

# VI.3

---

## **Demographic trends in the *Alouatta palliata* and *Cebus capucinus* populations of Santa Rosa National Park, Costa Rica**

L. M. FEDIGAN

### **Introduction**

With 30% of its land in national parks, the small Central American country of Costa Rica is a leader in conservation in Latin America. Three species of neotropical primates occur in Santa Rosa National Park in the northwestern province of Guanacaste: *Ateles geoffroyi*, the red spider monkey; *Alouatta palliata*, the mantled howling monkey; and *Cebus capucinus*, the white-faced cebus monkey. Guanacaste Province has undergone extensive deforestation that has negatively affected all three primate species, in particular spider monkeys, which are not reliably reported outside of the national parks, and cebus monkeys, which have disappeared from many previously known ranges. Thus, along with a number of other public and privately owned and protected areas, Santa Rosa represents a major refugium for the primates in Guanacaste.

Demographic trends in the Santa Rosa howling and cebus monkey populations are compared in this paper with the population and group composition data from two well-studied sites in Central America: La Pacifica in Guanacaste (Glander, 1980; Clarke & Glander, 1984) and Barro Colorado Island in Panama (Carpenter, 1964; Froehlich & Thorington, 1981; Milton, 1982; Oppenheimer, 1982).

### **Methods**

An exhaustive census of monkeys in all parts of the 100 km<sup>2</sup> park was conducted by a team of three to four researchers during the wet season of 1983 and the dry season of 1984. A detailed description of census techniques and results will be provided in Fedigan, Fedigan & Chapman (in preparation).

Twenty-two groups of the total 25 *Alouatta* groups counted in the park, and 22 of the total 28 *Cebus* groups counted, are used in this analysis. These are the groups for which the most reliable counts were obtained, and all of the group counts used in the major analysis were made in April–May 1984. As a first step, group compositions were compared between the wet season of 1983 and the dry season of 1984 to test for birth seasonality. Then population parameters for *Alouatta* and *Cebus* at Santa Rosa in 1984 were compared with findings from other sites. Finally, demographic characteristics of *Alouatta* and *Cebus* at Santa Rosa were compared with each other for species differences.

### Results and discussion

The infant to adult female ratios in 10 of the better-known groups of *Alouatta* were compared between the wet season of 1983 and the dry season of 1984. A similar analysis was performed for 10 groups of *Cebus*. In neither case was there a significant difference between the two seasons in the ratio of infants to adult females (*Alouatta*: Wilcoxon  $T = 25$ ,  $P > 0.05$ ; *Cebus*: Wilcoxon  $T = 17$ ,  $P > 0.05$ ). Thus, given the presently available evidence, there does not appear to be birth seasonality in howling or cebus monkeys at Santa Rosa, a finding confirmed for these species by Clarke & Glander (1984) and Oppenheimer (1982) at nearby Central American sites.

Table 1 summarizes some population parameters for *A. palliata* at Santa Rosa, compared to the same species at other sites. Although we have not yet monitored the primate populations in the park over a sufficient time period to establish definite patterns of growth, there are three lines of evidence to suggest that the Santa Rosa howler population is stable, and that it may be stationary or only slowly increasing in size. First, Freese (1976) censused the monkeys in the park in 1972, and although he found fewer howlers in fewer places in the park than we did, the age/sex composition in 1972 was very similar to values from 1984. A stable age distribution is characteristic of a stable population. Secondly, there is a wealth of data on mantled howler populations from other research sites, including census information covering a 50-year period for Barro Colorado Island (BCI) in Panama, which has been summarized by both Milton (1982) and Froehlich & Thorington (1981). From these data one can extract the demographic characteristics of *A. palliata* populations which are known to be declining or increasing in size.

For example, data are available which were obtained prior to, soon after, and some years following, a 1951 population crash at BCI. From

Table 1. Population parameters for *Alouatta palliata* at Santa Rosa and other sites

Study site	Mean group size	Mean group composition (%)				Mean sociometric ratios		
		AdM	AdF	Juv	Inf	M:F	F:Inf	F:Imm (Juv & Inf)
Santa Rosa 1984 (This study)	13.6	22	44	20	14	1:2.03	1:0.31	1:0.77
Santa Rosa 1972 (Freese, 1976)	8.1	20	44	25	11	1:2.23	1:0.29	1:0.79
BCI, declining 1951 (Collias & Southwick, unpublished)	7.8	15	58	13	14	1:3.75	1:0.24	1:0.46
Los Tuxtlas, Mexico 1982 (Estrada, 1982)	9.1	33	45	9	13	1:1.37	1:0.28	1:0.48
BSI, expanding 1959 (Carpenter, 1964)	18.5	18	49	17	16	1:2.75	1:0.33	1:0.77
Modeled stable population (Heltné <i>et al.</i> , 1976)	15.0	-	-	-	-	-	1:0.25	1:0.75

AdM = adult males; AdF = adult females; Juv = juveniles; Inf = infants; Imm = immatures.

this information, both Carpenter (1964) and Heltne, Turner & Scott (1976) proposed that there are four indicators of a declining or recently declined *A. palliata* population: a small mean group size, of less than eight; an elevated number of adult females per male; a low proportion of females with infants; and a low proportion of immatures to adult females. Further, Estrada (1982) has argued that the low proportion of immatures in the howler population at Los Tuxtlas, Mexico, and the skewed sex ratio (although in the opposite direction from BCI) both suggest a population in decline and under stress.

