A Preliminary Study of Mantled Howling Monkey (*Alouatta palliata*) Ecology and Conservation on Isla de Ometepe, Nicaragua

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Introduction

In this paper we examine the ecology and conservation status of mantled howling monkeys (*Alouatta palliata*) on Isla de Ometepe, Nicaragua (Fig. 1). Ometepe (11°40'N and 85°50'W) is a volcanic island located within the southeastern edge of Lake Nicaragua. It is the largest island in the world (276 km^2) situated in a fresh water lake, and is characterized by zones of dry deciduous forest, cloud forest, forest-shaded coffee plantations, agricultural fields, and other areas cleared for human use. Human impact has been most severe in zones between the lake and the foothills of the volcanoes. The cloud forest that covers the slopes of the volcanoes is characterized by abrupt changes in elevation and habitat, and remains relatively undisturbed. Two volcanoes dominate the island. Concepción, the tallest, is active and rises to a height of 1,610 m. Maderas, the other volcano is dormant and measures 1,394 m at its summit (Salas Estrada, 1993). It is estimated that Ometepe has been separated from the mainland for approximately 10,000 years (Gillespie,1994), however, little is known concerning when nonhuman primates first arrived on the island, and the degree to which howling monkey populations on Ometepe differ genetically, behaviorally, or ecologically from howling monkey populations in other regions of the Neotropics. White-faced capuchins (*Cebus capucinus*) also occur naturally on the island.

Nicaragua is a country rich in natural resources, with approximately one-third of its tropical lowland rainforest remaining intact. However, as a result of political instability and civil war, there have been virtually no published studies of the ecology and conservation status of Nicaraguan primates over the past 25 years (Crockett *et al.*, 1997). With the assistance of the Nicaraguan Government, the University of Illinois, Universidad Nacional Autonoma (Managua), Universidad Nacional Autonoma (Leon), Universidad Centro Americana, Universidad de Mobile (Nicaraguan Campus), and the Molina family, a research and educational foundation (Fundación Ometepe) was established in Nicaragua. One of the main goals of Fundación Ometepe is to study the behavior, ecology, and demography of primate populations in Nicaragua in order to develop both community-based and internationally-based plans for the conservation and management of Neotropical forests.

In December 1997, we established a biological field station on the eastern part of the island (Estación Biológica de Ometepe) near the settlement of San Ramón (see Figure 1), and initiated a preliminary field investigation of the behavioral ecology of mantled howling monkeys (*Alouatta palliata*). The genus *Alouatta* represents the most geographically widespread taxon of New World primates (Strier, 1992; Crockett, 1998). Howling monkeys range from southern Mexico, throughout Central America and the Amazon Basin, and as far south as northern Argentina (Hershkovitz, 1977). Although most of the six currently recognized howler species are reported to live in relatively small groups composed of 1-2 adult males and 1-2 adult females (mean group size <10 individuals; Crockett and Eisenberg, 1987; Chapman and Balcomb, 1998; Fedigan *et al.*, 1998), mantled howlers (*A. palliata*) are unusual in that group size tends to be large (12-20), containing 2-4 adult males and 3-9 adult females (Crockett and Eisenberg, 1987; Chapman and Balcomb, 1998; Fedigan *et al.*, 1998). Compared to other *Alouatta* species, sexual dimorphism in body weight (Ford and Davis, 1992) and hyoid size (Crockett and Eisenberg, 1987) in *A. palliata* are reported to be low, suggesting that factors contributing to reproductive competition and mate choice in this species may differ significantly from those present in more dimorphic howler species.

