FINAL REPORT

"SURVEY AND ASSESSMENT OF PRIMATE POPULATIONS IN CHOCOCENTE WILDLIFE REFUGE, NICARAGUA"

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I. INTRODUCTION

The tropical dry forest is one of Central America's most threatened ecosystems [Janzen 1988]. More than half of Central America's human population resides along the pacific slope where tropical dry forests are distributed [UNWFP 2005]. Human activities such as logging, firewood collection and agriculture have resulted in dry forest fragmentation and degradation. This habitat loss, along with hunting and human disturbance, has contributed to a decline in wildlife populations associated with dry forests. Primates are particularly vulnerable to habitat loss due to their large body size, slow reproductive rates, and dispersal requirements [Chapman and Peres 2001]. Additionally, primates are often hunted for food or the pet trade, making their populations even more at risk. Not surprisingly, primates are believed to be locally extinct across many dry forest patches in Central America. Loss of primates in these habitats is of particular concern, both because of their intrinsic value and role in successional processes via seed dispersal [Andresen 2000; Chapman and Onderdonk 1998]. This research, funded in part by the Primate Action Fund, describes primate populations and their conservation status (*Alouatta palliata, Cebus capucinus, Ateles geoffroyi*) in an important dry forest protected area.

The Chococente Wildlife Refuge (4800 ha) in southwestern Nicaragua is one of the largest remaining fragments of tropical dry forest in Central America [Sabogal 1992]. Recent observations have indicated that all three of Nicaragua's primate species are found there [Otterstrom 2001, unpublished data]. This study was particularly timely, as Chococente faces a number of threats related to changes in land tenure, human population density, and tourism development in the area. Here we report on the results of an intensive primate survey in the park and the research priorities suggested by our findings. Our goals were to augment our limited knowledge of Nicaragua's primates, determine this population's long-term viability, and identify priorities for improving primate habitat quality and connectivity in the western portion of Central America's largest country.

METHODS

Study Area

The Chococente Wildlife Refuge is located at 11°32'N, 86°12'W, along the southwestern coast of Nicaragua (Fig. 1). The reserve is primarily composed of deciduous upland forests and semi-perennial riparian forests [Sabogal 1992]. Two large watersheds border the southern and northern edge of the reserve where wildlife congregate during dry season months. Patches of non-forested areas are also scattered throughout the reserve (Fig. 2) due to clearing for agriculture and

cattle pasture. In spite of this fragmentation, Chococente is a conservation priority because it maintains stands of high quality dry forest [Sabogal 1992], presents the highest bird diversity along Nicaragua's Pacific slope [Gillespie and Walter 2001], and is a major nesting site for Olive Ridley and Pacific Leatherback turtles [National Marine Fisheries Service and U.S. Fish and Wildlife Service 1998].

In Nicaragua, the government does not hold ownership of land within the majority of its designated protected areas. This poses a challenge to management because human activities such as farming, grazing and tourism may continue despite the need to protect wildlife and vegetation. At Chococente, two groups of investors own approximately 70% of the reserve, including the majority of the forested areas. The remaining land is distributed among 71 subsistence-farming households, which are grouped in small communities throughout the inland portion of the reserve [Otterstrom, unpublished data]. Small farms can increase landscape heterogeneity, but may disrupt forest canopy connectivity and inhibit primate movement.

Primate Surveys

To characterize the primate populations in Chococente, we used line transect sampling [Buckland and others 2001] along with opportunistic directed searches in areas where we expected to find primates based on habitat type or prior reports. We established seven straight-line transects with lengths of 1.25 to 2.5 km (Fig. 2; Table 1). Although longer transects are recommended for primate surveys [Peres 1999], conflicts between landowners (i.e., inability to cross property boundaries in some cases) and landscape heterogeneity (i.e., large pastures and agricultural fields in the line of transects) prevented us from establishing longer transects. Using a year 2000 habitat map based on remote sensing of habitat types, we placed transects such that passage through non-forested areas was minimized, with four transects oriented on a roughly north-south axis and sampling riparian and closed canopy forest, and three transects oriented on a roughly east-west axis and sampling more diverse habitats. Transects were periodically cleared of regrowth during the study period.

Transect data were collected by a team of local investigators. We trained an initial team of four data collectors in June and July 2005 in the methods used in line transect surveys (below), and their proficiency was evaluated several times in July to ensure that they understood all methods and were adept at describing primate group compositions and taking measurements and bearings. The four data collectors are local residents and were employees of Servicios Generales, S.A. (a group of

investors with the largest property holdings in Chococente), which helped fund salaries for the data collectors. Transects were divided into a western (Fig. 2, transects 1-3) and eastern (Fig. 2, transects 4-7) sector. Within each sector, transects were visited on a rotating basis by teams of two local investigators; each team visited one transect per day. Weather permitting, each transect was visited approximately eight times per month, during the periods of August – December 2005 and February – June 2006; an unusually strong wet season forced transect visits to be curtailed in September and October 2005. Observers moved quietly and slowly along the transects, searching for primates. When primates were sighted, location on the transect and perpendicular distance to the center of the primate group were measured. Observers also recorded information on group size, age/sex composition, and trees used for feeding, resting, or locomotion. The chance of groups being counted twice was low, given the rather sedentary nature of howler monkeys. However, observers made certain to note primate movements to avoid double-counting of animals moving in front of data collectors.

