

IMPACTS OF SUBSISTENCE HUNTING ON THE FORAGING ECOLOGY OF
JAGUAR AND PUMA IN THE MAYA BIOSPHERE RESERVE, GUATEMALA

By

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Abstract of Thesis Presented to the Graduate School
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This study assessed the effects of subsistence hunting on the foraging ecology of jaguar (*Panthera onca*) and puma (*Puma concolor*) within the Maya Biosphere Reserve (MBR), Guatemala. Food habits were determined from analysis of 76 jaguar and 145 puma scats collected within hunted and protected areas of the MBR from February 2000-August 2001. Diets of jaguar and puma were compared (1) within species between areas with and without hunting to evaluate effects of subsistence hunting, and (2) between species to evaluate resource partitioning between these sympatric carnivores. Origin of predator scat was determined from mitochondrial DNA, diets were identified from prey remnants found within scats, and frequency of prey in scats was compared to expected values based on prey density estimates to test the hypothesis of non-selective predation. Density of major prey was estimated using line-transect sampling. Diets of jaguar and puma, as measured by percent biomass occurrence of prey species, did not differ between protected and hunted areas. Jaguar diets were dominated by medium-sized prey, particularly armadillos (*Dasypus novemcinctus*) and coatis (*Nasua nasua*), in both protected and hunted areas. Jaguar in the protected area selected for armadillos and coatis in greater proportion than expected based on their availability. Medium-sized mammals also dominated puma diets, but large mammals constituted approximately 50% of prey biomass in both hunted and protected areas. Deer (*Odocoileus virginianus* and *Mazama* sp.) and large rodents (*Agouti paca* and *Dasyprocta punctata*) were the most important prey. Puma in the non-hunted region consumed agoutis and white-tailed deer in greater proportion than expected based on their availability while puma in the hunted region consumed agouti, pacas and brocket deer in greater proportion than expected. A low degree of dietary overlap existed between jaguar and puma in both study areas. White-lipped peccary (*Tayassu pecari*), collared peccary (*Tayassu tajacu*) and brocket

deer were less abundant, and coatis more abundant, in the hunted area. Jaguar and puma in both study areas obtained similar contributions from large prey to their respective diets despite changes in the abundance of those prey. The relative abundance of jaguar and puma, and a density estimate for jaguar, was estimated in protected areas (where hunting was prohibited) of the MBR using infrared-triggered camera-traps. Puma (3.9 captures/100 trap nights) were relatively more abundant than jaguar (2.0 captures/100 trap nights). A minimum density estimate of 0.7 jaguar/100 km² occurred in the protected area. Minimum density estimates were not calculated for puma, which lack distinctive markings. Assuming adult jaguar male home ranges overlap exclusively with at least two females, a conservative approximation for jaguar density in the study area was 1.7 jaguar/100 km².

CHAPTER 1

IMPACTS OF SUBSISTENCE HUNTING ON THE FORAGING ECOLOGY OF JAGUAR AND PUMA IN THE MAYA BIOSPHERE RESERVE, GUATEMALA

Introduction

The jaguar (*Panthera onca*) is the largest extant cat in the Western Hemisphere. Mean weight varies geographically and ranges from 56-105 kg for adult males and 41-77 kg for adult females (Hoogesteijn et al., 1996). Jaguar inhabit most tropical forest types, including evergreen forest, deciduous forest, and thornscrub, and can be found in seasonally flooded swamp and pampas grasslands. At the time of European arrival to North America, this species was found in suitable habitat from the southwestern United States, throughout Mexico and Central America, and south to Patagonia and northern Argentina (Hall, 1981). However, jaguars have been extirpated from large portions of their range and by the 1980's the range of the jaguar was reduced by two-thirds in North and Central America (Swank & Teer, 1989). A more recent and rigorous range-wide assessment of jaguar distribution determined that they are restricted to 46% of their former range, with insufficient information to determine status on 12% of historic range (Sanderson et al., 2002).

Throughout most of Central and South America, the jaguar is sympatric with another large felid, the puma (*Puma concolor*). Where these two species coexist, puma are of smaller size and stature than jaguar, ranging in size from 53-72 kg for males and 34-48 kg for females (Anderson, 1983; Pall et al., 1988). The puma's smaller size is postulated to be an evolved response that serves to reduce competition with jaguar (Taber et al., 1997). The smallest puma are found in equatorial forests, whereas the largest are found in temperate zones along the northern and southern limits of their range (Emmons, 1987; Iriarte et al., 1990).

Puma are more adaptable than jaguar and, consequently, are more widely distributed. Puma are found at elevations ranging from sea level to 5,800 meters (Redford & Eisenberg, 1992). Habitats used by puma are more diverse than those of jaguar and include desert, rainforest, montane forest and arid scrub. The geographic range of puma extends from the Yukon Territory, Canada, to the southern tip of Argentina and Chile (Emmons & Feer, 1990).

Both jaguar and puma are legally protected throughout Central America and almost all countries within their geographic range have laws that forbid the killing of these large carnivores. Unfortunately, law enforcement varies among countries and is generally non-existent or lax outside of the United States and Canada (Swank & Teer, 1989).

Throughout most of their combined range, jaguar and puma are killed primarily by recreational hunters and by ranchers attempting to protect livestock but, only rarely by subsistence hunters (Yanez et al., 1986; Hoogesteijn et al., 1996; Novack, 2003a). In some areas, ranchers are responsible for more than half of all puma deaths (Cunningham et al., 1995). Additional harvest pressure is exerted on jaguar because of the illegal

market for their pelts (Aranda, 1991). In November, 2002, the author observed a jaguar skin for sale at a leather shop in Flores, Guatemala. Besides direct persecution, habitat fragmentation and declining prey populations threaten jaguar and puma populations. Of these three factors, habitat loss and fragmentation are considered to be the most critical (Medellin et al., 2000; Logan & Sweanor, 2001).

Little information is available regarding the ecology and predatory patterns of large carnivores in the Neotropics (Weber & Rabinowitz, 1996). Jaguar and puma, like other felids, are adaptable and opportunistic hunters. Where available, large and medium-sized terrestrial mammals are reportedly the preferred prey for both of these felids (Emmons, 1987; Iriarte et al., 1990; Crawshaw, 1995; Taber et al., 1997; Nunez et al., 2000; Polisar et al., 2003). Large felids are morphologically specialized to take prey as large or larger than themselves (Kleiman & Eisenberg, 1973; Kruuk, 1986). However, carnivores will shift to alternative prey or “buffer species” when preferred prey are scarce (Murdoch, 1966; Bergerud, 1983; Jędrzejewski et al., 2000). For example, in southern Chile, puma preyed on European hares (*Lepus capensis*) when guanaco (*Lama guanicoe*) populations were low, but when the guanaco population increased, pumas increased their take of guanacos (Yanez et al., 1986; Iriarte et al., 1990).

The fitness of any individual predator is determined largely by the quality and quantity of its prey (Sunquist & Sunquist, 1989). The social dynamics of large carnivores are believed to be sensitive to natural or human-induced variations in the relative densities of different size classes of prey (Karanth & Sunquist, 1995). Hunting, logging, or agricultural activities usually alter the dynamics and structure of large ungulate populations (Hunter, 1990; Madhusudan & Karanth, 2000) and, depending on the scale of human activity, can negatively impact the foraging ecology of large felids that depend on ungulates as their primary prey.

Humans also compete directly with jaguar and puma for prey, particularly where subsistence hunting is important. In the Neotropics, both Indian and colonist groups rely heavily on wild game, especially mammals (Leopold, 1959; Redford & Robinson, 1987; Escamilla et al., 2000). The diets of subsistence hunters have been shown to overlap with those of puma and jaguar (Jorgenson & Redford, 1993) and subsistence hunting has depleted populations of major prey in areas lacking strict protection (Carrillo et al., 2000). Typically, as human populations increase, wildlife populations are depleted because hunter behavior is guided by efforts to maximize immediate harvest success and not long-term conservation (Stephens & Krebs 1986; Robinson & Redford 1991; Alvard, 1993).

The primary objectives of this study were to evaluate the impact of subsistence hunting on prey availability and, consequently, on the food habits of jaguar and puma in hunted and protected areas within the Maya Biosphere Reserve (MBR), Guatemala. I tested the hypotheses that diets of jaguar and puma reflect availability of prey, that diets differed between hunted and protected areas of the MBR, and that large prey were less abundant in diets of jaguar and puma in areas open to subsistence hunting compared to areas where hunting is prohibited. A secondary objective was to describe how jaguar and puma partition prey resources interspecifically, and to determine if the degree of interspecific competition differed between protected and hunted areas.

Materials and Methods

Study Area

The MBR encompasses 11,600 km² of lowland tropical rainforests in northeastern Guatemala. The altitudes in the study area range from 100-400 m above sea level. Mean monthly temperature varies from 22° C in January to a high of 34° C in June. Annual rainfall averages 1200-1500 mm and falls mainly during the wet season (June-January). Most of this rain drains into the watershed of the Rio Azul River. During the pronounced dry season (February-May), surface water is limited and available only at scattered waterholes, lakes, and in the deeper sections of the Rio Azul River.

