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Population Density and Use of Space in Howling Monkeys (*Alouatta villosa*) in Southwestern Panama

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ABSTRACT. Eight troops of *Alouatta villosa* (=*A. palliata*) were studied for 10 weeks in a natural forest in southwestern Panama. This is one of the few extended studies on the species to be conducted in a location other than Barro Colorado Island. The 151 animals belonging to 8 troops and 6 additional isolates utilized 37 acres of forest. This population density was 21 times greater than on Barro Colorado in 1932 and 12 times than on Barro Colorado in 1967. The average troop size was 18.9 animals; the average home range was 12.1 acres. Home ranges overlapped extensively and on the average troops had only 6% of their home range for exclusive use. There were no signs that the howling monkeys were exhausting their food supply or were experiencing decreased fertility. Several factors that could function in population control are evaluated.

INTRODUCTION

Since 1931 several studies on howling monkeys (*Alouatta villosa* [=*A. palliata*]) on Barro Colorado Island in the Panama Canal Zone have yielded longitudinal data on ecology, population dynamics and behavior (CARPENTER, 1934; COLLIAS & SOUTHWICK, 1952; ALTMANN, 1959; SOUTHWICK, 1962; BERNSTEIN, 1964; CHIVERS, 1969). Howling monkeys have been of interest to primatologists for at least 3 reasons: (1) since they were the first species systematically studied in their natural environment (by CARPENTER in the early 1930's), they have had an established position in the literature on primate biology and behavior; (2) the monkeys' ritualized intertroop howling exchanges are both impressive to experience and important to theories of utilization of space by animals; (3) the longitudinal data on population dynamics on Barro Colorado Island are among the best available for any wild primate species which is of great value to ecologists and primatologists.

This report will present comparative data on howling monkeys (*Alouatta villosa*) observed by the authors in a natural forest in southwestern Panama. This is the first extended study on howling monkeys in a natural environment other than Barro Colorado Island. Comparative studies on primates have been of great value since many primate species show significant variance in social organization and behavior in different environments. DEVORE (1965), JAY (1968) and others have emphasized that a thorough description of a species should be based on studies in different environments in order to delineate the range of variance and adaptability of that species. The data from our recent study on howling monkeys in southwestern Panama contain several findings that are significantly different from those made on Barro Colorado Island. This report will present comparative data on population density, troop size, home range size, and home range overlap.

BARRO COLORADO ISLAND

For the reader who is unfamiliar with the howler research, the present section reviews the findings and theoretical questions concerning the population dynamics on Barro Colorado Island.

Table 1 presents the population and range data for the howling monkeys on Barro Colorado Island and the data from the present study. CARPENTER (1934) counted 398 animals in 1932 and 489 in 1933. COLLIAS and SOUTHWICK (1952) and SOUTHWICK (1963) postulated that the population grew from 1932 until 1948 or 1949 when an epidemic drastically cut back the total population size to 239 howlers. Since 1951 the population grew to around 1000 animals in 1967 (CHIVERS, 1969). The increasing population density has raised questions about how the animals will adapt to greater crowding. The troops do not show friendly association or even mutual tolerance of each other: they tend to avoid each other; and when troops do converge on the same area, they engage in vocal confrontations, which CARPENTER (1934) described as 'vocal battles.' SOUTHWICK (1963) summarized the major research questions for the Barro Colorado howlers as: "(1) What levels will this howler population attain? (2) What will happen behaviorally and socially at higher population densities? (3) What will be the ultimate mechanism of population control?" Since little is known about the ecology, epidemiology or behavior of primates living in high population densities, Barro Colorado is a unique natural laboratory for research on population dynamics.

During the years that the Barro Colorado animals have been observed there have been changes in intertroop interactions that have correlated with the population

Table 1. The howler population data for Barro Colorado Island in 1932, 1967, and CHIVERS' estimated potential population. These are compared with the data for the present study.