Primates other than howlers were very rarely observed in the transects (see Results); we therefore also conducted directed searches in forested areas and areas where spider and capuchin monkeys had previously been reported. Directed searches were conducted at the height of the dry season (March 2006) along watercourses and dry river beds (Fig. 2): because many of the trees in tropical dry forest shed their leaves, primates are known to congregate in riparian forests during the dry season [Fedigan and Jack 2001]. Whenever primates were encountered, the location was recorded with a GPS unit, and the group size and composition were determined.

Vegetation

Forest vegetation was surveyed in order to develop a description of habitat quality along primate survey transects. Using the point-centered quarter method [Cottam and Curtis 1956], we recorded woody vegetation greater than 10 cm DBH at 50 meter intervals along the entire length of each of the primate survey transects. The height, DBH, and species of individual trees were recorded. Additionally we took note of any evidence of recent wildfires or grazing. Woody vegetation was surveyed during the month of January when trees still had leaves and many were in fruit to enable easy identification. Local names were used to identify trees in the field and then we referred to previous botanical collections from the Chococente reserve to positively identify the species [Otterstrom and others 2006].

Data Analysis

Line transect data were analyzed using the program DISTANCE 5.0. Sightings for all transects were combined to determine species-specific effective strip width, density per hectare, and total population size for the study area. Observations more than 50 m perpendicular from the transect (N=12) were censored, since it is improbable that primates could be seen this far off the line; such distances more likely represent recorder error through accidental use of the feet (versus meter) side of the measuring tape. For analyses of seasonality in detection, observations were divided into wet (May-November) and dry (December – April) seasons. To determine if howlers were sighted more often than expected with respect to season, we used a chi-square goodness-of-fit test to compare the actual number of sightings by season with expected number as calculated based on the proportion of transect distance walked in each season. Similarly, to determine if howlers were found more often than expected in certain forest types, we used a goodness-of-fit test to compare the actual number of sightings in different forest types with expected numbers based on the contributions of each forest type to the proportion of transect distance walked in each habitat. Forest vegetation was divided into three classes: semi-perennial riparian forest, upland dry forest, and secondary forest. We classified vegetation at each 50 meter sample point through a combination of several variables, these were: 1) floristic composition 2) vegetation height, diameter and density, 3) observations of vegetation in the field, and 4) topography and distance to rivers.

RESULTS

Vegetation Survey

Results of the vegetation survey confirm that transects covered a wide range of habitat types. Of the sample points 11% were riparian forest, 59% were upland dry forest, and 30% were classified as secondary forest. These classifications were consistent with those made in maps based on remote sensing imagery (Figure 2), although there were some discrepancies. For example, our classification system placed more sample points in upland dry forest than the vegetation map does. This is likely because remote sensing makes classifications based on forest cover, while our classification emphasized species compositions; in many upland dry forest areas the canopy is open and cover is relatively low, even when the majority of trees are mature and late successional tree species are present.

Transect Surveys

Between August 2005 and June 2006, a total of 666.9 km of transect data was collected, and primates were recorded a total of 168 times. Transects differed somewhat in encounter rates (Table 1), with rates of 0.05 to 0.36 encounters per kilometer. Mantled howlers were encountered 162 times, for an overall encounter rate of 0.24/km. Effective strip width (ESW) was estimated to be 32.7 m. Based on these calculations, the density of howlers is estimated to be 0.43 individuals/ha. Given a study area of approximately 4,800 ha, an estimated 2,066 howlers are estimated to live in and around Chococente reserve. In contrast, capuchins were encountered only six times during line transect walks, for an encounter rate of <0.01/km. All but one of the capuchin sightings took place on the transect near the Escalante River, which forms Chococente's southeastern border. In spite of scattered reports by reliable community members, and our own directed searches (see below), spider monkeys were never observed by the PI's or the project's data collectors.

Of the howlers sighted during transect visits, two appeared to be sick (due to lethargy and a tendency to remain in the same area over several days); a dead howler (cause of death unknown, but not shot) was also found on one transect walk. Other mammals were observed; these included white-tailed deer, porcupines, and squirrels. A cat sign (size consistent with ocelot or jaguarondi) was observed during transect walks. In all transects, signs of extensive cattle grazing and trampling were observed, and cattle were frequently encountered in all transects, both in more remote areas of dry forest and in the riparian forests which comprise favorable primate habitat in Chococente.

During the transect runs, lone male howlers were sighted 3 times, lone females 3 times, and lone females with associated juveniles 3 times. One group of two females was also observed. Bisexual groups of howlers were sighted a total of 152 times. Observed group sizes ranged from 2 to 40 individuals, with between 1 and 6 adult males, 1 and 20 adult females, 0 and 8 juveniles, and 0 to 8 infants in each group. Average group compositions are presented in Table 4, with each sighting treated as an independent observation. Many of these sightings probably represent repeated encounters over time with groups whose home ranges overlap with areas sampled by the transects. Our data do not allow us to discriminate between repeat counts of groups, so the average values in Table 3 may include repeated counts of some groups.