The MBR is almost completely covered by mature forest classified as Subtropical Moist (Holdridge et al., 1971). Schulze and Whitacre (1999) recognized 11 habitat types within the MBR based upon the variables of topographic position, slope, soil clay content, and soil rock content. These habitat types can be simplified into three categories; upland forest, bajo or lowland forest, and transitional forest. Upland forest is found in areas of greater relief, and is characterized by a high, closed tree canopy. Bajo forest has a low, somewhat open canopy, thick underbrush, and is seasonally inundated. Transitional forest consists of an intermediate stage between upland and bajo forest types.

Many small villages and towns can be found within the confines of the MBR. The village of Uaxactun is inhabited by approximately 700 individuals and is the only permanently inhabited settlement within the hunted study site. Inhabitants are primarily mestizo and derive most of their subsistence and financial earnings from the harvest of forest products and small-scale agriculture. The village has been granted a 25-year concession to an 836 km² area of forest within the MBR. This concession permits village inhabitants to benefit economically from the sustainable management of natural resources inside the concession limits. Individuals travel widely throughout the concession area and northern limits of Tikal National Park to collect fronds from the xate palm (*Chaemaedorea* sp.), harvest resin from the chicle tree (*Manilkara zapota*), and engage in subsistence hunting. Hunters take a wide variety of taxa but prefer large and medium-sized mammals (McNab, 1998). Small-scale selective cutting of timber began in year 2000. No cattle are produced in Uaxactun. A few poorly maintained logging roads and an extensive network of trails and temporary camps provide access to the forest. Less than 10% of the Uaxactun Forest Concession has been converted to agriculture, and most of the fields are located within 15 km of the village of Uaxactun.

Jaguar and puma are the largest carnivores residing within MBR. Smaller mammalian carnivores include ocelot (*Leopardus pardalis*), margay (*Leopardus wiedii*), jaguarundi (*Herpailurus yagouaroundi*), tayra (*Eira barbara*), grey fox (*Urocyon cinereoargenteus*), and raccoon (*Procyon lotor*). Potential large-bodied prey (>15 kg) are represented by ungulates, including tapir (*Tapirus terrestris*), collared and white-lipped peccary (*Tayassu tajacu* and *T. pecari*), white-tailed deer (*Odocoileus virginianus*), and brocket deer (*Mazama pandora* and *M. americana*). A variety of medium-sized (2-15 kg) and small (<2 kg) prey are also available.

The MBR is subdivided into various management units administered by different institutions (Figure 1.1). The four management units where data were collected included portions of El Mirador-Rio Azul National Park (1,177 km²), Tikal National Park (576 km²), Biotope Dos Lagunas (296 km²), and the Uaxactun Community Forest Concession

(836 km²). The combined area of these management units is approximately 2,885 km². The contiguous area encompassed by Biotopo Dos Lagunas and the eastern portion of Mirador-Rio Azul National Park is a protected, uninhabited region of the MBR and serves as an un hunted or very lightly hunted control area. The area encompassed by the Uaxactun Community Forest Concession and northern half of Tikal National Park is moderately to heavily hunted (Polisar et al., 1998).

Methods

Estimation of Prey Availability

Line-transect sampling (Buckland et al., 2001) was used to estimate densities of prey species in the study area. This method has been effectively used by previous researchers in the Neotropics (Peres, 2000) and in the Maya Biosphere Reserve (Kawanishi, 1995; Baur, 1998). Six transects, each 2.5 km long, were established in forested habitats within the hunted area at distances of 6-10 km from the village of Uaxactun. Transects traversed equal proportions of upland, transitional and bajo habitat such that one third of the total transect lengths sampled each habitat type.

Transects were surveyed periodically, usually at 5-day intervals between August 2000 and July 2001. A total of 1,045 km of transects were surveyed in the hunted area. Surveys began immediately after daybreak with one observer walking the transect at 1-2 km/hr. Observers recorded all mammals observed from the transect, the perpendicular distance of each animal/group from the transect line (visually estimated), group size, sex, and age class of individuals (when possible).

Prey species in the protected area were surveyed along six transects, using identical methods. A total of 1,414 km of transects was surveyed during February 2000 – March 2001. These data were collected and compiled for a separate research project. Encounter rates are presented in Baur et al. (2002). Data were reanalyzed with permission for inclusion in this paper.

Population densities were estimated for each species using DISTANCE version 3.5 (Laake et al., 1998). Model selection and the degree of truncation were determined separately for each species and site. To avoid bias associated with visual estimates of sighting distance, observations were grouped into 4-6 distance-class intervals that varied in range for each species and site. Individual and group density estimates for each species were compared between hunted and protected areas using a student t-test (Rao, 1998).

Diet Analyses

Scats were analyzed to determine proportions of different prey species consumed by jaguar and puma. Scats were collected opportunistically between February 2000 and July 2001 by the author, park guards, and members of the community of Uaxactun. A financial reward was offered as an incentive for villagers and park guards to participate in the scat collection effort. A reward of \$1.25 (US) was offered to anyone bringing in a suspected feline scat with accompanying information on the date and location where the scat was found. Scats located inside the hunted site but >15 km from the community of Uaxactun, were not considered for analysis. Limiting the area from which scats were

collected in the hunted portion of MBR ensured that scats came from nearer the village where hunting pressure is greatest (Figure 1-2). A distance of 12 km separated the control and treatment sites. The areas from which scats were collected were large enough to guarantee that numerous individual jaguar and puma contributed to the overall sample.

Scats were initially dried on a raised platform in open sunlight and then placed in paper envelopes for temporary storage. Scats were later dried for 2-4 days at 48 °C and stored in a water-resistant container until processed for genetic and prey-content analyses.

A random subsample of 350 large diameter scats (width >19mm) evenly divided between hunted and protected sites, was selected for analysis. Nineteen millimeters is considered the minimum size for an adult jaguar or puma scat (Farrell et al., 2000). Scats were broken apart, and the bile powder was carefully sifted through a sanitized wire mesh and separated from prey contents. Bile powder from the selected scats was placed into a wide mouth polyurethane bottle, sealed and shipped to the laboratory (Wildlife Genetics International, Canada), where mitochondrial DNA was extracted and used to identify species of predator (Wasser et al., 1997). Predator identity was confirmed using a sequence-based analysis at the 16S gene of mtDNA (Johnson & O'Brien, 1997; Paetkau, in press).

Following removal of bile, scats were washed and sifted to isolate hair, bone, hooves, teeth and other undigested remnants of consumed prey. Scat contents were examined macroscopically and microscopically. Hairs, hooves, bone, and teeth from prey were compared with reference samples made available from the Florida Museum of Natural History at the University of Florida in Gainesville, Florida, and the Guatemalan Natural History Museum of the University of San Carlos, Guatemala City, Guatemala. Length, color, width, medullar structure, and cuticle pattern of hair found in scats were used to identify prey (Moore et al., 1974).

Food habits of jaguar and puma were calculated using frequency of occurrence and estimated mean biomass of each species consumed (Ackerman et al., 1984; Taber et al., 1997). Biomass calculations were transformed using a correction factor ($Y = 1.98 + 0.035 X$) experimentally derived by Ackerman et al. (1984) during feeding trials of puma, where Y represented the weight of food consumed per scat, and X is the mean prey weight. Mean prey weights were derived from previous studies of subsistence hunting in the MBR (Baur, 1998; McNab, 1998), Mexican Yucatan (Jorgenson, 1993), and Central America (Reid, 1997). Mean vertebrate weight of prey was calculated as a grand geometric mean following the methods of Jaksic & Brakker (1983).

The observed prey frequency of items in scats was compared to expected values to test the hypothesis of non-selective predation for both jaguar and puma in hunted and protected areas. Expected values were derived from group densities (d_i) of prey species and the estimated number of field collectible scats (λ_i) produced by each prey species as derived from mean prey weight and the correction factor developed by Ackerman et al (1984). Densities of pacas (*Agouti paca*) and armadillos (*Dasypus novemcinctus*) were derived from data obtained in an adjacent region of the MBR (Baur, 1998). Species of birds and mammals whose densities could not be reliably estimated were eliminated from consideration. The values for d_i , SD d_i , λ_i , SD λ_i and the frequency of prey item appearance within scats were entered into the computer program SCATMAN (Hines & Link, 1994). When more than one prey item appeared in a scat, each was given an equal contribution to frequency (e.g., two items would be assigned 0.5 each). Unknown deer

were divided proportionally between the categories for brocket deer and white-tailed deer. Observed and expected prey frequencies were compared using Fisher's exact test.