The 1984 Santa Rosa values for mean group size, sex ratio, and female to infant ratio, fall between those of declining mantled howler populations and BCI values for time periods when that population was expanding. In the last few years at BCI, the birth rate has been unusually high, but the total population size appears to have remained stationary, and Milton (1982) has argued that the control of population size there is achieved through the counter-balancing effects of high juvenile mortality against high birth rates. I will return to the seemingly low numbers of juvenile howlers at many study sites later in this paper.

The third line of evidence for a stable howler population in Santa Rosa is the relatively good fit between empirical values obtained for this population in 1984 and the theoretical values derived from a model proposed by Heltne *et al.* (1976) for a stable population of *A. palliata*. The assumption used in their '11 year model' seems closest to what is known today about reproductive and life-history parameters in female howlers. From this model, they argued that a stable mantled howler population should have mean group sizes of around 15, a female to infant ratio of at least 1:0.25, and a female to immature ratio of 1:0.75; all values which are close to those found in our study population.

Table 2 summarizes data for *Cebus* in the park, and compares them to the only other published demographic data on white-faced cebus monkeys, those of Oppenheimer's (1982) 4-year study of two groups on BCI. These two sets of demographic data are quite similar, especially the female to immature ratios. During Oppenheimer's study in Panama, his local population was increasing at a mean rate of 23% a year, that is, growing rapidly. Thus, although only future censuses will finally determine the growth pattern of the *Cebus* population in Santa Rosa, the comparative data and the current structure do suggest an expanding population.

Table 2. Comparison of demographic data for *Cebus capucinus* at Santa Rosa and Barro Colorado Island

Study site	Mean group size	Mean group composition (%)				Mean sociometric ratios			
		AdM	AdF	Juv	Inf	M:F	F:Inf	F:Imm (Juv & Inf)	
Santa Rosa 1984	14.1	16	37	35	12	1:2.24	1:0.33	1:0.27	
BCI 1966-70 (Oppenheimer, 1982)	14.4	17	32	36	15	1:1.71	1:0.43	1:1.38	

Table 3 compares some howler demographic characteristics to those of cebus at Santa Rosa. One major difference lies in the proportions of juveniles, particularly young or 'small' juveniles in the two populations. Although both species are reported to have similar maturation rates, and both currently experience similar birthrates at Santa Rosa, there is a greater proportion of juveniles in the cebus population than in the howler population. Lifetable statistics cannot yet be calculated for these animals. However, a simplified estimation of survivorship compares the observed to the expected number of juveniles in each group, assuming that these monkeys are juveniles for 3 years, and that the mean number of adult females in each group and birthrate have remained constant over the last 3 years. Milton (1982) originally proposed this measure, and she found that at BCI 39% of the expected immature howlers were 'missing'. Similarly, the observed number of juvenile howlers in each group at Santa Rosa is much lower than expected (2.8 compared to 5.6, or almost 50% 'missing'). However, there are nearly as many cebus juveniles observed as expected. Low numbers of juvenile howlers also have been reported from several other studies (e.g. Rudran, 1979; Froehlich & Thorington, 1981; Estrada, 1982).

Thus, the question presents itself: where have all the juvenile howlers gone? One obvious answer is that the juveniles have dispersed and are living as solitaries, rather than as group members. Various studies have reported that female as well as male howlers transfer between groups (e.g. Rudran, 1979; Glander, 1980), and one study of red howlers found that many immatures of both sexes may leave their natal group without immediately joining a new group (Crockett, 1984). However, we did not encounter temporary heterosexual associations made up of emigrants, like those described for red howlers, nor did we find sufficient numbers of solitaries to begin to correct for their low representation in groups.