The capuchin groups sighted ranged in size from 3 to 19 individuals (average size = 13.0 ± 6.2 S.D.; N = 6). All groups were bisexual, with an average of 2.5 ± 1.2 adult males (range 1-4), 6.7 ± 2.4 adult females (range 3-10), 2.7 ± 1.6 juveniles (range 0-5), and 1.3 ± 1.0 infants (range 0-2).

Because capuchins would flee immediately upon sighting human observers, it was difficult to obtain complete group counts, and the above numbers may significantly underestimate capuchin group sizes at Chococente.

Directed Searches

In March of 2006, we covered over 23 km of roads, trails, and streambeds as part of an opportunistic, directed search of primates (Fig. 2). During this time, a total of 192 howlers and 5 capuchin monkeys were observed during 24 encounters with primate groups, primarily along the Río Escalente (Fig. 3). Additional sightings were recorded in riparian habitat of the Talolinga, Tempate, Acayo, and La Palma watersheds. As reported at other forested sites, it did appear that howlers at least were congregating in riparian habitats, with at least 116 individuals sighted in one morning during a ~3 km walk along the banks of the Río Escalente. Of the individuals sighted, 61 were adult males, 87 adult females, 27 juveniles, and 22 infants, belonging to approximately 21 groups; one adult male was sighted alone, and a bachelor group of two males was also observed. In some areas, particularly along the banks of the Escanlente, the density of howlers was so high during the search period that it was not possible to determine how many groups of howlers there were – the riparian forest had become so crowded with howlers that there was often not more than 50 m separating clusters of primates, making it difficult to characterize the composition of bisexual groups. The group compositions (counting clusters of animals as separate groups, even when separated by <50 m) are presented in Table 3. The group compositions observed during these periods are notable for their relatively low proportions of males to females, although ratios of immatures and infants to females are similar to those observed for groups encountered during line transect surveys.

Seasonal Effects

Although primates were encountered slightly more often than expected in the dry season, primate encounter rates did not differ significantly from expected frequencies with respect to season ($\chi^2 = 0.47$, $P = 0.492$, N = 168). However, the encounter varied greatly from month to month (Table 3), and encounter rates on a monthly basis differed significantly from those expected based on proportion of transects walked per month ($\chi^2 = 43.37$, $P < 0.001$, N = 168). In particular, the number of encounters was lower than expected in August and September 2005, and higher than expected in November 2005 and May and June of 2006. In spite of the perception by investigators

and data collectors of increased primate density during the dry season (particularly in riparian habitat), these differences do not have a clear relationship with seasonality. They do, however, emphasize the importance of collecting data over several months in order to obtain a more accurate estimate of primate density in an area.

Vegetation Effects

Transects sampled all available forest types within the reserve, to better investigate the relationship between habitat type and primate density. Primates were encountered significantly more often than expected in riparian habitat, and less often than expected in secondary forest (χ^2 = 13.00, P = 0.005, N = 168; see also Fig. 3). These differences are reflected in differing density estimates for each habitat type from DISTANCE: 0.44 ind/ha with an ESW of 32.3 m in dry forest, 0.64 ind/ha with an ESW of 32.4 m in riparian forests, and 0.29 ind/ha with an ESW of 42.4 m in secondary forest. The larger effective strip width of transect segments in secondary forest presumably reflects higher primate visibility in areas with more open canopies. The low densities of howlers (and presumably other primate species) in secondary versus dry and riparian forests in particular emphasize the importance of the latter habitat types in maintaining Chococente's primate populations.

DISCUSSION

In 2001, a Nicaraguan biology student conducted a preliminary survey of primates in Chococente along short (none longer than 500 m) transects placed in areas where locals reported monkeys being present. This initial survey found several groups of spider and capuchin monkeys (Figure 3); howlers were so abundant that they were not recorded (Otterstrom, unpublished data). The methods used in this small study differed from ours in that transects were located specifically where primates were expected to be found, thus encounter rates should be higher than with the more random placement of our transects. Nevertheless, based on these data and on previous experience in the reserve we expected to find high numbers of monkeys, particularly since our transects covered some of the same areas as the previous survey. It has therefore come as a surprise to us that our observations are largely limited to howler monkeys and only a few capuchins largely confined to riparian forest along the border of the Río Escalente. Although some reliable informants report the presence of spider monkeys, no evidence of any sort was recorded during our survey, suggesting that only a handful of individuals remain in Chococente. It thus appears that the

primate population in Chococente has suffered a decline during the last few years; below we discuss population characteristics, threats to conservation, and future outlook for management in Chococente.

Comparison to Other Primate Populations

The group sizes and compositions of primates in Chococente reveal to a certain extent the kinds of threats they face; because of limited sample sizes, we will consider only the demographic characteristics of Chococente howlers in depth. The demographic characteristics of howler populations often reflect recent group history [Chapman and Balcomb 1998]: parameters such as group size and age-sex structure change in response to habitat disturbance or degradation. For example, howler densities are reduced in areas where they are hunted [Peres 1997] or during periods of resource shortages [Milton 1982]; densities may become elevated in areas rapidly being deforested as animals become crowded in remaining habitat [Baldwin and Baldwin 1972]; and deforestation may limit dispersal, resulting in changes in group composition and mortality of certain age-sex classes [Clarke and others 2002a; Clarke and others 2002b; Cristóbal-Azkarate and others 2005]. Therefore, demographic parameters can be considered to infer the suitability of a habitat for long-term occupancy by primates, in that primates in unfavorable environments are not expected to demonstrate demographic patterns characteristic of healthy populations (e.g., larger group sizes or high reproductive rates).