In this paper, we present the results of a preliminary field study of mantled howling monkeys conducted on Isla de Ometepe, Nicaragua. In particular, we examine: 1) group size and composition; 2) feeding behavior and the plant species composition of the diet; 3) the physical structure of the habitat

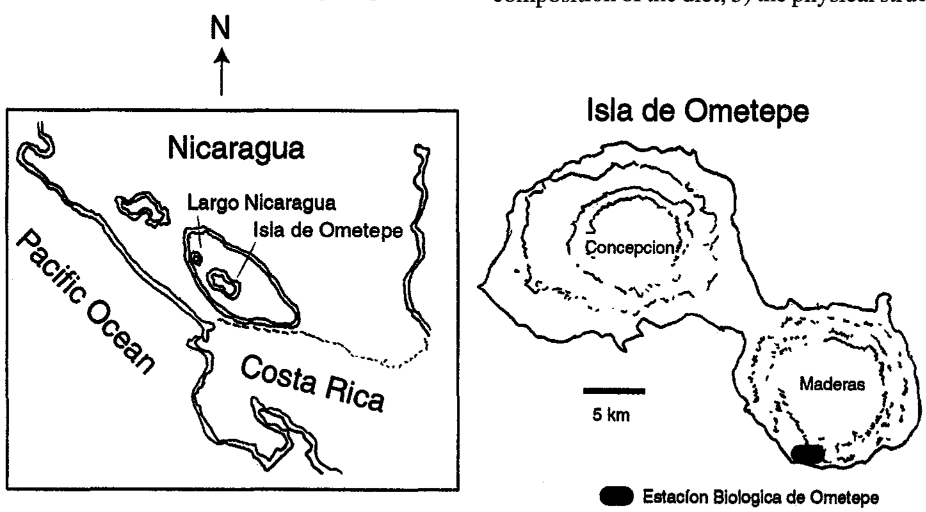

Figure 1. Map of Nicaragua showing Isla de Ometepe and the location of the Estación de Ometepe.

of the study group. In addition, we have developed an initial set of recommendations for effective community-based conservation efforts to protect the wild primate populations on Ometepe.

Methods

From December 1997 through January 1998 and July through August 1999, we conducted a field study of a group of approximately 20 mantled howling monkeys (Volcano Group) inhabiting a 4 ha area on the foothills of Volcan Maderas. Additional observations of this group were conducted in July and August, 1999. The group's home range is part of Estación Biológica de Ometepe, and was characterized by a dry semideciduous forest of low to medium stature (Salas Estrada, 1993). Rainfall in this part of Nicaragua averages from 1200-1900 mm per year, with most rain falling during the months of May through November (Salas Estrada, 1993). Tree species characteristic of this type of forest include *Albizia guachapele* (Mimosaceae), *Brosimum alicastrum* (Moraceae), *Coccoloba floribunda* (Polygonaceae), *Ficus cotinifolia* (Moraceae), *Hymenaea courbaril* (Caesalpiniaceae), *Bursera simaruba* (Burseraceae), *Lonchocarpus latifolius* (Fabaceae), and *Malpighia* sp. (Malpighiaceae) (Salas Estrada, 1993).

Howlers in our main study group were observed for 62 hours on 23 days. Data on activity budget, ranging patterns, diet, and the location of feeding trees were compiled. Behavioral data were collected at 2-minute intervals throughout the day using a focal animal time sampling technique. We also noted the size of the group or subgroup, identified, marked and mapped the location all trees howlers were observed to feed in, and collected data on the size, diameter at breast height (DBH), and crown diameter of the feeding trees. Subgroups were recorded as the number of howlers simultaneously visible to the observer. We estimate that each subgroup represented the number of howlers present within an area with a radius of 25 m.

A trail system and map of the study group's home range was constructed using a Brunton transit mounted on a tripod. In all, the coordinates of 116 trail markers and 84 trees were included on the field map (total of 200 mapped points). These points encompassed an area of 48,125 m² (4.8 ha). The distances between nearest neighbor trees of the same species and the distances that howlers traveled between successive feeding sites were calculated directly from the field map.