	Barro Colorado Island			Present study
	1932 (CARPENTER, 1934)	1967 (CHIVERS, 1969)	Potential (CHIVERS, 1969)	Southwestern Panama, 1971
Number of troops in the utilized area	23	63–87	262	8
Average troop size	17.3	14.7	14.7	18.9
Population in the utilized area	398	926–1278	3,860	157
Acres of utilized area	2,000[1]	3,150[2]	3,150	37
Estimated home range size (in acres)	90–150[3]	36–50	36	12.1
Home range overlap	5% per 5 mo.	3% per 1 mo 62.5% per 3 mo	assumed at 67%	94%
Population density (howlers per 100 acres)	20	29–41	123	417

1) Apparently in 1932 about 3 of the 6.5 square miles of Barro Colorado Island were primary forests used by howlers. This number is estimated from Figures 1 and 2 in CARPENTER (1934) and pages 146–147 in COLLIAS and SOUTHWICK (1952).
2) CHIVERS' data imply that in 1967 the howlers were using around 3,150 acres, since 504 acres were 16% of the utilized island area (pp. 80–81).
3) Although CARPENTER (1934) gives the range 200 to 300 acres on page 33, on page 31 he states that the troops used a range roughly like a circle with "a radius slightly over 600 yards," which would be 105–110 acres; and on page 38 the observation that there were 23 troops in 1932 and 28 in 1933 in the 2,000 acres of howler habitat indicates an average home range of 86 acres, assuming no home range overlap. Adding 5% overlap, the mean home range (exclusive plus overlap) equals 90 acres. (Page numbers refer to the 1934 article reprinted in CARPENTER, 1964.)

changes. SOUTHWICK (1963) made observations in 1951 and 1959. "In eight years the primate population had increased almost four fold." "The amount of intergroup vocalization had increased at least ten fold from 1951. In 1951 it was very rare to hear daytime howling. In 1959 howling was heard throughout the day." In 1967 CHIVERS (1969) observed that in spite of the increasing population and decreasing home range size, there had been a decrease in overlap in the home range used in any given month. In CHIVERS' 1967 study there were drifts in home range boundaries from month to month, but during any given month each group had exclusive use of its own area. CHIVERS concluded that "this suggests the recent perfection of a spacing mechanism."

The howlers we observed in southwestern Panama were 21 times denser than those originally observed on Barro Colorado by CARPENTER in 1932 and 12 times more crowded than those observed by CHIVERS in 1967 (calculated on howlers per unit area). Also, the intertroop interactions and home range overlap differed from those one would predict from the Barro Colorado data.

THE STUDY SITE IN SOUTHWESTERN PANAMA

The study site consists of a 50 acre (0.20 km^2) subset of a continuous, undisturbed forest of over 1,000 acres (4 km^2) in southwestern Panama (8°, 19′ N. latitude; 82°, 38′ W. longitude). During the study the following primates used the 50 acre area: 1 troop of *Cebus capucinus,* 2 troops of *Saimiri oerstedii* and 11 troops of *Alouatta villosa.* The forest extends along the Pacific coast and varies from 0.25 to 1 mile in width. The forest is bordered by an estuary to the Escarrea River on the north, and by grasslands that are flooded in wet season on the south. In wet season, part of the forest floor is covered with water, but approximately 85% is elevated above the wet season high water level. Surrounded by water most of the year, the study site has been effectively isolated from human molestation, and species of animals now rare elsewhere in southwestern Panama were present in the forest. Figure 1 shows the forest and the 5 mile trail system that was opened to follow the monkeys. The eight troops of howlers that were studied extensively used 37 acres of the study site. The howlers habituated to the observers in less than two weeks and could be observed continuously from ranges of 20 to 50 feet. Further description of the forest is presented elsewhere (BALDWIN & BALDWIN, in press).

The study was conducted between December 19, 1970, and February 25, 1971; and a total of 513 hours were spent in contact with the howlers. Observations were made with 7 × 35, 11° wide angle and 8 × 30 binoculars. Observations were recorded on note cards and tape recorders and were typed and annotated daily. Other data were collected via vocalization tapes, daily travel maps, plant collections, still photography and motion pictures. Squirrel monkeys and capuchin monkeys were also studied for 263 and 170 hours respectively.