The density and group compositions of howlers at Chococente seem to fall well within the range of variation demonstrated by the species (Table 4). Howler densities are "average" for the species, suggesting that populations are experiencing neither chronic resource scarcity nor rapid range contraction. Although the ratios of immatures to adult females and infants to adult females are towards the low end of the range of values observed for the species, they are higher than those observed for populations clearly under high pressure, and are very similar to those observed in the nearby site of Mombacho Volcano, Nicaragua. Thus, the population of Chococente howlers is apparently reproducing at a normal rate. Taken together, these results suggest that forests in Chococente are suitable for occupation by howler monkeys, at the very least. The low density of primates in Chococente may reflect not a deficiency of resources *per se*, but rather other kinds of pressures (e.g., hunting) which impact the populations.

Possible Causes of Declines in Chococente's Primate Populations

The decline in primate populations in Chococente over the last five years has coincided with a period of highly unstable land tenure in the reserve and little to no formal management and monitoring of forested areas by the Nicaraguan environmental ministry. Until the late 1990's, land in Chococente was in the hands of cooperatives of small farmers. However, many cooperatives and holders of small parcels have sold off their land, usually to foreign investors hoping to develop resorts and/or ecotourism ventures. Some landowners have demonstrated genuine interest in wildlife conservation; others are primarily interested in recouping financial investments as quickly as possible through development projects. Oversight of the reserve by the environmental ministry (MARENA) is non-existent. MARENA maintains a ranger station in Chococente for monitoring of turtle populations; we have invited rangers from the MARENA to participate in data collection (this would be the only patrolling activity by the rangers in the forest areas), and although they expressed interest and attended a training meeting, they never did accompany our team of data collectors on any transect visits.

In fact, MARENA itself had recently proposed changing the reserve's boundaries in order to better accommodate the development of a luxury housing complex planned inside the southeast of the reserve. MARENA has formally approved this development which will abut the riparian habitat of the Río Escalente. Our data clearly demonstrates that this riparian habitat is vital for both howlers and capuchin monkeys. Other organizations currently working within the reserve (primarily FFI) have expressed interest in collaborating with us to extend the primate monitoring into a three-year program in order to measure the efficacy of management plans. Unfortunately, at this point FFI is redirecting their available research funds towards collecting expeditions, and it is unclear if they will maintain monitoring programs of primates and other organisms that they had initially planned.

As cooperative members leave their lands, they cease to monitor resource use in what were once their forested areas, meaning that there is no local, community-based control on logging and hunting. For example, during our study we learned that a cooperative in the process of selling their lands and had therefore (illegally) logged an area of old growth forest prior to sale. While consolidation of lands into a few hands potentially makes it easier to arrive at agreements about how land is used, it can also leave these forests vulnerable to overexploitation if landowners do not maintain a constant presence in the area. These problems have been exacerbated by the construction of a paved road into the western sector of the reserve; while this has greatly facilitated

travel for the reserve's communities, there is no monitoring of wildlife going in or out, and this has become a major route for the traffic in sea turtle eggs (and presumably other wildlife products).

Local people repeatedly cited deforestation and habitat fragmentation as also being behind primate declines in the area. Although there are still large areas remaining of tropical dry and riparian forest, these suffer from extremely high levels of disturbance. Cattle are found throughout the reserve, including in forested areas, with unknown (although probably negative) consequences for ecological processes in the reserve. Deforestation outside of the reserve also has serious impacts on primates: as more of the areas surrounding protected areas are converted from forest and traditional "biodiversity-friendly" production systems to highly modified anthropogenic land uses, the connectivity between reserves is reduced, isolating small populations and leaving them vulnerable to extirpation due to disease, predation, or other processes which reduce population size. Low reproductive rates, hunting pressure, and habitat fragmentation/isolation have probably acted synergistically to result in a primate crash in the reserve. Additionally, improved roads within Chococente have made primates vulnerable to human predation pressure through improved access for poachers. Within the reserve, high quality forest and riparian fragments may not be large enough to support species such as spider monkeys, which have large home ranges and specialized diets. Even when sufficient resources do exist, spider monkeys in particular are being removed from the population more quickly than they can reproduce themselves; and deforestation outside of the reserve has left Chococente isolated and without sources of emigrants to reestablish primate populations. Such vulnerabilities make projects such as the housing development along Chococente's southeastern border all the more worrisome.

As a case study, the situation of primates in Chococente is exemplary of scenarios playing out throughout western Central America, in which weak central governance coupled with growing population pressure and socioeconomic inequities have resulted in the defacto management of parklands by private landowners, many of whose priorities are at odds with the goals of biodiversity conservation. The Chococente case also illustrates the apparent failure of diffuse conservation initiatives funded through multi-lateral organizations to protect wildlife in the face of rapid land development and radically shifting land tenure.