In order to identify the structural characteristics of the forest, we divided the study group's home range into seventy-seven 25 x 25 m quadrats. Each quadrat was plotted on the field map, and measurements of tree height, density, and degree of human disturbance were compiled. We interviewed members of the local community in order to identify whether trees important in the howling monkey diet were among the set of species commonly cut by island inhabitants for firewood, canoes, house construction, or other purposes. A second group of howlers (Beach group) was also monitored for information on group size, composition, and the presence of dependent young.

Results

Size and Composition of Study Groups

Two groups of howlers were censused daily to determine the size and composition of the groups. The Beach group contained five adult males, five adult females with dependent offspring, six adult females without dependent offspring, two preadults, and five infants (total 23 individuals). This group was found to spend much of its time each day exploiting a small (1 ha) isolated patch of tall remnant forest adjacent to the lake. This fragment contained a large number of fig trees that were fruiting in December and January. The howlers reached this forest patch by going to the ground and crossing the main road on the island. In July and August 1999, however, this group was never observed to cross the road and spent all of its time in an adjacent 8 ha patch of forest.

The Volcano group contained at least 5-6 adult males, five adult females, five preadults, and two infants (18-20 individuals). This group was frequently observed to split into smaller subgroups during the day. Mean subgroup size was 8.4 individuals (±3.5; range 3-17). Subgroups represent the number of howlers simultaneously visible to the observer. The average number of adults males per subgroup was 3.1 (±1.4) and the average number of adult females per subgroup was 2.9 (±1.5). Although we failed to observe any aggressive encounters between members of the same or neighboring groups, several of the adult males in each study group showed evidence of facial scars, cut lips, and broken digits, which would suggest that although adult males tolerate the presence of several other adult males in a group, fighting among adult males can be extremely severe.

Feeding Patterns and the Distribution of Feeding Sites

During the course of the dry season study (December-January), 84 trees which the howlers fed in were marked, identified, and mapped. Seventy-four of these trees were of nine species (87%). They included *Spondias mombin*, *Cecropia* spp., *Bursera simarouba*, *Gliricidia sepium*, *Calycophyllum candidissimum* and *Lonchocarpus parviflorus*. The howlers consumed leaves from 53% of these trees, flowers from 32%, and fruits from 14%. On average, each howler subgroup fed in 3.0 trees per observation hour. Subgrouping may enable members of a single large group to exploit more effectively a set of small clumped feeding sites that are scattered across their home range (see below).

In order to examine howling monkey feeding and ranging patterns, the nearest neighbor distances between feeding trees of the same species and distances traveled between feeding sites were calculated. As indicated in Table 1, tree species exploited by howlers tended towards a clumped distribution. Mean nearest neighbor distances in five of 10 species were less than or equal to 35 m, and in two of the remaining cases mean nearest neighbor distances was less than 50 m. The greatest distance howlers traveled between successive feeding sites within a resource clump was 20 m.

We also examined the distribution of feeding sites by counting the number of trees in each of the seventy-seven 25 x 25m

Table 1. Spatial distribution of feeding trees exploited by mantled howlers on Ometepe.

Tree Species	No. of trees	Mean NN distance m	Range NN distance m
Gliricidia sepium	21	9	4-25
Chaperno	12	41	5-97
Spondias mombin	11	29	9-140
Purple Flower	9	24	2-27
Cecropia sp.	8	35	7-88
Bursera simaruba	5	30	12-63
Melastomaceae	4	84	64-142
Schizolobium sp.	3	106	17-201
Hymenaea courbaril	2	49	-
Calycophyllum candidissimum	2	225	-

NN = Neareast Neighbor

quadrats overlain on our field map. As indicated in Table 2, 45 of 84 howler feeding trees (53.5%) were distributed in only 10 quadrats (an area of 0.64 ha or 13% of the home range). The greatest number of feeding trees in any single quadrat was seven. In contrast, howlers were not observed to feed in 42 of these quadrats (2.6 ha or 54% of the home range). The distribution of feeding trees exploited by the howlers on Ometepe differed significantly from a Poisson or random distribution (χ^2= 21.805, df = 3, p<0.01). Based on calculations of the coefficient of dispersion (CD = 1.4574), these resources are best characterized as local aggregations of clumped feeding sites. Given the relatively large concentration of feeding trees in circumscribed areas of their home range, even during the dry season, these howlers were able to exploit small forest fragments successfully.