POPULATION DENSITY

Table 2 presents the population and range data for the 8 troops of howling monkeys

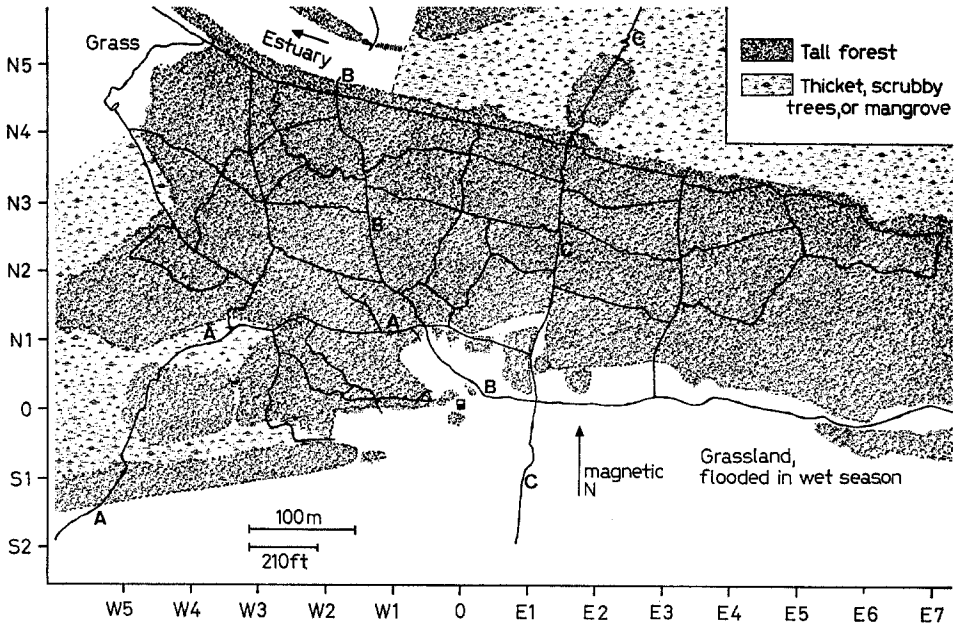

Fig. 1. The study site and trail system at Hacienda Barqueta. The tent site (0,0) was 2.4 miles east of the mouth of the Escarrea River and 0.25 miles north from the Pacific coast line.

that were studied extensively. Several other troops lived in the 50 acre study area, but the data on these troops are too incomplete to be included. The average howler troop size of 18.2 is not notably different from the averages reported on Barro Colorado Island. The largest troop of 28 was smaller than the largest troops observed on Barro Colorado, which have at times reached 40 monkeys. However, the first three troops in Table 2 occasionally joined and traveled together, partially intermingling, to produce 'supertroops' of 38, 45, 47 or 65 animals depending on which troops combined. The relations between these 3 troops appeared to be friendly and

Table 2. The population size and home range data for the troops in the present study. Troops are listed from those living in the far west to far east.

Troop	No. of howlers	Range: acres	Exclusive range: Acres	Exclusive range: Percent
Planta	20	15.7	0.00	0.0%
Boca	18	16.5	0.00	0.0%
27-4-2	27	17.2	0.00	0.0%
Pata	16	8.0	0.75	9.4%
Saco	16	8.0	0.70	8.8%
7-2-0	7	?	?	?
Cola	28	8.7	3.00	34.5%
L.D.	19	10.5	?	?
Totals	151	84.6	4.45	
Averages	18.9	12.1	0.74	6.0%
Loners	6			
	157			

behavioral observations suggest that these 3 troops may have been fragments of a common original troop. The behaviors observed in all the other intertroop relationships showed the existence of mutual fear and avoidance, even though the home ranges of all these troops overlapped extensively.