Conservation Action and Management Recommendations

This survey project has resulted in a number of synergistic activities which will enhance and improve primate conservation in the region of southwestern Nicaragua. This project has coincided

with the formation of Paso Pacífico, an non-profit organization founded by co-PI Otterstrom and dedicated to conservation of Central America's remaining tropical dry forests. Paso Pacífico's early research will focus on spider monkey conservation in this highly fragmented area. Otterstrom has been working with a number of private landowners with holdings to the south of Chococente near the Costa Rican border. These properties have large forest fragments with populations of spider monkeys. Paso Pacífico will advise landowners on developing conservation plans. Related to this, Suzanne Hagell (Northern Arizona University) is planning on carrying out her doctoral thesis on spider monkeys in the area. This work will focus on the extent to which spiders are able to occupy disturbed habitats and identify characteristics of habitat fragments and corridors associated with use by spider monkeys. This research will relate to longer-term plans by Paso Pacífico to identify remaining forest fragments in southwestern Nicaragua suitable for primate occupation, improve connectivity between these areas, and increased protection for these primates.

Initial Management Recommendations

We continue to work with landowners, community members, and local NGO's to develop a viable management plan for the Chococente area. However, based on our initial study, a number of management recommendations can be immediately made:

- Remove cattle from forested areas in Chococente. Although landowners have put up fencing and have demanded that local residents remove cattle from their property, illegal grazing within the reserve remains a problem and impacts forest regeneration in otherwise intact secondary forest. Encouraging landowners to adopt stricter measures, such as seizure of cattle, may be necessary to curtail these activities.
- Institute immediate protection of riparian and dry forest to prevent further conversion and limit human traffic within riparian areas, particularly as the disturbance impacts behavior of sensitive capuchin and spider monkeys.
- Manage development outside of the reserve to maintain/improve matrix quality and connectivity. In particular, limit development to already-degraded areas of the park, and prevent development from abutting the Escalente's riparian forest.
- Develop an independent management entity for the reserve whose primary goal is biodiversity conservation and who can mediate the interests of the large landowners and local stakeholders.
- Investigate more specifically resource availability as it pertains to capuchins and spiders; if there is enough high-quality habitat, a reintroduction program may be warranted.

In general, this year-long study highlights the need for immediate action to safeguard western Nicaragua's last primate populations. This will require improved protection of primates and their habitats in already established protected areas such as Chococente. It will also involve an assessment of the few remaining primate populations that are scattered across the pacific slope on private farms. Paso Pacífico will be working with both primatologists and private landowners in the coming years to develop effective strategies for primate conservation in western Nicaragua..

PROJECT TIMELINE

- June – July 2005: Established transects in Chococente and trained data collectors.
- August 2005: Follow-up training of data collectors and beginning of data collection.
- August – December 2005: Repeated transect walks and data collection (heavy rains reduced data collection in September and October 2005).
- January 2006: Collection of vegetation data along transects.
- February 2006: Resumption of line-transect data collection.
- March 2006: Line-transect data collection and directed searches for primates along watercourses.
- May – June 2006: Collection of line-transect data.
- August 2006: Completed data analysis and write up
- September 2006: Manuscript to be submitted for publication.
- October 2006: Presentation of study results at 10th Congress of the Mesoamerican Society for Biology and Conservation, Antigua, Guatemala.

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Table 1. Line transects established in Chococente Wildlife Refuge. Numbers correspond to numbers on map in Figure 1. "No. Encounters" indicates the total number of times primate groups were recorded in each transect during walks; all encounters are with howlers unless otherwise indicated. "Habitats (GIS)" indicates the percent length of the transect passing through different vegetation types, based on intersection of transect with habitat map in ArcView; "Forest Type" indicates the percent of the vegetation points in each transect classified as classified during our

				Habitats (GIS)				Forest Type			
Transect	Length (m)	No. Visits	No. Encounters	% Open	% Closed	% Riparian	% Other	% Dry	% Secondary	% Riparian	% Not Forested
1. Río Escalente	2350	58	48*	44.3	0.0	55.7	0.0	68.9	6.7	24.4	0.0
2. Finca Barbarena	2550	50	26	34.8	35.8	7.6	21.8	72.0	16.0	12.0	0.0
3. Río Chococente	2400	54	31	37.6	50.1	0.0	12.3	57.1	40.8	2.0	0.0
4. Talolinga	1800	45	22	42.9	40.0	9.3	7.8	24.3	67.6	8.1	0.0
5. La Leona	1250	43	16	68.5	31.5	0.0	0.0	73.3	16.7	10.0	0.0
6. Río Acayo	1250	47	21	0.6	50.9	25.2	23.3	46.2	30.8	11.5	11.5
7. Punta Piedra	2000	40	4**	48.3	51.7	0.0	0.0	60.0	34.3	5.7	0.0

* 5 of 48 encounters were with capuchins.
** 1 of 4 encounters were with capuchins.

Table 2. Monthly variation in observed versus expected encounter rates based on total kilometers of transects walked per month of transects walked.