Table 2. Distribution of feeding trees used by howlers at Ometepe.

No. of feeding Trees per quadrat	No. of quadrats
0	42
1	11
2	14
3	3
4	3
5	2
6	0
7	2

Comparison of Howler Feeding Trees and Sample Trees

A comparison of the height and DBH of howler feeding trees with the height and DBH of trees sampled within twelve 15 x 4 m quadrats (720 m²) is presented in Table 3. Of the 67 trees measured in the sample quadrats, mean tree height was 9.2 m and mean DBH was 17.5 cm (range 5-52.5 cm; trees of diameter <5cm were not included in the sample). In contrast, data collected on 74 trees fed in by howlers indicate a very different height/DBH profile. Howler feeding trees were significantly taller (13.7 m ±2.9; χ^2 = 547, df = 3, p<0.001) and had a greater DBH (110 cm ±78; χ^2 = 2 314, df = 3, p<0.001) than trees in our sample plots. In the case of Ometepe howlers, 80% of trees fed in had a DBH >41 cm. Trees of this diameter accounted for only 10% of the trees sampled in the groups' home range.

Forest Characteristics

A major focus of our research was to determine the degree to which the forests exploited by howlers were impacted by human activity. This was accomplished by evaluating the vegetation and structural characteristics of 67 contiguous 25 x 25 m quadrats (4.1 ha) within the home range of the study group. This area represents over 85% of the study group's range. Within each quadrat the following were recorded: canopy height, the number of trees of at least 2 m in total height, degree of understorey vegetation, the number of *Cecropia* trees (an early successional plant species), and evidence of human disturbance.

Table 3. Dimensions of trees in sample plots and trees fed in by howlers.

	Tree height (m)						
	0-5	6-10	11-15	16-20	>20	Total	
Sample plot							
(N)	10	38	17	2	0	67	
%	14.9	56.7	25.3	2.9	0		
Feeding trees							
(N)	0	8	54	17	2	81	
%	0	9.8	66.6	20.9	2.4		
	DBH (cm)						
Total	**5-20**	**21-40**	**41-60**	**61-80**	**81-100**	**100+**	
Sample plot							
(N)	46	14	7	0	0	0	67
%	69.6	20.8	10.4	0	0	0	
Feeding trees							
(N)	2	14	14	2	9	40	81
%	2.4	17.2	17.2	2.4	11.1	49.3	

Quadrats that evidenced recent human activities such as cut trails and forest cleared for pasture, agriculture, and logging were scored as human-impacted zones. These accounted for 40.3% (N = 27 quadrats) of the study area (three additional quadrats showed evidence of both human disturbance and natural edge habitat; Table 4). Human-impacted areas were characterized by trees of low stature and a well developed understorey. In over 51% (N = 14) of these quadrats, 75-100% of the forest floor was covered with low shrubs and grasses. Quadrats that included stream beds and tree fall gaps are referred to as natural edge zones (Table 4). Natural edge zones made up 14.9% (N = 11 quadrats) of the study area. Trees of between 10-15 m in height were found in 64% (N = 7) of these quadrats. Natural edges tended to have limited ground cover (55% [N = 6] of the quadrats within this zone were characterized by 0-25% ground cover). This may reflect the fact that many of these quadrats bordered seasonally dry stream beds formed from volcanic rock which served as a barrier to plant growth. *Cecropia* trees were found in eight of 11 natural edge quadrats and averaged 4.9 trees per quadrat (range = 0-19). This shade-intolerant, pioneer genus requires high light levels for growth and is commonly associated with gap-phase regeneration (Denslow and Hartshorn, 1994). Fifty-six percent (N = 54) of all reported *Cecropia* trees were located within this zone.