Prey selection was evaluated using SCATMAN when the number of scat samples was greater than 30. SCATMAN uses a chi-squared goodness of fit test to test the null hypothesis of zero prey selection (Manly et al., 1972; Chesson, 1978) and adds a parametric bootstrap to correct for overdispersion (Link & Karanth, 1994). To test for prey selection and comply with the assumption of a chi-square goodness of fit test, some prey species were combined with their nearest taxonomic relative into a single group. Both species of peccary, for example, were combined into the group TASP. For jaguar in the protected area, large rodents (i.e., pacas and agoutis) were combined into the group AGPA+DAPU. A value of 0.5 was added to the observed frequency of all cells in the analysis of jaguar in protected area and puma in the hunted area following Agresti (2002) so that all cell frequencies would be greater than zero.

Fisher's exact test was used to determine if the diets of jaguar and puma differed between protected and hunted areas. Prey frequency was used with $P < 0.05$ defined as a significant difference. Interspecific differences in the relative prey frequency consumed by jaguar and puma for each site were tested with a student t-test for differences of proportions. Overlap of diets was determined using Pianka's (1973) equation.

Results

Prey Availability

Densities and group densities were compared for the eight most important mammalian prey species in hunted and protected areas (Table 1-1). Most mammals species appeared to be less abundant in the hunted areas with the exception of agoutis, white-tailed deer and coatis. The mean densities of white-lipped peccaries ($t = 2.25$, $df = 10$), collared peccaries ($t = 5.24$, $df = 10$), and brocket deer ($t = 4.00$, $df = 10$) were less abundant ($\alpha < 0.05$) in the hunted zone, whereas coatis ($t = 4.70$, $df = 10$) were more abundant. The density of agoutis and white-tailed deer did not differ between areas. Similar results were obtained from a comparison of mean group densities. Monkeys (*Alouatta pigra* and *Ateles geoffryii*) were not recorded during surveys in the hunted area but their densities would not be expected to differ between areas because local hunters rarely harvest monkeys (McNab, 1998).

Diet Composition and Prey Selection

A sample of 800 scats was collected between February 2000 and July 2001, 95% of which were obtained from December through July. A random subsample of 350 scats (175 each from hunted and protected areas) was selected for mtDNA identification of species origin. Two hundred and sixty-four samples were successfully identified, of which 145 were puma, 76 were jaguar, and 43 were non-focal species including ocelot, jaguarundi and domestic dog (*Canis familiaris*).

Jaguar diets

I identified 13 species of prey from 76 jaguar scats. Jaguar scats contained an average of 1.36 identifiable prey items per scat. No small mammals (<2 kg) were found in jaguar scats. The mean weight of vertebrate prey (MWVP) consumed was similar for the protected (6.18 kg) and hunted (6.34 kg) areas.

The diets of jaguar within both the protected and hunted areas of the MBR were dominated by medium-sized mammals. In the protected area, medium-sized mammals were frequently identified in scats (85%) and contributed 66% of the total biomass consumed. Ungulates occurred much less frequently (7%) and comprised 30% of biomass consumed, whereas birds, mostly Cracidae, occurred in 9% of scats and comprised 4% of the relative biomass consumed (Table 1-2). In the hunted area, medium-sized mammals occurred in 91% of scats and comprised 69% of biomass consumed. Ungulates occurred less frequently (9%) and constituted 31% of the biomass consumed, birds were absent (Table 1-2).

At the species level, armadillos contributed the largest amount of biomass to jaguar diets in both protected and hunted areas, contributing 39% and 25%, respectively. In the protected area, the second largest contributor of biomass to jaguar diets were coatis (19%), followed by white-tailed deer (9%), collared peccaries (8%) and white-lipped peccaries (7%). In the hunted area, collared peccaries (23%) were the second largest contributor of biomass to jaguar diets followed by coatis (22%), pacas (8%), and monkeys (6%).

Based on comparison of observed versus expected prey frequency in scats (Table 1-3), I rejected the hypothesis that jaguar in the protected (unhunted) area were non-selective (Fisher's exact test, $P < 0.001$). Jaguar consumed coatis and armadillos in greater proportion than expected based on their availability ($P < 0.001$), whereas most other species of prey were consumed less than expected by their availability (Table 1-4). In the protected areas, jaguar consumed significantly fewer monkeys ($P = 0.011$) and brocket deer ($P = 0.043$) than expected, and to a lesser extent, peccaries ($P = 0.099$) and large rodents ($P = 0.097$). However, in the hunted area, jaguar diets did not differ from expected (Fisher's exact test, $P = 0.461$), nor did the observed prey frequency in jaguar diets differ between protected and hunted areas (Fisher's exact test, $P = 0.289$).

Puma diets

I analyzed 145 puma scats that contained at least 14 species of prey and averaged 1.29 identifiable prey items per scat. No mammals <2 kg were found in puma scat. The MVWP was 8.59 kg and 7.20 kg for the protected and hunted areas, respectively.

A comparison of observed prey frequencies (Table 1-3) revealed puma diets did not differ between hunted and protected areas (Fisher's exact test, $P = 0.271$). Puma diets within the protected area were dominated by medium-sized mammals which were identified in 67% of scats and contributed 42% of the biomass consumed. Ungulates occurred less frequently (15%) and contributed 51% to biomass consumed, and birds occurred in 18% of scats and comprised 6% of biomass consumed by puma. For puma within the hunted area, medium-sized mammals were frequently identified (79%) and

contributed 57% of biomass consumed. Ungulates occurred in 11% of scats and comprised 49% of biomass consumed, while birds were less frequently identified in scats (10%) and contributed 4% to the biomass consumed.

White-tailed deer and brocket deer were the most important prey in puma diets in the protected area and contributed the largest proportion of biomass, 20% and 21%, respectively (Table 1-5). Brocket deer were also the most frequently occurring prey item (25%). Agoutis were the next most important component of puma diets contributing 15% of biomass, followed by pacas at 13%. Birds, monkeys, and collared peccaries each contributed 6-7% of the total biomass consumed by puma in the protected area. Brocket deer, agoutis and pacas dominated puma diets in the hunted area, with each species contributing 20% of prey biomass consumed. The fourth most important prey item in the hunted area, as measured by biomass, was white-tailed deer (12%), followed by monkeys (10%).

I rejected the hypothesis that puma in either protected or hunted areas were non-selective of prey (Fisher's exact test, $P = 0.024$ and $P < 0.001$, respectively) based on comparisons of observed and expected prey frequencies in diets (Table 1-3). Puma in the protected area consumed agoutis ($P = 0.003$) and white-tailed deer ($P = 0.043$) in greater proportion than their availability, and consumed armadillo ($P = 0.013$) and peccaries ($P = 0.089$) less than expected based on their availability (Table 1-6).

Puma in the hunted area also selected agoutis ($P = 0.003$). Additionally, they selected for pacas ($P = 0.002$) and brocket deer ($P = 0.004$) whereas puma living in the protected area did not. Armadillos were taken less than expected based on their availability ($P = 0.003$), as were coatis ($P = 0.002$). Peccaries and white-tailed deer were taken in proportion to their availability.

Dietary Overlap Between Jaguar and Puma

The degree of dietary overlap between jaguar and puma was relatively low and varied little between protected (Pianka index 0.30) and hunted (Pianka index 0.33) areas. A value of 0 indicates complete dissimilarity, and a value of 1 indicates complete similarity. Using an equality of proportions test (Rao, 1998), jaguar in the protected area consumed more armadillos ($t = 5.84$, $P < 0.001$) and coatis ($t = 3.62$, $P < 0.001$) than did puma. Puma in the protected area consumed more brocket deer ($t = 2.92$, $P < 0.001$) and pacas ($t = 2.80$, $P < 0.001$) than did jaguar. The dietary overlap of jaguar and puma was marginally different in the hunted area. Jaguar in the hunted area consumed significantly more armadillos ($t = 5.08$, $P < 0.001$), collared peccary ($t = 2.65$, $P < 0.001$), and coatis ($t = 5.19$, $P < 0.001$), but fewer brocket deer ($t = -2.71$, $P < 0.001$) than puma.

Discussion

Diets of Jaguar and Puma in the MBR

The effects of subsistence hunting on large carnivores are of particular concern since hunters compete directly for large and mutually preferred prey (Jorgenson & Redford, 1993). Diets of jaguar and puma, as measured by percent biomass occurrence of prey species, did not differ between protected and hunted areas. Large prey (>15 kg) were consumed in equivalent proportions between areas. The contribution of large prey

to the diets of jaguar was 31% in the hunted and 28% in the protected area. The food habits of puma in the hunted area had marginally less large prey, 39% of biomass occurrence, compared to 50% in the protected area. However, 3 of the 4 species of large prey were significantly less abundant in areas subjected to subsistence hunting. Consequently, jaguar and puma in both hunted and protected areas obtained similar contributions to their diets from large prey despite changes in the abundance of those prey.

The MWVP varied little for jaguar between areas whereas the MWVP of puma was smaller by 1.3 kg in the hunted area. Prey selection relative to prey abundance, varied little for jaguar and puma between hunted and protected areas, and suggested minimal apparent impact from subsistence hunting pressure at current levels.

