the 22.5 mo mean reported for Costa Rican *A. palliata* [Glander, 1980]. This difference may be related to lower quality, less abundant, and/or seasonally scarce foods at the Costa Rican site. For example, fig trees, an important howler food at Hato Masaguaral and at Barro Colorado Island [Milton, 1980], are rare at Glander's [1978, 1981] site.

Variation in food availability appears to affect IBI length and natality in some Old World monkeys. The mean IBI after births of surviving *P. entellus* infants in an area where the monkeys were regularly provided with food by local people was 14.9 mo, a considerably shorter period than the 19–24 mo typical of other areas where breeding is more seasonal [Vogel & Loch, 1984]. Captive *P. entellus* also had shorter IBIs, averaging 15.4 mo [Harley, 1985]. Birthrate in *M. fascicularis* was more than twice as high in a year of food abundance than in 2 yr of lower food availability [van Schaik, 1983; van Schaik & van Noordwijk, 1985]. In a similar vein, Sugiyama and Ohsawa [1982] found that the annual birthrate of Japanese macaques, *M. fuscata*, declined from 60% to 34% after provisioning was terminated. Wild *C. aethiops* birthrate was positively correlated with adult female rank in an area where preferred foods were clumped and food intake was rank related [Whitten, 1983], although this relationship was not found at another site [Cheney et al, in press]. In baboons (*Papio anubis*), birthrate declined as food competition with ungulates increased [Strum & Western, 1982]. In our study site, birthrate was positively correlated with annual rainfall, and food abundance varies with rainfall. For example, three GF tree species experienced fruit crop failures after the dry year of 1977 [Robinson, 1986].

The red howlers at Hato Masaguaral had a median of 0.73 births per female year. This value exceeds most estimates for cercopithecine monkeys [Andelman, 1986], and birthrates this high among wild populations are usually associated with high infant mortality [Altmann et al, 1985] and concomitant shortening of birth intervals. Provisioned rhesus have shown similar or higher birthrates and infant survival than our population [introduced island free-ranging: Drickamer, 1974; Rawlins & Kessler, 1985; and wild: Malik et al, 1984]. However, for a natural, undisturbed monkey population, the red howlers at Hato Masaguaral have high rates of natality and infant survival. Not surprisingly, the population has been growing. Between 1979 and 1981, the annual growth rate was 6% for W and 21% for GF [Crockett, 1984, 1985].

Differential Investment in Offspring and Birth Timing

As outlined in the introduction, mothers might vary their investment in offspring as a function of offspring sex. This differential investment might be expressed in longer interbirth intervals associated with one sex than with the other depending upon the condition of the mother. Thus, the timing of a particular birth might be

influenced by whether its preceding sibling were male or female. However, greater investment in one sex could also result from producing more offspring of that sex and/or spending more time and energy rearing individual offspring of that sex post-weaning, eg, through agonistic support or social grooming.

In our study, maternal age class was the only measure available that might correlate with bodily condition or social rank. It was found to be unrelated to IBI length, and mean IBIs for the three age classes were almost identical. Furthermore, no interactions were found to suggest that mothers invested differentially in male versus female offspring depending on maternal age. Differences in IBI length related to infant sex were complex and varied somewhat between habitats. However, there was some evidence that longer intervals after female infants might increase their chances of breeding natively and most likely give them (and their mothers) a reproductive advantage over emigrating females. The average of more than 3 mo delay in conceiving a new infant after bearing a female who ended up being a natal breeder might reflect additional "investment" of some sort. For example, since red howler infants are nursed through about 11 to 14 mo of age, infants with longer IBIs after their birth might be weaned before conception of their next sibling; their mothers might be able to devote more energy to lactation. In contrast, infants with shorter IBIs are invariably still suckling when gestation of the next infant begins; they possibly receive less milk and might not grow as fast. There are insufficient data to examine this possibility, but measurements taken during tagging in 1981 revealed no sex differences in weight or head-tail length through 18 mo of age.

The longer length of IBIs after female infants that eventually bred natively might also reflect some behavioral differences on the infants' part compared to eventual emigrants. They might have been, for example, more demanding or aggressive in ways which might have suppressed conception of their mother's next infant. Such behavior might not necessarily garner them more "investment" measured in milk consumption, but may have made them more successful in female-female competition (thought to be important in determining who breeds natively [Crockett, 1984]). Regardless, this would still qualify as PI as defined by Trivers [1972].

However, the significant difference in IBIs depending on whether or not females emigrated might be related to the sex of the next sibling. All eight natal breeders had sisters as the next sibling, whereas the eight emigrant females were followed by six brothers and only two sisters. The biological significance of this is not readily apparent. Sex ratios at birth were not significantly different from 50:50, and there was no convincing evidence for facultative adjustment of offspring sex ratio.