The interior forest zone is comprised of quadrats that exhibited little to no evidence of recent human-disturbance or natural edges. These quadrats made up 37.3% (N = 26) of the study area. Trees of 10-15 m in height were found in 92% (N = 24) of interior zone quadrats. More than half of these quadrats also contained trees that were greater than 15 m in height. Understorey density was highly variable in these quadrats. *Cecropia* averaged 1.2 trees per quadrat (range = 0-6).

Table 4. Comparison between habitat types found within the howler home range and the distribution of feeding trees.

Habitat type	% Area	% Howler feeding trees
Human Edge	40.3%	16.0%
Natural Edge	16.4%	23.2%
Forest Interior	38.8%	58.9%
Human/Natural Edge	4.4%	1.7%

As indicated in Table 4, there was a significantly greater number of howler feeding trees in the interior forest zone than expected based on the availability of this habitat type in the group's home range ($\chi^2 = 5.8$, df = 1, $p<0.02$). For example, 58.9% of trees fed in by howlers were located in areas of minimally disturbed forest. This area accounted for only 38.8% of the group's range. There was a significantly smaller number of howler feeding trees in areas of the forest altered by human interference ($\chi^2 = 8.1$, df = 1, $p<0.01$). Areas impacted by human activities accounted for 40.3% of the home range but contained only 16.0% of feeding trees. In natural edge zones, however, the howlers used feeding trees in proportion to the size of the area exploited ($\chi^2 = 1.6$, df = 1, $p>0.10$). These data suggest that tree species regenerating in areas heavily impacted by recent human activity are unlikely to provide sufficient resources to support mantled howling monkeys.

Deforestation

Many of the families living near the field station regularly enter the forest to extract wood for cooking and as building materials. We therefore interviewed members of the local community to identify which trees were most frequently harvested. Several tree species important in the howling monkey diet, such as *Gliricidia sepium* and *Calycophyllum candidissimum*, were among the most common tree species used for firewood. Effective conservation policies on Isla de Ometepe must include working with local residents in finding alternative sources of cooking fuel.

Discussion

Based on our preliminary findings, it appears that the remaining forests on Isla de Ometepe support a large population of mantled howling monkeys. These howlers were found to exploit patches of fragmented forest located near the margins of the lake, on the foothills of the volcano, in areas impacted by the cultivation of shade coffee, and in undisturbed cloud forest going all the way up to the top of the volcano. Areas clearcut for pastures or cultivated for other crops such as corn, plantains, and rice do not support howling monkeys. However, we have observed howlers using extremely small strips of forest and tree-lined fence rows to move from one area to another or to migrate between groups. From a conservation perspective, even small corridors connecting forest patches appear to be effective in facilitating dispersal.

The size and composition of the two study groups observed on Ometepe were generally consistent with reports of mantled howling monkeys from several sites in Mexico, Costa Rica, and Panama (Estrada, 1982; Chapman and Balcomb, 1998; Fedigan *et al.*, 1998). Both of our howler study groups were large, however, and both contained at least 5-6 adult males. In fact, we have counted as many as nine adult males residing in the same group (Bezanson, pers. comm.). Based on a comparative study of howler population demography, Fedigan *et al.* (1998) proposed that under conditions of low population density and during the initial stages of forest regeneration, males may exhibit enhanced survivorship resulting in an increase in the number of males per group. On Ometepe, however, it still remains unclear how howler groups are distributed across the island, the degree to which individuals in fragmented forests are isolated from neighboring groups, and whether limited dispersal opportunities frequently result in subadult males and females remaining in their natal groups. A goal of our continued research is to examine age and sex-based patterns of howler dispersal on Ometepe in order to understand better how the density, distribution, and isolation of established social groups impact on individual survivorship and the genetic diversity of howler populations on the island.