No small prey (<2 kg) were found in jaguar or puma scats collected during this study. That all scats were identified as jaguar or puma by molecular assay casts doubt on the reported observance of small prey (<1 kg) in the diets of jaguar and puma from previously cited research (Emmons, 1987; Taber et al., 1997). The veracity of using tracks associated with scat as a technique for identifying species origin is suspect because accurate identification of tracks under field conditions is dependant on soil conditions, track age and observer experience since track sizes of puma and jaguar overlap.

Medium-sized mammals, especially armadillos and coatis, dominated the diets of jaguars in Guatemala. Mean vertebrate weight of prey consumed by jaguar from this study was greater than for the Chaco, Paraguay (Taber et al., 1997), but less than that found in Mexico or Venezuela (Nunez et al., 2000; Scognamillo et al., 2003). The percentage occurrence of coatis in the diets of jaguar in Guatemala is the highest recorded for any area. Jaguar and other felids have been reported as important predators of coatis (Booth-Biznik, 2001), and were the most important cause of mortality among radio-collared coatis in Arizona and Mexico (Hass & Valenzuela, 2002; Valenzuela & Ceballos, 2000). The higher densities of coatis in the hunted area of this study (Table 1-1) did not coincide with a greater percentage occurrence of biomass consumed by either jaguar or puma.

Jaguar consumption of armadillos was less than that reported in Belize (Rabinowitz & Nottingham, 1986). Puma clearly avoided armadillos. Puma may be avoiding armadillos because they are infrequently encountered or, because larger, more profitable prey are available. Additionally, the differences in prey selection may be partially attributed to the ability of jaguar to handle armored prey. . Although puma teeth can probably penetrate the armadillo shell, handling time is probably much greater than for a jaguar. Jaguars have disproportionably greater bone crushing capability than do puma (Biknevicius & Valkenburgh, 1996); hence, armadillos are relatively more profitable to obtain. Interestingly, a strong correlation exists between the historical distribution of jaguar at its northern geographic limit and the overlapping distributional limits of armadillos, coatis, and collared peccary.

Puma prefer deer as prey throughout most of their range (Iriarte et al., 1990). Consistent with this finding, puma consumed both species of deer in greater proportion than their availability in both hunted and protected areas. Contrary to expectation, however, white-tailed deer were not selected for in the hunted area, where their relative abundance was greater in proportion to the total number of ungulates available. Populations of ungulates in the hunted area of MBR were lower than those in the

protected area, with the exception of white-tailed deer. Presumably, lower densities of peccaries and brocket deer are attributable to human hunting pressure. The higher densities of white-tailed deer in the hunted area may be explained by human induced changes to habitat. Approximately 10% of the Uaxactun concession area has been converted to secondary forest or agriculture, both of which provide habitat favorable to white-tailed deer. These human-modified habitats are concentrated within the hunted area.

Dietary Overlap Between Jaguar and Puma

Interspecific differences in jaguar and puma diets for both protected and hunted areas suggest that these sympatric felids have co-evolved to partition prey resources in such manner as to reduce competition. Similar findings have been reported for jaguar and puma in the llanos of Venezuela (Scognamillo et al., 2003) and for tiger (*Panthera tigris*), leopard (*Panthera pardus*), and dhole (*Cuon alpinus*) in India (Karanth & Sunquist, 1995). The low degree of dietary overlap between jaguar and puma in both protected and hunted areas is largely a reflection of differences in selection for armadillos and coatis by jaguars and brocket deer by pumas.

Where prey species are found in different habitats, and there is selection for different prey, habitat partitioning can facilitate food resource partitioning by sympatric carnivores. Armadillos and coatis, the primary prey species of jaguar in MBR, are both insectivores dependant upon arthropods living in organic litter of the forest floor. During the dry season, these arthropods are more abundant in areas of greater soil humidity (Janzen & Scheoner 1968; Pearson & Derr, 1986). Jaguars tend to use mesic habitat (Emmons, 1987; Quigley & Crawshaw, 1992), which likely facilitates encounters between coatis and armadillos with jaguar.

Conservation Implications

A lack of prey can be detrimental to the populations of large carnivores. Prey availability can influence carnivore densities, survival, reproduction and behavior in ways that effect population viability (Fuller & Sievert, 2001). Lower densities of large prey were reported in the hunted area, presumably due to hunter harvest. Consequently, reduced availability of large prey may result in reduced survival rates, larger home ranges and, consequently, a lower carrying capacity for jaguar and puma in hunted areas of the MBR. Such effects have been demonstrated with other large felids (Knick, 1989; Maehr et al., 1989). Additionally, predators or their prey may respond to hunting activity by altering their distribution in space or time (Sunquist & Sunquist, 1989). Puma in Florida (Janis & Clark, 2002) and Arizona (Van Dyke et al., 1986) reacted to human activity by avoiding areas of human presence and altering their periods of peak activity. Similar behavioral responses have been documented in prey species such as white-tailed deer (Kilgo et al., 1998) and coati (Gompper, 1995).

It is surprising that jaguar, the largest terrestrial carnivore in this system, could be fulfilling its energetic needs by consuming mostly medium-sized prey. To fulfill its energetic needs, a jaguar should daily consume an average of 34 g meat kg cat/day (Altman & Dittmer, 1973). Jaguars in Central America are relatively small compared to those of South America (Hoogesteijn & Mondolfi, 1996). Average weights for jaguar in the Calakmul Biosphere of Mexico, which adjoins the study area, were 56 kg for males

and 41 kg for females (Aranda, 1992). If energetic needs of jaguars are calculated from these values, the typical Guatemalan jaguar requires 1.9 kg meat/day for males and 1.4 kg meat/day for females. The caloric intake of females will increase during gestation and lactation and when providing for cubs. In domestic cats, and presumably other felids, the intake of metabolizable energy during pregnancy can increase 1.5-fold during pregnancy. During peak lactation, the intake will increase up to 2.5-fold for litters of 2-4 cubs (Loveridge, 1986).

The consumable fraction of larger prey (> 15 kg) (Messier & Crete, 1985; Emmons, 1987) and armadillos, whose armored shell is indigestible, is assumed to be 75%. Prey items smaller than 10 kg in size would be entirely consumed (Nunez et al., 2000). Thus, an individual coati or armadillo could only meet the energetic needs of an adult jaguar for 1-3 days. In the case of a female during peak lactation, a single medium-sized prey item of this type may not fulfill even daily caloric needs. The availability of large-sized prey then becomes potentially critical to the survival of nursing cubs.

The evidence from this study is consistent with the suggestion of Gonzalez and Miller (2002) that jaguar cannot compensate for a decrease in large-sized prey by eating greater quantities of medium-sized prey. Although the abundance of large ungulates was less in the hunted area than in the protected area, the relative contribution of ungulates to jaguar diets did not differ. Jaguar in this study appeared to minimally fulfill their caloric needs by preying on coatis and armadillos, while consumption of ungulates was maintained at a minimum threshold of approximately 28-30% of biomass consumed.

Energetic costs may increase when the availability of large prey is reduced. Large prey animals, such as an adult white-tailed deer, cannot be fully consumed by either jaguar or puma at one sitting and will be revisited on consecutive days (Logan & Sweanor, 2001). During the time a carcass is intact, further foraging activity is probably curtailed while the cat stays in vicinity to the remnants. By contrast, small prey items like armadillo and coati can satisfy little more than immediate energetic needs of jaguar and once consumed, the jaguar would likely continue to search for other prey. When large prey are scarce, therefore, foraging effort by jaguar will presumably increase. The more time spent foraging in search of prey, the greater the energetic costs and potential for encounters with humans or their livestock. Animals that depredate livestock or encounter people will frequently be killed (Hoogesteijn et al., 1996).

Hunting activity appears to have minimal effects on the diets and prey selection patterns of jaguar and puma in the MBR, but the full impact of hunting activity on the feeding ecology of these cats is still not completely understood. Unregulated subsistence hunting appears to be having an impact on densities of some prey, particularly large species such as brocket deer and white-lipped peccaries. Similar effects have been reported by other studies (Carillo et al., 2000; Peres, 2000). As such, the unregulated activity of subsistence hunters inside the MBR may pose a potential threat to carrying capacity and ultimately, the long-term persistence of jaguar and puma in this region. A community wildlife management program, such as that proposed by Bodmer & Puertas (1999) and currently under development in the Uaxactun forest concession, should be enacted to prevent the possible overexploitation of large prey, by hunters in the MBR. A successful program that regulates hunting activity in the MBR would likely benefit populations of jaguar and puma and ensure that sustainable harvests are available for subsistence hunters in the future.

Table 1-1. Comparison of mean density estimates for individuals and groups of principal prey species in protected and hunted regions during February 2000 – July 2001.