The home range sizes varied from 8.0 to 17.2 acres, with an average of 12.1 acres per troop. This is approximately one-tenth the size of the home ranges observed by CARPENTER (1934) for similar sized troops, and 3 to 4 times smaller than those observed by CHIVERS (1969) for troops of 11 to 18 monkeys. Not only were the home ranges the smallest yet observed for howlers, the home ranges overlapped extensively and 3 of the troops for which there are adequate data had no exclusive area which was not utilized by other troops (Fig. 2). Most troops traversed their entire home range every 3 to 10 days. On the average, 94% of each troop's home range was utilized by other troops at least several times a month, and multiple use of certain areas was common. This contrasts sharply with the 3 to 5% home range overlap per month on Barro Colorado. Figure 3 compares the relative topography of the home ranges observed in three studies. After the first 2 weeks of research spent in ascertaining the home range boundaries in the present study, the boundaries did not vary during the remaining 8 weeks of observations. This suggests that these howlers may not be as 'nomadic' as those on Barro Colorado Island (CHIVERS, 1969).

Clearly the howlers at the study site had adapted to living in much closer contact than has yet occurred on Barro Colorado Island.

The remainder of the 1,000 acre forest could not be easily surveyed since there were few trails. Having walked for miles along various perimeters of this forest and others along the Pacific coast of southwestern Panama, we believe that the population

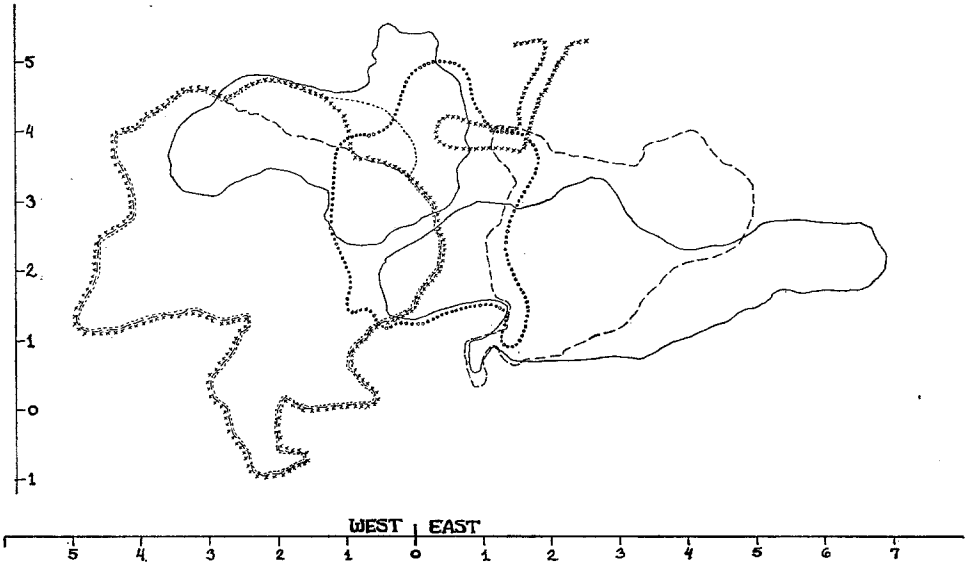

Fig. 2. The home ranges of the 8 troops at Hacienda Barqueta, 1971. Additional troops entered the study area from the east and west but could not be well studied.