Month	Season	Km transect walked	Number of Encounters	Expected Number
August 2005	Wet	103.65	2	27
September 2005	Wet	67.85	10	17
October 2005	Wet	42.55	7	10
November 2005	Wet	57	23	13
December 2005	Dry	49.5	15	12
February 2006	Dry	65.75	18	17
March 2006	Dry	73	18	18
May 2006	Wet	103.6	40	27
June 2006	Wet	104	35	27

Table 3. Group composition (average and standard deviations) of counts of bisexual *Alouatta palliata* groups observed during line transect surveys (top two rows, N = 152) and directed searches (bottom two rows, N = 21) in Chococente Wildlife Refuge.

		Total#	Males	Females	Juveniles	Infants	Imm:F	Inf:F	F:M
Line	Average	12.30	2.06	6.32	2.20	1.78	0.62	0.28	3.22
Transects	S.D.	6.09	0.98	3.27	1.60	1.35	0.31	0.20	1.30
Directed	Average	9.00	2.71	4.00	1.24	1.05	0.58	0.28	1.68
Searches	S.D.	5.67	2.00	2.74	1.26	1.12	0.26	0.30	1.25

Table 4. Population characteristics of mantled howlers (*Alouatta palliata*) in Chococente and at other sites in Central America[a].

Site	Density (ind/ha)	Group Size	Mean No.				Imm/F	Inf/F	F/M	Source
			Males	Females	Juveniles	Infants				
Chococente (Nic)	0.43	12.30	2.06	6.32	2.20	1.78	0.62	0.28	3.22	Current study
La Luz (Nic)	0.51	17.62	1.88	9.12	4.12	2.50	0.73	0.28	5.94	[Williams-Guillén 2003]
Los Tuxtlas (Mex)	0.54	7.82	2.84	3.65	1.13	1.16	0.58	0.33	1.47	[Chapman and Balcomb 1998; Cristóbal-Azkarate and others 2005; Fedigan and others 1998]
Ometepe (Nic)	--	20.50	5.50	8.00	3.50	3.50	0.88	0.44	1.45	[Garber and others 1999]
Cabo Blanco (CR)	0.08	12.85	2.40	7.25	2.25	1.90	0.57	0.26	3.02	[Fedigan and others 1998]
La Pacifica (CR)	0.70	12.74	2.28	7.33	2.95	2.20	0.63	0.37	3.19	[Chapman and Balcomb 1998; Clarke and others 2002b; Fedigan and others 1998]
La Selva (CR)	0.13	12.33	3.30	4.00	2.30	1.30	0.90	0.33	1.21	[Chapman and Balcomb 1998; Fedigan and others 1998]
Palo Verde (CR)	0.90	13.77	--	--	--	--	0.78	--	2.38	[Chapman and Balcomb 1998]
Santa Rosa (CR)	0.05	12.53	2.79	5.25	2.52	1.93	0.85	0.35	1.94	[Chapman and Balcomb 1998; Fedigan and Jack 2001; Fedigan and others 1998]
Toboga (CR)	--	11.48	2.41	5.58	--	--	0.65	--	2.35	[Chapman and Balcomb 1998; Crockett and Eisenberg 1987]
BCI (Pan)	0.58	16.46	2.77	7.61	2.76	3.36	0.78	0.42	2.84	[Chapman and Balcomb 1998; Fedigan and others 1998]

[a] Values at each site calculated from means of groups and, when applicable, of repeated censues.