Species	Mean animal density per km ²				Mean group density per km ²			
	Protected ^a	Hunted ^a	t	P	Protected ^a	Hunted ^a	t	P
Agouti (<i>Dasyprocta punctata</i>)	10.5 (2.99)	7.52 (2.42)	1.60		8.44 (2.50)	7.52 (2.42)	0.65	
White-nosed coati (<i>Nasua nasua</i>)	22.58 (3.93)	52.89 (15.31)	4.70	< 0.05	4.04 (0.52)	10.59 (2.03)	7.65	< 0.05
Brocket Deer (<i>Mazama sp.</i>)	3.11 (0.74)	1.76 (0.35)	4.00	< 0.05	3.08 (0.73)	1.76 (0.35)	3.95	< 0.05
White-tailed deer (<i>Odocoileus virginianus</i>)	1.18 (0.38)	1.32 (0.52)	0.54		1.18 (0.38)	1.16 (0.43)	0.10	
White-Lipped Peccary (<i>Tayassu pecari</i>)	9.59 (7.38)	0.00 (7.38)	2.25	< 0.05	0.49 (0.36)	0.00 (0.36)	3.38	< 0.05
Collared Peccary (<i>Tayassu tajacu</i>)	8.12 (2.49)	2.38 (1.01)	5.24	< 0.05	2.58 (0.78)	1.38 (0.56)	3.10	< 0.05
Howler Monkey (<i>Alouatta pigra</i>)	6.14 (2.64)	N/A	-	-	1.53 (0.65)	N/A	-	-
Spider Monkey (<i>Ateles geoffryii</i>)	52.52 (16.59)	N/A	-	-	8.34 (2.63)	N/A	-	-
Nine-banded Armadillo (<i>Dasypus novemcinctus</i>)	N/A	9.49 (7.68) ²	-	-	N/A	9.49 (7.68) ²	-	-
Paca (<i>Agouti paca</i>)	N/A	3.65 (3.03) ²	-	-	N/A	3.65 (3.03) ²	-	-

^a— Point estimate with standard deviation shown in parentheses

² - Data from Baur (1999)

N/A – Estimates not available

Table 1-2. Frequency of occurrence, relative biomass, and number of prey consumed by jaguar in hunted (n=23 scats) and protected (n=53 scats) areas of the Maya Biosphere Reserve, Guatemala, February 2000-July 2001.

Prey	<u>Frequency of occurrence(%)</u>		<u>Prey weight (kg)</u>	<u>Correction Factor</u>	<u>Relative Biomass Consumed (%)</u>	
	Hunted	Protected			Hunted	Protected
Collared Peccary (<i>Tayassu tajacu</i>)	30.43	9.43	17.53	2.59	23.35	8.05
White-Lipped Peccary (<i>Tayassu pecari</i>)	4.35	7.55	29.38	3.01	3.88	7.49
White-tailed deer (<i>Odocoileus virginianus</i>)	4.35	7.55	35.28	3.21	4.14	7.99
Brocket Deer (<i>Mazama sp.</i>)	0.00	5.66	16.70	2.57	0.00	4.80
Nine-banded Armadillo (<i>Dasypus novemcinctus</i>)	39.13	54.72	4.69	2.14	24.81	38.61
White-nosed coati (<i>Nasua nasua</i>)	34.78	28.30	3.18	2.09	21.53	19.50
Agouti (<i>Dasyprocta punctata</i>)	8.70	7.55	2.81	2.08	5.36	5.18
Paca (<i>Agouti paca</i>)	13.04	1.89	6.04	2.19	8.46	1.36
Monkeys	8.70	0.00	7.30	2.24	5.77	0.00
Birds	0.00	5.66	2.30	2.06	0.00	3.84
Porcupine (<i>Coendou mexicana</i>)	0.00	0.00	2.00	2.05	0.00	0.00
Northern Tamandua (<i>Tamandua mexicana</i>)	0.00	1.89	6.15	2.20	0.00	1.37
Kinkajou (<i>Potos flavus</i>)	4.35	0.00	3.30	2.10	2.71	0.00
Grey Fox (<i>Urocyon cinereargenteus</i>)	0.00	0.00	2.65	2.07	0.00	0.00
Unknown Deer	0.00	1.89	26.00	2.89	0.00	1.80

¹ - From Ackerman et al., 1984

Table 1-3. Prey frequency of items found in jaguar and puma scats collected in hunted and protected regions of the Maya Biosphere Reserve, Guatemala. Expected frequencies were derived from point estimates of the number of collectible scats and prey density.

Prey species	<u>Jaguar</u>				<u>Puma</u>			
	<u>Observed prey item</u>		<u>Expected prey item</u>		<u>Observed prey item</u>		<u>Expected prey item</u>	
	<u>frequency</u>		<u>frequency</u>		<u>frequency</u>		<u>frequency</u>	
	Hunted	Protected	Hunted	Protected	Hunted	Protected	Hunted	Protected
<i>Collared Peccary</i> (<i>Tayassu tajacu</i>)	4.16	3.83	1.82	7.26	4.33	4.50	6.20	8.03
White-Lipped Peccary (<i>Tayassu pecari</i>)	1.00	3.33	0.02	1.99	1.00	0.50	0.06	2.20
White-tailed deer (<i>Odocoileus virginianus</i>)	1.00	3.13	2.48	5.39	6.66	10.9	8.46	5.96
Brocket Deer (<i>Mazama sp.</i>)	0.00	2.03	2.24	8.36	16.34	14.1	7.63	9.24
Nine-banded Armadillo (<i>Dasypus novemcinctus</i>)	6.33	11.83	3.14	2.56	0.00	2.00	10.7	2.83
White-nosed coati (<i>Nasua nasua</i>)	6.33	22.00	4.05	8.65	0.50	1.00	13.81	9.56
Agouti (<i>Dasyprocta punctata</i>)	0.83	3.00	1.99	4.76	18.49	12.00	6.80	5.26
Paca (<i>Agouti paca</i>)	1.50	0.50	1.96	4.19	16.65	7.00	6.69	4.64
Monkey	1.33	0.00	3.35	7.15	9.83	4.0	11.41	7.90

Table 1-4. Results of chi-square test for zero prey selection from scat data of jaguar in the protected region Maya Biosphere Reserve, Guatemala. The row labeled “Prey Freq” gives the number of scats containing the specified prey items. Expected frequencies were derived from point estimates of the number of collectible scats (λ_i) and prey density (d_i), and assumed no selectivity. Adjusted P-value based on B = 200 parametric bootstrap replicates to correct for overdispersion.

	Prey species ¹						
	AGPA+ DAPU	MASP	ODVI	DANO	NANA	TASP	MONK
Prey Freq. ²	4	2.53	3.63	22.5	12.33	4.33	0.5
Expected	8.85	8.28	5.34	8.57	2.53	9.17	7.08
X_i^2	3.2283	4.7919	0.6126	27.335	39.9288	3.128	7.1291
Adjusted P-value	0.097	0.043	0.454	<.001	<.001	0.099	0.011
(SE)	0.002	0.001	0.003	<.001	<.001	0.002	0.000
λ_i	1.78	6.52	10.97	2.19	1.52	7.24	3.27
SD (λ_i) ³	0.71	2.61	4.39	0.88	0.61	2.90	1.31
d_i	12.05 ⁴	3.08	1.18	9.49 ⁴	4.04	3.07	5.25
SD (d_i)	5.53	0.73	0.38	7.68	0.52	1.14	1.76

¹- AGPA+DAPU: Paca (*Agouti paca*) and Agouti (*Dasyprocta punctata*); MASP: Brouket deer (*Mazama sp.*); ODVI: White-tailed deer (*Odocoileus virginianus*); DANO: Armadillo (*Dasypus novemcinctus*); NANA: Coati (*Nasua nasua*); TASP: Peccary (*Tayassu tajacu* and *T. pecari*.); MONK: Monkeys (*Ateles geoffreyi* and *Alouatta pigra*)

²- A value of 0.5 was added to all cells (Agresti, 2002)

³- Assumed to be 40% of λ_i (see Link & Karanth, 1994)

⁴- Data from Baur (1999)

⁵- Hunted region not analyzed due to small sample size.

Table 1-5. Frequency of occurrence, relative biomass, and number of prey consumed by puma in hunted (n=82 scats) and protected (n=63 scats) areas of the Maya Biosphere Reserve, Guatemala, February 2000-July 2001.