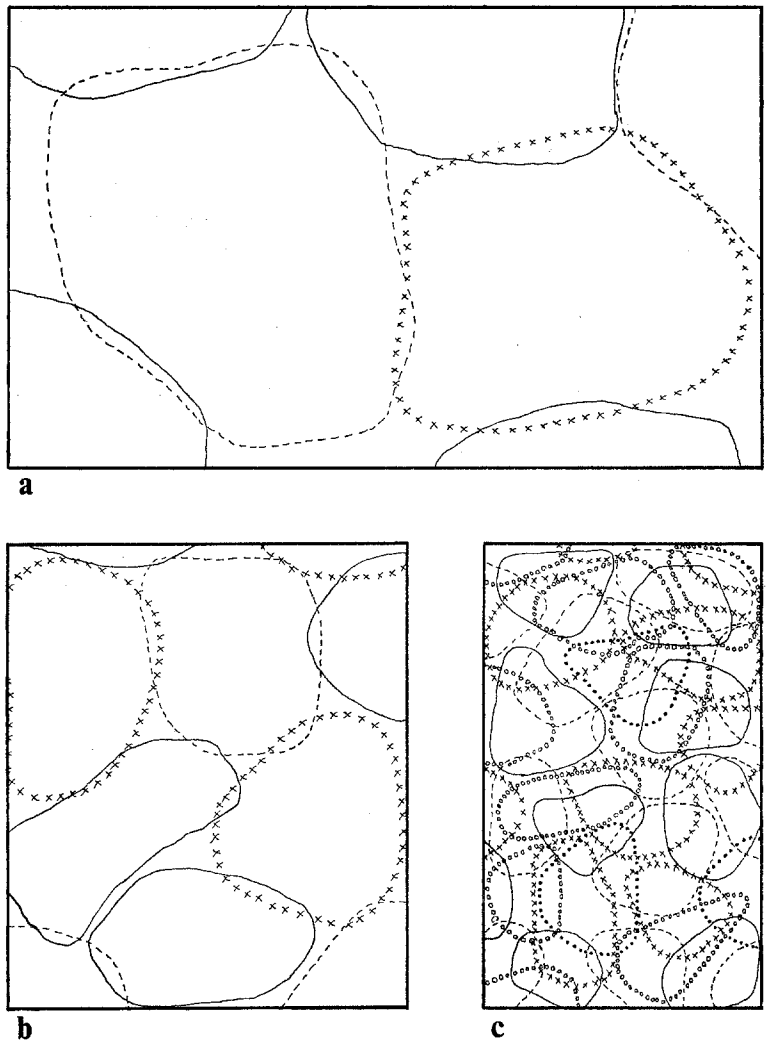

Fig. 3. Comparison of the home ranges of the howlers, (a) on Barro Colorado Island, 1932 (CARPENTER, 1934); (b) on Barro Colorado Island in 1967 (CHIVERS, 1969); and (c) southwestern Panama, 1971.

density found in the 50 acre study area is similar to that found throughout hundreds if not thousands of acres of forest of the area.

DISCUSSION OF POPULATION DENSITY

Three major questions have recurred several times in the literature on Barro Colorado howlers (SOUTHWICK, 1962, 1963; CHIVERS, 1969): how large can the population grow, will growth cause behavioral and social changes, and what will limit further growth? The data from the present study indicate that population density can exceed the level which has been observed on Barro Colorado by at least 12

times. There are several possible mechanisms of population control in howlers and other primates. The combined data from Barro Colorado and the present study lead to a consistent evaluation of these mechanisms.

Limited food resources could possibly establish the ceiling of population growth; but none of the observations on Barro Colorado or at the southwestern Panama site indicate that these populations have reached the limits set by food abundance. Howlers' preference for such abundant foods as the leaves of common trees, along with flowers and fruits, would seem to set a very high population ceiling. The high population density in the present study showed no sign of exhausting or damaging the food trees even in dry season when several species lost their leaves.

CARPENTER (1934) reported that he may have seen an ocelot attack and injure a young howler. No other reports of natural predation on howlers are known by the authors. In many areas of Central and South America, humans trap or hunt howlers for food or sport; but on Barro Colorado Island and at the present study site there has been no indication of recent molestation by man.