Previous studies have indicated that howlers can successfully exploit small patches of fragmented and disturbed forest (Crockett, 1998). In part, this may reflect their ability to use a diet that contains a high proportion of both immature leaves and leaves of early successional plant species. The home range of the Volcano group contained areas of natural edge forest that were characterized by approximately five *Cecropia* trees per hectare. The leaves and fruits of these trees are commonly eaten by howlers (Milton, 1980). However, the ability of howlers to persist under conditions of severe habitat fragmentation has been questioned (Crockett, 1998). Crockett (1998), for example, has suggested that increased exposure to parasite loads, natural disasters, and inbreeding may limit the long-term viability of fragmented howler populations (see also Horwich, 1998). Our impression of the distribution of howlers on Isla de Ometepe is that areas of more continuous canopy cover, including areas of shade-coffee, support a higher density of individuals and groups. In areas of highly fragmented forest, group size may be large, but individuals tend to spend the majority of their time in subgroups composed of 4-8 individuals. Leighton and Leighton (1982) also reported subgrouping in mantled howlers. They suggested that howlers form subgroups when exploiting "locally high densities of preferred food sources that occur in small patches" (Leighton and Leighton, 1982, p.88).

The large number of males residing in our howler study groups may be indicative of limited opportunities for male migration. Given the low levels of genetic diversity which are reported to characterize island populations in general (Crockett, 1998) and isolated groups in particular, effective primate conservation and management programs on Ometepe may require a sustained effort to regenerate forested corridors between isolated forest patches, and in extreme cases the translocation of individuals from the mainland to increase the genetic diversity of the population.

Howlers are not hunted for food or killed as agricultural pests on Ometepe. Occasionally infants are captured by local people as pets. There is no evidence, however, of any organized pet trade on the island. Habitat destruction and forest fragmentation remain the major conservation problems faced by both animal and plant species on Ometepe.

Based on archaeological evidence, humans first colonized Isla de Ometepe some 4000 years ago (Haberland, 1992). The island was used principally as a ceremonial center and its precontact population was small. Today, there are some 40,000 inhabitants on Ometepe (this is double the population just 30 years ago). Although most of the population is concentrated in a few towns (Altagracia, Moyagalpa), the impact of human activity is pervasive. In the area near our field station, clearing of land between the lake and the foothills of the Volcan Maderas has been so extensive that even selective logging is likely to have a severe negative impact on the survival of local howler populations. In order to address these problems, the Fundación Ometepe has purchased several parcels of land between the foothills and the volcano. This area will serve as a buffer zone to limit continued forest destruction, promote forest regeneration, and provide corridors for howler migration and colonization.

Compared to other atelines, *Alouatta* is characterized by an early age at first reproduction and a high intrinsic rate of population increase (Fedigan and Rose, 1995; Strier, 1996; Crockett, 1998). Given their relatively fast life history pattern and ability to colonize regenerating habitats (Crockett, 1998; Fedigan *et al.*, 1998; Horwich, 1998), we are hopeful that our efforts to protect and conserve mantled howling monkey populations on Isla de Ometepe will succeed. However, in order to safeguard the continued survival of wild primate populations in Nicaragua and other areas of Latin America members of the local community, National governments, and International Aid Agencies must work together to develop informed and successful wildlife management policies.

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Testis Symmetry in the Mantled Howling Monkey

Clara B. Jones

Markow *et al.* (1996) studied fluctuating asymmetry (random deviations from symmetry in traits on opposite sides of the body) in the sex combs of two *Drosophila* species and found no evidence for sexual selection in this secondary sexual character, contrary to the predictions of Moller and Pomiankowski (1994). The latter authors argued that symmetry would be positively related to male copulation success and that secondary sexual characteristics would exhibit the