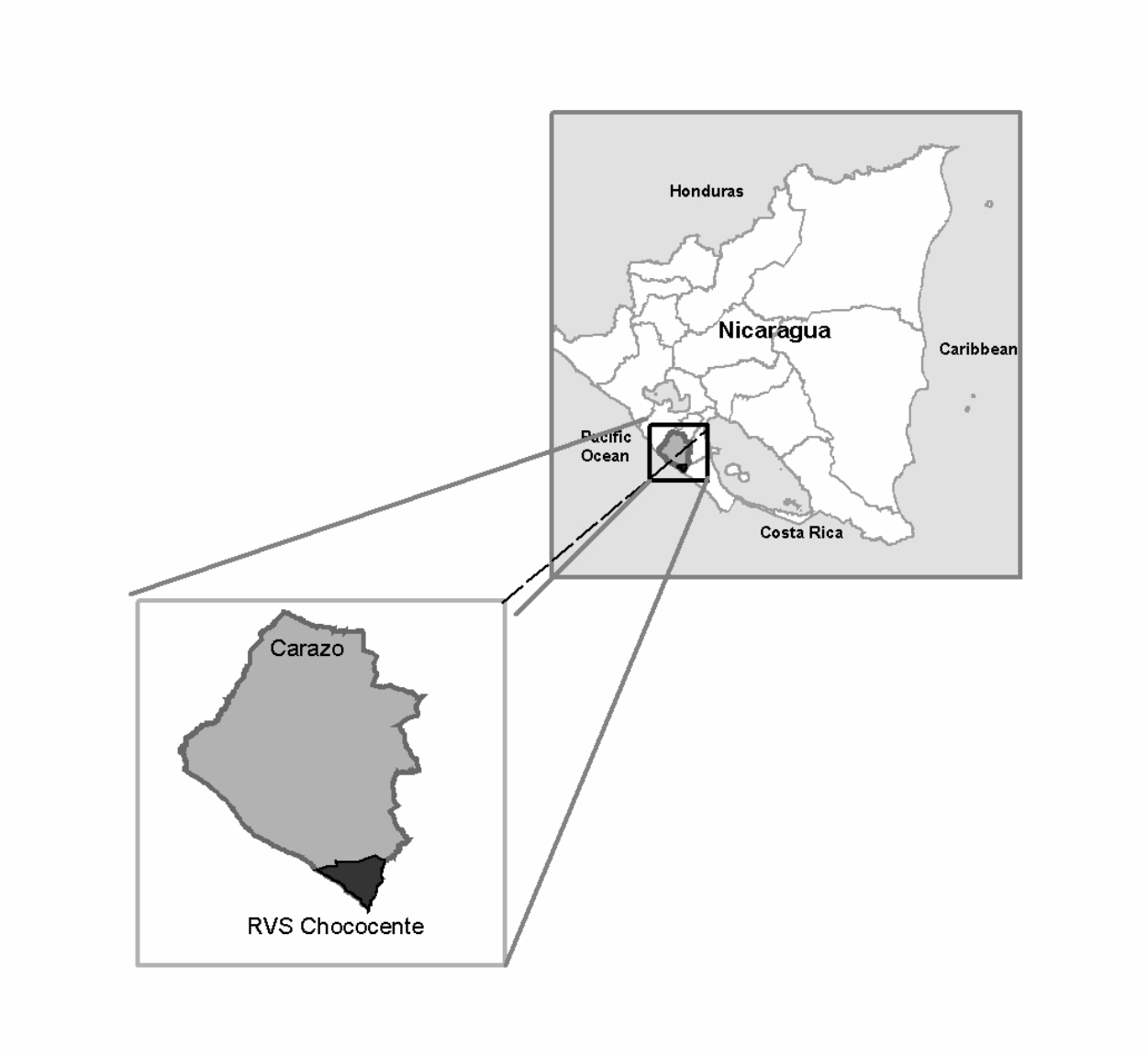

Figure 1. Nicaragua, with the location of the department of Carazo and of Chococente Wildlife Refuge.