Intraspecific aggression appears to be uncommon in howlers. Most observers have found wounded animals, but such injuries could have resulted by falling from the trees. CARPENTER (1934) reported an incident that strongly indicates that a solitary male was wounded by troop males in the process of becoming assimilated into a troop. COLLIAS and SOUTHWICK (1952) saw an adult male attack an infant, bite its tail in half and throw it to the ground. In the present study we observed a troop come across a resting solitary juvenile. The juvenile made a quick, inaccurate jump, fell 30 feet to the ground and incurred multiple injuries on the face and leg. The bleeding juvenile crawled from the forest edge to a tree near our tent. After a week it was recovering strength and returning to the forest for several hours each day. Due to the differences in observers and reporting, it is difficult to compare the precise frequency of aggression on Barro Colorado Island with the present study; but there do not seem to be any major differences in aggression between the studies. Mild threats, lunges, play fights, etc., have been reported by all observers, but severe aggression among howlers is rare. There is no indication that the high population density of the present study caused increased aggression compared with Barro Colorado. At present there is no evidence that serious fights or attacks occur often enough in howler troops to limit population growth.

Howlers fall from trees for reasons other than those related to aggressive interactions. CARPENTER (1934) observed infants that fell to the ground and were retrieved by their mothers. On several occasions during the present study, infants and juveniles were observed to make hazardous jumps in order to travel with their troops. The adults often made long jumps between trees with no 'concern' for older infants and juveniles that traveled with the troop. These young animals often showed prolonged hesitancy—making numerous incipient jump movements or looking for easy alternative routes—before following after their troops. The young animals that eventually made the long jumps sometimes landed in low scrubby undergrowth or on the ground. None were visibly injured; but such falls could conceivably result in injury, separation from the troop or death. The fact that 4 of the 6 lone howlers were juveniles does suggest that animals at this age are prone to becoming separated from their troops and

that they may not survive long once separated. It is difficult to evaluate what importance this cause of mortality might play on Barro Colorado or at the present study site.

COLLIAS and SOUTHWICK (1952) presented strong evidence that parasites and disease can reduce howler populations in a brief period of time. With higher population density, serious epidemics are more likely to affect larger percentages of the population. This higher risk does set probabilistic ceilings on population growth; but some populations may far exceed expected ceilings before suffering an epidemic. The populations in southwestern Panama could represent such a case.

There may exist physiological or behavioral responses to high population density that could limit population growth. WYNNE-EDWARDS (1962) lists several types of social stimuli that could operate to control population growth by triggering physiological changes to decrease fertility. For howling monkeys WYNNE-EDWARDS identifies the loud intertroop vocal interactions as a likely social stimulus that might inhibit reproductive success at higher population densities. The fact that all the troops except 7-2-0 had one or two infant-1's and several older infants suggests that the reproductive capacity of the animals in the present study was not inhibited. CALHOUN (1962a,b) observed that crowding in rats led to the development of pathological behaviors—such as inappropriate reproductive behavior, poor mothering, and cannibalism—that lowered reproductive success. No such aberrant behaviors were observed in the present study, and conditions were ideal for prolonged behavioral observations at close range (20 to 50 feet). Thus, if there are any physiological or behavioral changes induced by high population density in howlers, they are not apparent at the density observed in this study. Primates have long been typified as adaptable; it may be that primates can tolerate greater variance in crowding without developing physiological or behavioral abnormalities than would be predicted from other species.

SUMMARY

Since 1931 several studies have been conducted on howling monkeys (*Alouatta villosa*) on Barro Colorado Island. There have been significant changes in population size and intertroop interactions over the decades; and several researchers (SOUTHWICK, 1962, 1963; CHIVERS, 1969) have raised such questions as (1) How much crowding can the troops tolerate? (2) Will behavioral adaptations occur as crowding increases? (3) What mechanisms will limit the population growth?

The present study on the same species of howling monkeys in a different part of Panama has yielded data relevant to these questions. The population density was 21 times greater than that on Barro Colorado in 1932 and 12 times that on Barro Colorado in 1967. The average home range size was 12.1 acres, and troops traversed their entire range every 3 to 10 days. Three troops occasionally joined and traveled together, partially intermingling, to produce 'supertroops' of 38 to 65 animals. All other troops showed mutual fear and avoidance. Home ranges overlapped extensively: the average troop shared 94% of its home range with other troops, and most troops had little or no area of exclusive use. There were no signs that the howling

monkeys were exhausting their food supply or were experiencing decreased fertility. Several factors that could function in population control are evaluated.

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