Prey	Frequency of occurrence (%)		Prey weight (kg)	Correction factor	Relative biomass consumed (%)	
	Hunted	Protected			Hunted	Protected
Collared Peccary (<i>Tayassu tajacu</i>)	7.32	7.94	17.53	2.59	5.99	6.74
White-Lipped Peccary (<i>Tayassu pecari</i>)	1.22	1.59	29.38	3.01	1.16	1.57
White-tailed deer (<i>Odocoileus virginianus</i>)	12.20	19.05	35.28	3.21	12.37	20.04
Brocket Deer (<i>Mazama sp.</i>)	24.39	25.40	16.70	2.57	19.80	21.39
Nine-banded Armadillo (<i>Dasypus novemcinctus</i>)	1.22	3.17	4.69	2.14	0.82	2.22
White-nosed coati (<i>Nasua nasua</i>)	0.00	3.17	3.18	2.09	0.00	2.17
Agouti (<i>Dasyprocta punctata</i>)	29.97	22.22	2.81	2.08	19.69	15.14
Paca (<i>Agouti paca</i>)	29.27	17.46	6.04	2.19	20.24	12.53
Monkey	14.63	9.52	7.30	2.24	10.35	6.99
Birds	6.10	9.52	2.30	2.06	3.97	6.43
Porcupine (<i>Coendou mexicana</i>)	2.44	0.00	2.00	2.05	1.58	0.00
Northern Tamandua (<i>Tamandua mexicana</i>)	0.00	0.00	6.15	2.20	0.00	0.00
Kinkajou (<i>Potos flavus</i>)	4.88	4.76	3.30	2.10	3.24	3.28
Grey Fox (<i>Urocyon cinereargenteus</i>)	1.22	0.00	2.65	2.07	0.80	0.00
Unknown Deer	0.00	1.59	26.00	2.89	0.00	1.51

¹ - From Ackerman et al., 1984

Table 1-6. Results of chi-square test for zero prey selection from scat data of puma in protected and hunted regions of the Maya Biosphere Reserve, Guatemala. The row labeled “Prey Freq” gives the number of scats containing the specified prey items. Expected frequencies derived from point estimates of the number of collectible scats (λ_i) and prey density (d_i) and assumed no selectivity. Adjusted P-value based on B = 200 bootstrap replicates to correct for overdispersion.

	Prey Species ¹							
	AGPA	MASP	ODVI	DANO	DAPU	NANA	TASP	MONK
<u>Protected Region</u>								
Prey Freq.	7	14.1	10.9	1	12	2	5	4
Expected	4.67	9.31	6	9.63	5.29	2.85	10.3	7.96
X_i^2	1.27	2.96	4.49	9.34	9.38	0.26	3.34	2.29
Unadjusted P-value	0.26	0.085	0.034	0.002	0.002	0.607	0.068	0.13
Adjusted P-value	0.341	0.11	0.0432	0.013	0.003	0.617	0.089	0.157
(SE)	0.008	0.002	0.001	0.002	<.001	0.003	0.002	0.002
λ_i	2.76	6.52	10.97	2.19	1.36	1.52	7.24	3.27
SD (λ_i)	1.10	2.61	4.39	0.88	0.54	0.61	2.90	1.31
d_i	3.65 ²	3.08	1.18	9.49 ²	8.40	4.04	3.07	5.25
SD (d_i)	3.03	0.73	0.38	7.68	2.50	0.52	1.14	1.76
<u>Hunted Region</u>								
Prey Freq. ³	17.15	16.84	7.16	1	19	0.5	5.83	10.33
Expected	7.22	8.22	9.12	14.89	7.33	11.53	7.21	12.3
X_i^2	15.069	10.1	0.476	16.02	20.53	12.39	0.29	0.374
Adjusted P-value	0.002	0.004	0.522	0.003	<.001	0.002	0.636	0.583
(SE)	<.001	<.001	0.004	0.001	<.001	<.001	0.005	0.005
λ_i	2.76	6.52	10.97	2.19	1.36	1.52	7.24	3.27
SD (λ_i) ⁴	1.10	2.61	4.39	0.88	0.54	0.61	2.90	1.31
d_i	3.65 ²	1.76	1.16	9.49 ²	7.52	10.59	1.39	5.25
SD (d_i)	3.03	0.35	0.43	7.68	2.42	2.03	0.92	1.76

¹- AGPA: Paca (*Agouti paca*); MASP: Brocket deer (*Mazama sp.*); ODVI: White-tailed deer (*Odocoileus virginianus*); DANO: Armadillo (*Dasypus novemcinctus*); DAPU: Agouti (*Dasyprocta punctata*); NANA: Coati (*Nasua nasua*); TASP: Peccary (*Tayassu tajacu* and *T. pecari.*); MONK: Monkey (*Ateles geoffreyi* and *Alouatta pigra*)

²- Data from Baur (1998)

³- A value of 0.5 was added to all cells (Agresti, 2002)

⁴- Assumed to be 40% of λ_i (see Link and Karanth, 1994)

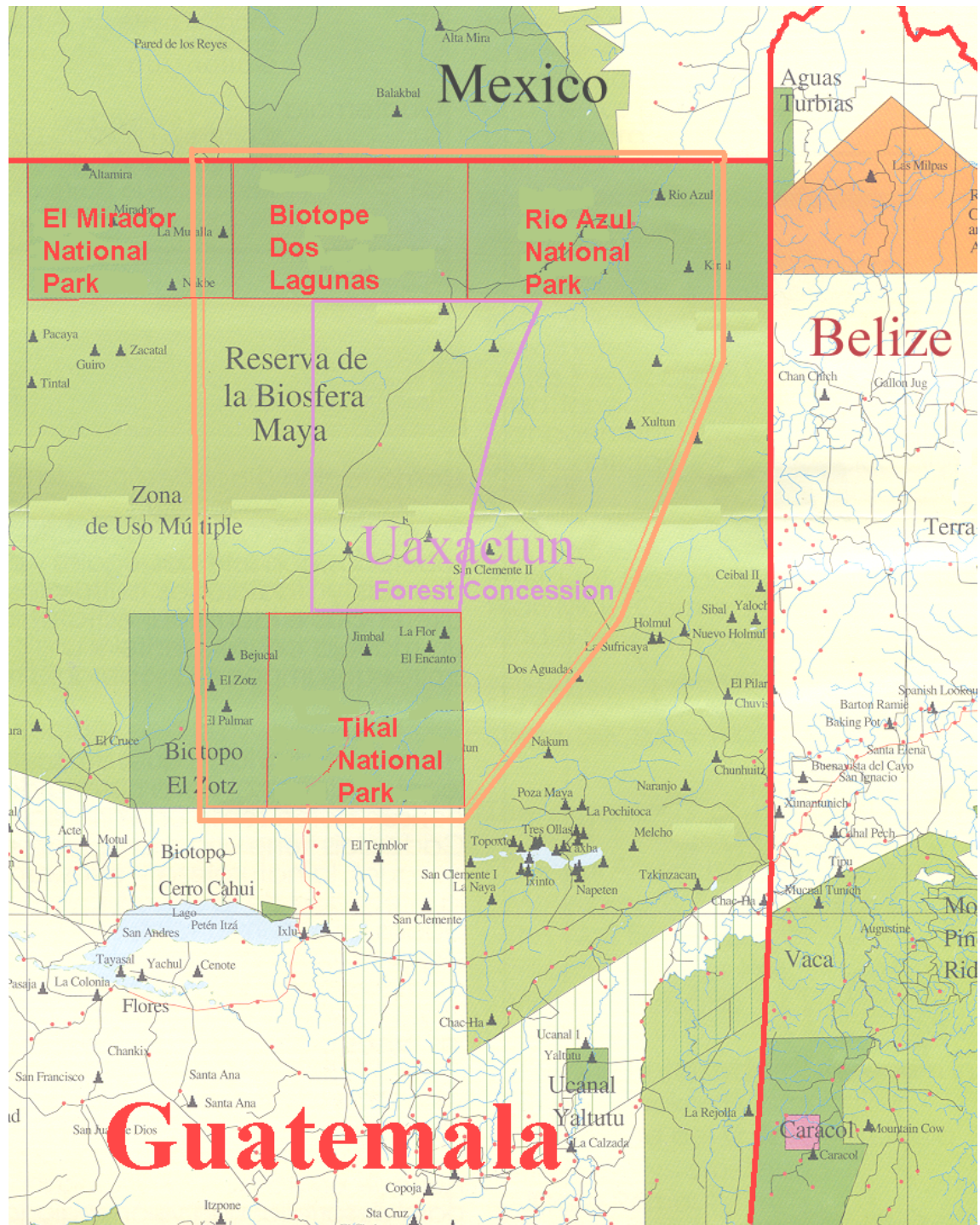


Figure 1-1. Map of management units within the Maya Biosphere Reserve, Guatemala, 2001.