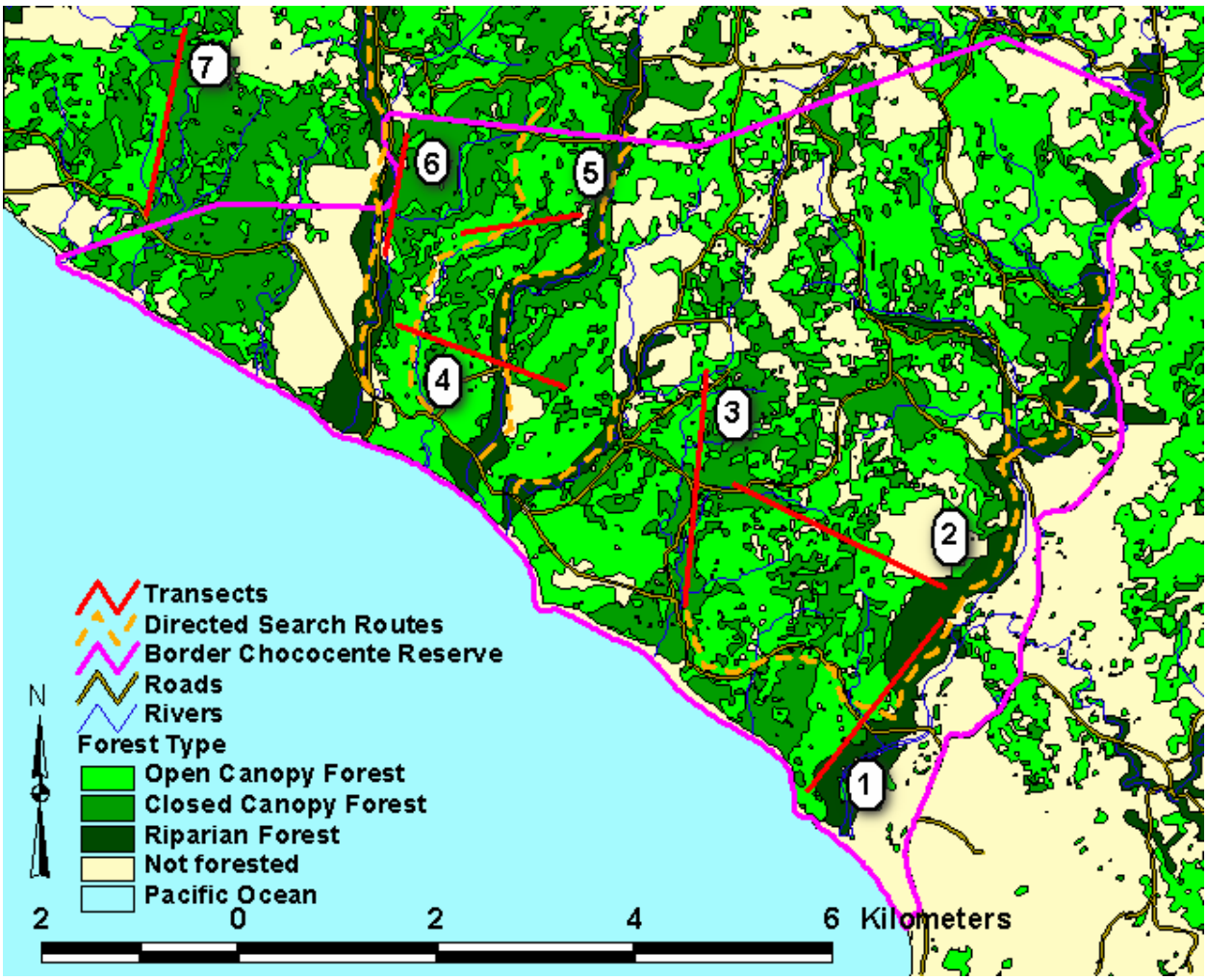

Figure 2. Map of transects (red lines) and opportunistic searches (orange dashed lines) in relation to habitat types in Chococente reserve. All forested habitat types are represented in the transects. Forested areas to the northwest of the reserve are also included in sampling.

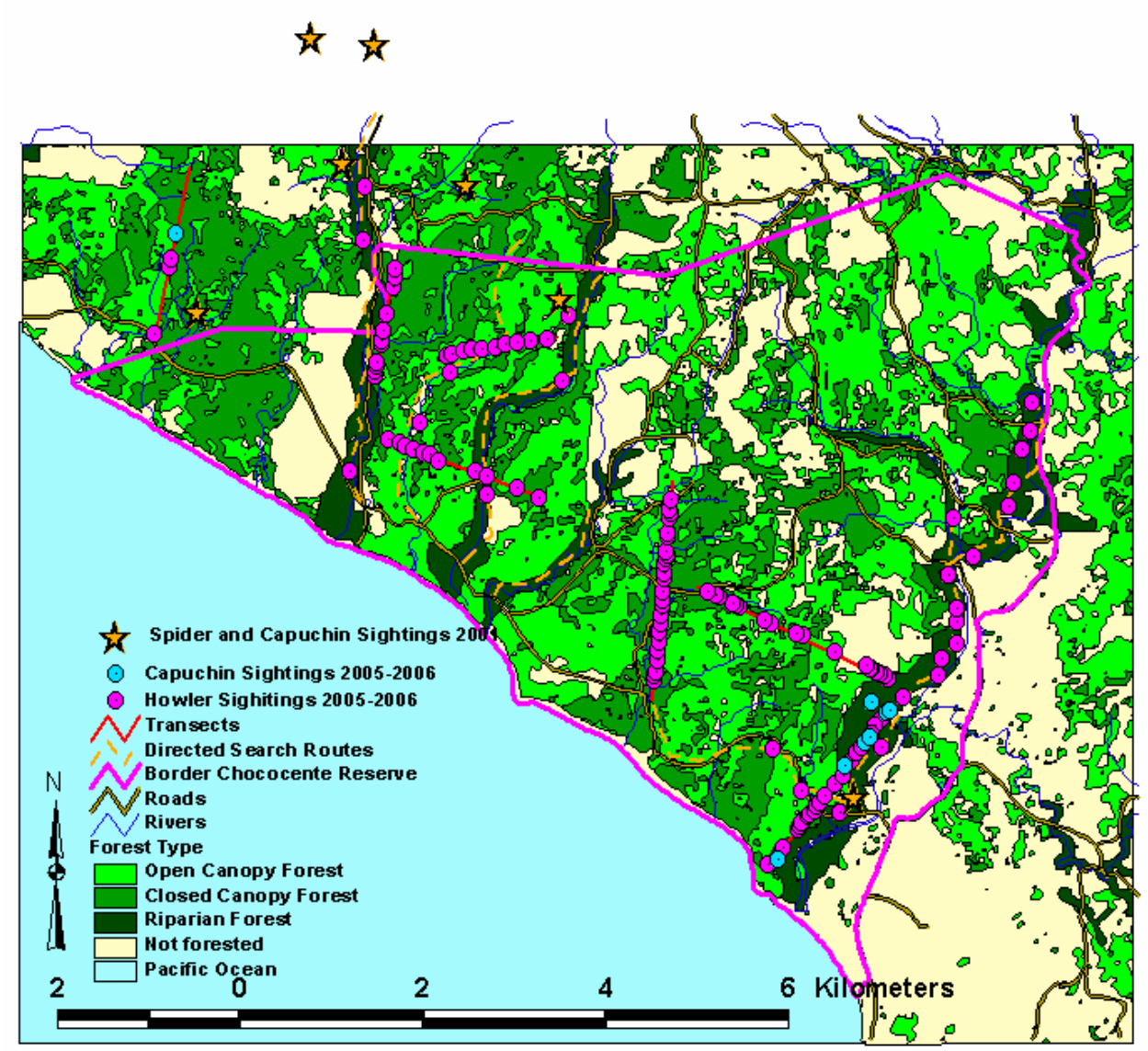

Figure 3. Locations of spider and capuchin monkey sightings during 2001 survey (orange stars), and sightings of capuchins (blue circles) and howlers (purple circles) along transects and directed search routes in 2005 and 2006.