The evidence for differential investment in natively breeding females, reflected in longer IBIs, is based on a small sample size and must be regarded tentatively. In support of the hypothesis, it is likely that variance in male and female RS is more similar in this species than in most polygynous species since so many female red howlers apparently die young or emigrate to uncertain reproductive fates. Thus mothers might be expected to be able to influence daughters' RS more than sons', by helping the former to breed natively. However, although female mantled howlers in Costa Rica are also thought to compete for breeding opportunities and both sexes emigrate [Jones, 1980], sex differences in infant mortality and age at emigration are the reverse of those at our site, with much higher male mortality and males emigrating at younger ages than females [Clarke & Glander, 1984]. Data on sex differences in IBI length have not been reported for the Costa Rican site, probably because so few male infants have survived there.

The red howler survival data are also inconsistent with Clutton-Brock and co-workers' [1985] theory that juvenile mortality should be higher in males than in females in sexually dimorphic mammals and birds. Higher juvenile female mortal-

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APPENDIX

SPSS Program SURVIVAL

SPSS program SURVIVAL [Hull and Nie, 1981] allows the user to specify which categories of cases (ie, individuals) are to be considered "terminal events" (deaths) and which ones are to be "censored." Censored cases are those that do not reach the terminal age, but are not considered "dead" at the time they leave the sample. In the analysis presented here, "censored" cases include a) those individuals who were alive but younger than the oldest possible age (84 + mo) in February 1984, b) those that were known to have emigrated, c) those that probably emigrated (animals that approximately fit their description were located), and d) those that were removed from the sample because they died tagging-related deaths (two cases) or because their troop could not be located in February 1984 (five cases in two troops). Terminal events included a) all known deaths, b) disappearances of individuals less than 18 mo of age (all presumed dead), and c) all other disappearances from natal troops. In all cases, individuals were considered to have attained the age when they were last seen. The probability of dying during a given age interval is calculated as number of terminal events during the interval divided by the number "exposed to risk" (see Hull and Nie [1981] for a more complete description).

Annual Birthrate

The annual birthrate was estimated by summing births per female-month (BFM)[see Crockett and Rudran, 1987, this issue] for 12-mo periods to yield births per female-year (BFY). These year-long periods comprised four consecutive seasons. In Table III, BFY years begin with late dry season (February). Somewhat different estimates were produced by beginning in late wet season (August). A problem arose in estimating GF birthrates for the first 2 yr. These birthrates may be artificially high due to the method used to determine the starting month for calculating females' BFM (see Crockett and Rudran, [1987, this issue]). Since females did not contribute female-months until the season that they first gave birth, a high proportion of primiparous births in GF undoubtedly inflated the birthrates. Nevertheless, the number of infants per female was much higher for GF than W in 1979 and this measure is unaffected by parity.

To provide an overall estimate of birthrate for the two populations, the median birthrate of all BFY estimates (beginning February and beginning August) was calculated (Table III). In W, a median of 0.68 infants were produced per female-year compared to 0.83 infants in GF. The overall median was 0.73 (N=19).

Birthrate can also be estimated by the equation

$$P_s (12/IBI_s) + P_d (12/IBI_d),$$

where P = proportion of infants, s = surviving, d = dying, and IBI = mean interbirth interval in months. Using $IBI_s = 17.5$ (W) and 15.3 (GF) (from Table IV), $IBI_d = 10.5$, $P_d = 0.162$ (W), and 0.192 (GF) (from Crockett and Sekulic [1984]), the estimated birthrates are 0.76 (W) and 0.85 (GF), similar to median BFY estimates.

IBI Analysis

The MOM AGE data set was a subset of the IBI data set, selected such that each female contributed only one IBI, phase 1 births were excluded and 1979–1981 (the main study period for both habitats) was given priority. The age classes were 1) young, the IBI after the first surviving infant to primiparous females (or the first accurate IBI); 2) older, the last accurate IBI recorded for greying, wrinkled females,

ending prior to 1982 unless no other IBI was available; 3) middle, all other females; the 1979–1980 IBI was selected over others when more than one IBI was available for “middle-aged” females. Of the 79 IBIs contributing to the MOM AGE sample, 91% began 1978–1980. The actual age of only the youngest females was known. The young females were about 5 to 8 yr old. The older females were probably about 18 to 25 yr old, suggested by preliminary analysis of tooth wear data from some of the females [Thorington, personal communication].

The ANOVA results summarized in Table IV are based on the following analyses:

HABITAT × BEG.SEX × END.SEX × SEASON (all phases, df = 126),

HABITAT × BEG.SEX × END.SEX × SEASON (phases 2–3, df = 114)

PHASE × BEG.SEX × END.SEX (all phases, W only, df = 100)

PHASE × BEG.SEX × END.SEX (phases 2–3, W only, df = 88)

MOM AGE × HABITAT × BEG.SEX (df = 78)