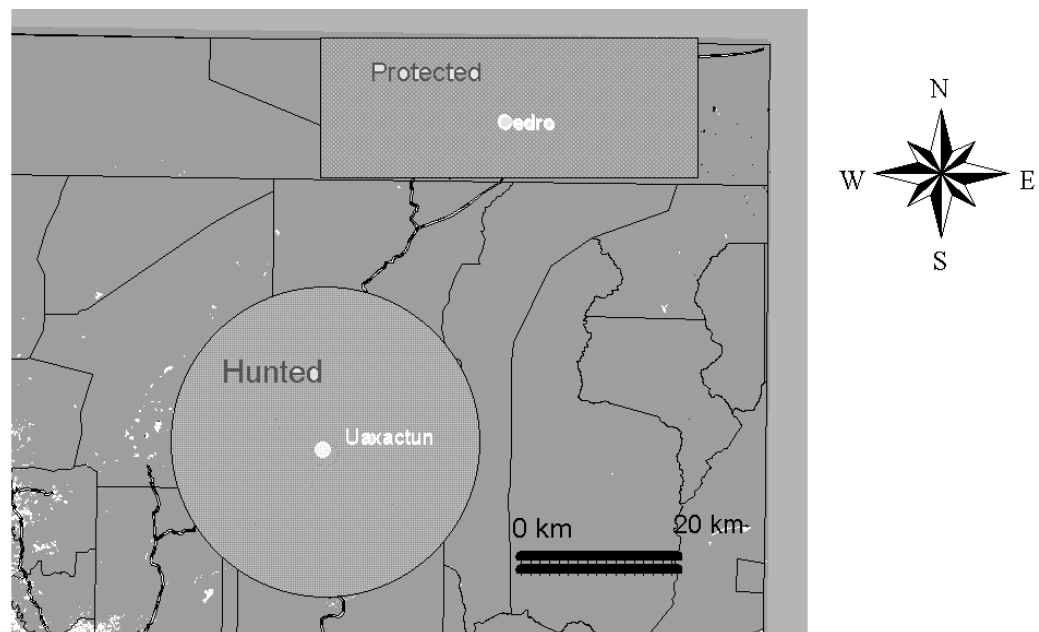


Figure 1-2. Map of hunted (represented by circle surrounding Uaxactun) and protected areas within the Maya Biosphere Reserve, Guatemala, 2001.

CHAPTER 2

THE USE OF REMOTE-TRIGGERED CAMERA SYSTEMS TO MONITOR JAGUAR AND PUMA IN THE MAYA BIOSPHERE RESERVE, GUATEMALA

Introduction

Large cats are notoriously difficult to survey due to their secretive habits, solitary nature, and low population densities. Most of the ecological research performed on large felids since the 1970's has relied on radio-telemetry to follow movement patterns and determine home range requirements and habitat preferences (Schaller & Crawshaw, 1980; Sunquist, 1981; Logan and Sweeney, 2001). However, telemetry studies are hampered by large requirements of capital and equipment, trained manpower, and logistical challenges associated with capture, monitoring, and length of time needed to obtain adequate data.

Remote-triggered cameras or "camera-traps" have become a useful tool in the study of wildlife ecology. Various types of camera-traps have been used to photograph wildlife since the early 1900's (Nesbit, 1926; Shiras, 1936). Early systems were crude and required mechanical trip mechanisms. Later models utilized trip-plates, photic cells, and infrared beams (Seydack 1984; Joslin 1986).

Research designs using camera traps recently have become more advanced and widely applied. Camera traps have been used to monitor nest predation (Buler & Hamilton, 2000), wildlife movement through highway underpasses (Foster and Humphrey, 1995), and to determine relative animal abundance (Main & Richardson, 2002). Recent studies have used cameras to estimate the population size of deer (*Odocoileus virginianus*) (Koerth et al., 1997) and grizzly bear (*Ursus arctos*) (Mace et al., 1994). Karanth & Nichols (1995) developed a statistically rigorous method for estimating tiger (*Panthera tigris*) populations that has since been replicated at other sites in India and Malaysia (Karanth & Nichols, 2000; Kawanishi, 2002), and with jaguar (*Panthera onca*) in Belize (S. Silver, in press). The objective of this research was to survey the abundance of jaguar and puma in northeastern Guatemala using camera-trap methodology.

Study Area

Fieldwork was conducted within the 11,600 km² Maya Biosphere Reserve (MBR) in the lowland tropical rainforests of the Department of Peten, Guatemala. Camera-trapping was conducted inside the Rio-Azul/El Mirador National Park, Biotope Dos Lagunas and along the boundary with the Uaxactun Community Forest Concession. Within the concession, inhabitants of the village of Uaxactun are allowed to benefit economically from the sustainable management of natural resources inside the concession limits. Subsistence hunting, timber harvest, small-scale agriculture, and the harvest of non-timber products are activities that occur within the concession boundaries. The national park and biotope (hereafter referred to as Rio Azul) are fully protected areas

where hunting is prohibited; park guards attempt to enforce the moratorium. The altitudes in the study area range from 100-400 m above sea level. Mean monthly temperature varies from 22°C in January to 34°C in June. Annual rainfall averages 1200-1500 mm and falls mainly during the wet season (June-January). Most of this rain drains into the watershed of the Rio Azul River. During the pronounced dry season (February-May), surface water is limited and available only at scattered waterholes, lakes, and in the deeper sections of the Rio Azul River.

The MBR is almost completely covered by mature forest classified as Subtropical Moist (Holdridge et al., 1971). Schulze and Whitacre (1999) recognized 11 habitat types within the MBR based upon the variables of topographic position, slope, soil clay content, and soil rock content. These habitat types can be simplified into three categories; upland forest, bajo, and transitional forest. Upland forest is found on higher sites and is characterized by a high, closed tree canopy. Bajo forest has a low, somewhat open canopy and is seasonally inundated. Transitional forest consists of an intermediate stage between upland and bajo forest types.

Materials and Methods

The field portion of this study began in March 2001 and continued until July 2001. Camera-traps were placed in locations, such as active game trails and other areas, where photo captures were likely to be maximized. Optimal camera-trap locations were identified during surveys along old logging roads, trails, ephemeral streambeds and the park boundary. Distribution of camera-trap locations followed mark-recapture design described by Karanth and Nichols (1998). Trap locations were spaced a minimum of 4 km apart. Six to nine pairs of cameras were positioned and activated for 10- to 23-day trapping sessions.

Two cameras were placed at each trap location, one opposite the other. The pattern of spots and rosettes on the pelage is unique to each jaguar, which allows them to be identified individually. Because the spot patterns are not symmetrical, both flanks of the animal have to be photographed; however, comparisons of pelage pattern differences between captured jaguars are made from the same flank. Puma do not typically possess distinguishing marks and usually could not be individually identified. Distance between cameras was 5-10 m, depending on trail width. The infrared beam was located approximately 41 cm (16 in) above the ground where it was most likely to be triggered by the body of an adult jaguar or puma. All vegetation within arms width of the infrared beam was removed with a machete to reduce the likelihood of the system being triggered by leaves or branches moving across the beam. New batteries and film were placed in all units before placement. Once a pair of camera-traps was placed at a trap location, both units were tested to ensure they were operating properly. A GPS location was taken for each trap locality and allowed for precise calculation of the polygon enclosed by the trap array. Traps were not checked again until the end of the trapping session, unless located on the primary road. Traps located along the road were checked once per week.

Both TrailMaster[®] TM-1500 (Goodson Associates, Inc., Kansas, USA) and Camtrakker[®] (CamTrak South Inc., Georgia, USA) brand remote camera systems were used in this study. The TrailMaster system utilizes an active infrared system with an electrical trigger that is activated when a narrow, infrared beam is broken by an object passing between the transmitter and receiver. The Camtrakker system uses a passive

infrared system. The thermal radiation produced by an animal will activate the camera when it enters into the conical infrared beam that is emitted by this system. Camera systems of a single brand were used for any given trap location. The TrailMaster system was used predominately. Four Camtrakker camera-traps were used only during the final trapping session as replacements for damaged and vandalized TrailMaster systems.

Relative abundance was calculated for jaguar and puma following Kawanishi (1995). The total number of photographic captures was divided by the total number of camera nights then, multiplied by 100 to give an index of captures per 100 trap nights. A camera night is defined as any 24-hour period where a trap site had functioning camera traps.

Results

Camera trapping was conducted during four separate trapping sessions in 2001: March 3-26, April 3-May 12, May 15-June 11 and June 21-July 17. A trap-night was tallied if at least one of the cameras was functioning during the time period from 1500 to 0900 hours. Using 32 different trap locations, a total area of approximately 300 km² was sampled during 814 trap nights (Figure 2-1). Thirteen different species of mammals and birds were captured during the sampling period (Table 2-1). Curassow (*Crax rubra*) were the most frequently captured animals (4.7 photo-captures per 100 trap nights), followed by puma (3.9 captures/100 trap nights), and ocellated turkey (*Meleagris ocellata*) (3.5 captures/100 trap nights).

Relative abundance of large cats was 2.0 jaguar and 3.9 puma/100 trap nights. Four individually identified jaguars were photographed ≥ 1 time during 16 separate capture events; three of which were male and one was of unknown gender. Puma were photographed on 32 different occasions. The number of individual puma could not be determined due to a lack of identifiable marks. Captures of both puma and jaguar occurred at 6 trap locations. No more than one felid of either species was captured at the same trap during any single trap night.

The first trapping session (106 trap nights) was conducted in an area dominated by lowland swamp forest called “bajo.” No jaguar were photographed during this trapping session nor from any subsequent traps placed within bajo habitat, but puma were captured in bajo habitat on two occasions (0.9 puma/100 trap nights). Excluding the few traps located in bajo habitat from the analysis, 27 trap locations produced 16 captures of jaguar during 585 trap nights (2.7 jaguar/100 trap nights).