If patterns of emigration do not fully account for the low proportion of juveniles, a second possibility is that of high mortality in the late-infant to early-juvenile stages. Rudran (1979) argued that this is indeed the pattern that occurs in red howlers, and that the high mortality is the result of frequent episodes of infanticide. The killing of infants by adult males has not been seen at Santa Rosa or BCI, but it has been reported by Clarke & Glander (1984) to occur in mantled howlers. In her consideration of juvenile mortality at BCI, Milton (1982) argued that the effects of parasites and unpredictable shortages of high-quality foods are far more important than infanticide in

Table 3. Comparison of demographic data for howlers and cebus monkeys at Santa Rosa, 1984

Species	Mean group size	Mean group composition (%)					Mean sociometric ratios		
		AdM	AdF	Large juv	Small juv	Inf	M:F	F:Inf	F:Imm (Juv & Inf)
Howlers	13.6	22	44	10	10	14	1:2.03	1:0.31	1:0.77
Cebus	14.1	16	37	14	21	12	1:2.24	1:0.33	1:1.25

Mean no. juv. howler per group: observed = 2.8, expected = 5.6  
 Mean no. juv. cebus per group: observed = 4.9, expected = 5.1  
 Expected howlers =  $3 \text{ yr} \times 6\text{F} \times 0.311$  per F per yr  
 Expected cebus =  $3 \text{ yr} \times 5.2\text{F} \times 0.331$  per F per yr

reducing numbers of immatures. In addition, Froehlich & Thorington (1981) argued that juvenile howlers suffer disproportionately high mortality during nutritionally poor years. All of these factors, as well as disease and predation, could limit the number of individuals that survive through the juvenile stage to reproductive maturity.

In conclusion, our preliminary findings suggest that the creation of Santa Rosa National Park 14 years ago, and the subsequent relaxation of some of the human-induced pressures on its wildlife, has resulted in local abundance of primate species. The howler population appears stable, and either stationary or only slowly increasing in size, whereas the cebus monkey population is likely an expanding one. While the park itself will continue to provide a secure habitat, with little hunting or encroachment pressure, the continuing deforestation and cattle-grazing in the areas surrounding the park will result in the increasing isolation of the primate populations, with new attendant demographic pressures. In the coming years, this investigation of Santa Rosa demography will continue, in addition to the monitoring of life-histories of selected individuals and groups in the park.

#### Acknowledgements

This research was supported by an NSERC (Canada) Operating Grant no. A7723. Colin Chapman, Larry Fedigan and Jeff Bullard helped to collect the census data. Daniel Janzen provided helpful criticisms of an earlier draft.

#### References

- Carpenter, C. R. (1964) *Naturalistic behavior of nonhuman primates*. University Park, Pa: Pennsylvania State University Press
- Clarke, M. R. & Glander, K. E. (1984) Female reproductive success in a group of free-ranging howling monkeys (*Alouatta palliata*) in Costa Rica. In *Female Primates: Studies by Women Primatologists*, ed. M. F. Small, pp. 111–26. New York: Alan R. Liss
- Crockett, C. M. (1984) Emigration by female red howler monkeys and the case for female competition. In *Female Primates: Studies by Women Primatologists*, ed. M. F. Small, pp. 159–73. New York: Alan R. Liss
- Estrada, A. (1982) Survey and census of howler monkeys (*Alouatta palliata*) in the rain forest of "Los Tuxtlas", Veracruz, Mexico. *Am. J. Primatol.*, **2**, 363–72
- Freese, C. (1976) Censusing *Alouatta palliata*, *Ateles geoffroyi* and *Cebus capucinus* in the Costa Rican dry forest. In *Neotropical Primates: Field Studies and Conservation*, ed. R. W. Thorington, Jr & P. G. Heltne, pp. 4–9. Washington, D.C.: National Academy of Sciences
- Froehlich, J. W. & Thorington, R. W., Jr (1981) The demography of howler monkeys *Alouatta palliata* on Barro Colorado Island, Panama. *Int. J. Primatol.*, **2**, 207–36
- Glander, K. E. (1980) Reproduction and population growth in free-ranging mantled howling monkeys. *Am. J. Phys. Anthropol.*, **53**, 25–36



- Heltne, P. G., Turner, D. C. & Scott, N. J. Jr (1976) Comparison of census data on *Alouatta palliata* from Costa Rica and Panama. In *Neotropical Primates: Field Studies and Conservation*, ed. R. W. Thorington, Jr & P. G. Heltne, pp. 10–19. Washington, D.C.: National Academy of Sciences
- Milton, K. (1982) Dietary quality and demographic regulation in a howler monkey population. In *The Ecology of the Tropical Forest. Seasonal Rhythms and Long-term Changes*, ed. E. G. Leigh, A. Stanley Rand & D. M. Windsor, pp. 273–89. Washington, D.C.: Smithsonian Institution Press
- Oppenheimer, J. R. (1982) *Cebus capucinus*: home range, population dynamics and interspecific relationships. In *The Ecology of the Tropical Forest: Seasonal Rhythms and Long-term Changes*, ed. E. G. Leigh, A. Stanley Rand & D. M. Windsor, pp. 253–72. Washington, D.C.: Smithsonian Institution
- Rudran, R. (1979) The demography and social mobility of a red howler (*Alouatta seniculus*) population in Venezuela. In *Vertebrate Ecology in the Northern Neotropics*, ed. J. F. Eisenberg, pp. 109–26. Washington, D.C.: Smithsonian Institution Press