Sixteen camera-trap stations operated for 378 trap nights and successfully sampled a polygon of 85 km² in compliance with established protocols for estimating absolute abundance (Karanth & Nichols, 1998). Within this polygon, no “holes” or gaps were sufficiently large to permit a jaguar to maintain a home range that did not overlap with at least one trap. The maximum distance between recaptures for identifiable male jaguars was 16.1 km and mean maximum distance moved (MMDM) between recaptures was 12.4 km. When a buffer area was calculated measuring one half MMDM extending outward from the trap polygon (Wilson & Anderson, 1985), the area sampled increased to 540 km² (Figure 2-2). Jaguars within this area appeared to have overlapping home ranges. All three males were photographed at two different camera stations, with two males being observed at each station. The number of individually identifiable jaguars (4) was too small to rigorously estimate population density with the program CAPTURE (Otis et al., 1978). However, minimum densities of jaguar computed from the data was

0.7 jaguar/ 100 km². Assuming each adult male has a home range that overlaps exclusively with at least two females (Schaller & Crawshaw, 1980), a conservative approximation for jaguar density in the study area was 1.7 jaguar/100 km².

Humans, not including tourists, park personnel, or members of this research project, were photographed on four different occasions and consisted of three different groups of people. Of the twenty-three camera traps used in this study, 6 cameras from four trap locations were vandalized or stolen. One camera was destroyed as it became inundated by rising water levels.

Discussion

Camera-traps as Survey Instruments

The use of camera-trap methodology to estimate abundance of jaguar and puma is a viable alternative to radio-telemetry studies, but is not without problems. Consideration must be given to the logistical difficulties associated with applying this method in remote areas with low jaguar population densities or the potential for vandalism and theft in areas with human activity. The remote nature of the Rio Azul and the lack of access trails and detailed maps of existing trails hampered this study. Only one poorly maintained jeep trail provides vehicular access through the site. Trap locations had to be surveyed on foot and mapped out before deploying camera-traps. Once trap locations were identified, it usually took 4-8 days to put 14-19 traps into operation. Other researchers have experienced similar difficulties. Kawanishi (2002) spent an enormous effort (14,054 camera-trap nights) to obtain the requisite number of tiger photographs needed to estimate density in a remote region within the Taman Negara National Park, Malaysia. Her study was hampered by the amount of time required to locate trap sites, the lack of footpaths or roads, and low tiger density. In contrast, Karanth and Nichols (2000) have used this method successfully in the forest reserves of India that have high tiger densities and easy access via vehicular roads and footpaths.

The potential use of camera-trap methodology is constrained by the possibility of theft or vandalism of camera units. The Trailmaster camera system consists of three separate components that are difficult to protect from vandalism, and are relatively expensive or difficult to repair in the field. Fewer trap nights will accumulate if a camera-trap is lost. Furthermore, if absolute abundance is the objective, stolen or vandalized cameras can create gaps in the trap spacing such that the data from adjacent traps are unusable for estimating population density. During this study, 6 cameras were stolen, all of which were located along roads or paths infrequently traversed by people. As a result of these thefts, data were lost and some areas had to be re-sampled. Furthermore, due to repeated losses of cameras to theft and vandalism, I concluded that trapping within the Uaxactun Forest Concession was impractical due to the higher amount of human activity and increased risk of theft. Other studies have encountered similar problems. Tikal National Park (576 km²) is located in Guatemala and borders the Uaxactun Forest Concession to the south. During 3 months in Tikal National Park, Kawanishi (1995) lost 7 TrailMaster cameras to theft, and had various components of the camera traps vandalized. Even in the remote Taman Negara National Park, Kawanishi (2002) lost 7 cameras to theft or vandals. Karanth (1995) has been able to reduce theft by removing cameras each morning following their placement the previous afternoon.

CamTrakker brand cameras consist of a single component encased in a durable housing and may be less vulnerable to vandalism, but this was not tested.

Jaguar and Puma Abundance in the Maya Biosphere Reserve, Guatemala

Estimates of abundance are critical to understanding potential impacts of human activity, habitat quality, and management activities on animal populations. This study calculated two estimates of abundance, including photographs/100 trap nights (both jaguar and puma) and individuals/100 km² (jaguar only). Jaguar densities estimated by this study may be conservative, because the MMDM used to establish buffer width around the 85-km² trap polygon was biased by the all male sample. Male jaguar, as with other felids, generally have larger home ranges than females (Crawshaw, 1995). Consequently, the buffer width calculated was larger than if females had been factored into the estimate. Thus, the resulting approximation of jaguar density in the Maya Biosphere Reserve is considered a conservative estimate.

Estimated jaguar density reported by this study (1.7 jaguar/100 km²) is equivalent to results reported from Jalisco-Mexico (1.7/100 km², Nunez et al., 2002), but less than recent estimates of 8.8 jaguar/100 km² reported for the Cockscomb Basin, Belize (Silver, in press). The similarity between estimates from this study and Mexico could be attributed to their corresponding environmental conditions. Both sites undergo extreme seasonal variations in rainfall that result in a dry season where standing water is limited to occasional waterholes. The size and distribution of these water sources could influence the distribution and abundance of jaguar and their prey. By contrast, the Cockscomb Basin in Belize has more water available with an annual precipitation that is 2-3 times greater than the study sites in Mexico or Guatemala.

The abundance of jaguar and puma reported during this study was substantially greater than was reported from Tikal National Park (Table 2-2). Camera-trapping in the Rio Azul/El Mirador National Park and Biotopo Dos Laguna resulted in a photographic index of jaguar abundance (2.0/100 trap nights) which exceeds estimates from Tikal (0.2/100 trap nights) by ten-fold. Similarly, puma abundance (5.1/100 trap nights) in this study was more than five times greater than Tikal (0.9/100 trap nights). These results suggest that the abundance of jaguar and puma is lower in Tikal National Park as compared to the more remote Rio-Azul/El Mirador National Park and Biotopo Dos Lagunas.

In Tikal, Kawanishi (1995) placed her camera traps along transect lines with varying degrees of human activity. Tikal National Park occurs at the southernmost border of the MBR, has access from Uaxactun to the north, and from various communities along the southern border. A greater number of people trespass into Tikal National Park to harvest wildlife and other non-timber products than they do in the northern part of the Maya Biosphere Reserve. Also, thousands of paying visitors enter the park every year to visit the archaeological ruins. The lower rates of photographic captures of jaguar and puma could potentially have been due to anthropogenic influences on cat behavior, although the nocturnal and secretive behaviors of these large predators makes this explanation unlikely.

The lower abundance of jaguar and puma in Tikal is more likely a consequence of reduced prey populations in that area. Hunting pressure from the communities bordering Tikal National Park apparently impact the populations of game animals inside the park borders (Polisar, 1998). Likewise, studies from the neighboring Uaxactun forest

concession reveal that subsistence hunting can significantly reduce the populations of brocket deer (*Mazama* sp.) and peccaries (*Tayassu tajacu* and *T. pecari*), all of which are important prey for both jaguar and puma. Peccaries and brocket deer constituted 23-34% occurrence in jaguar diets and 33-34% occurrence in puma diets within the Maya Biosphere Reserve (Novack, 2003b). Although, it was hypothesized that human hunting pressure within the Uaxactun forest concession would result in reduced numbers of jaguar and puma as a consequence of a depleted prey base, this hypothesis could not be tested directly due to the potential camera losses associated with vandalism and theft in the concession area. However, hunting activity that reduces prey availability can alter patterns of prey selection of carnivores such as wolves (Jędrzejewski et al., 2000), or jaguar and puma (Novack, 2003b). Prey availability can influence carnivore densities, survival, reproduction and behavior in ways that affect population viability (Fuller & Sievert, 2001). Additional research is needed to determine whether the abundance of jaguars and pumas is reduced in areas where unregulated subsistence hunting impacts prey populations. Until such studies are realized, the unregulated activity of subsistence hunters inside the Maya Biosphere Reserve should be considered as having an unknown impact on the long-term persistence of jaguar and puma. Wildlife managers should be cautious in allowing such unregulated hunting activity to continue indefinitely. Management plans should be developed that regulate the exploitation of game animals in areas where jaguar and puma reside.

Table 2-1. Number of photographic captures of 13 species from 32 trap locations and 814 trap nights in northeastern Guatemala, 2001.

Species	Number of photographic captures
Jaguar (<i>Panthera onca</i>)	16
Puma (<i>Puma concolor</i>)	32
Ocelot (<i>Leopardus pardalis</i>)	9
Brocket deer (<i>Mazama sp.</i>)	5
White-tailed deer (<i>Odocoileus virginianus</i>)	0
Tapir (<i>Tapirus bairdii</i>)	11
Collared Peccary (<i>Tayassu tajacu</i>)	1
White-lipped peccary (<i>Tayassu pecari</i>)	8
Opposum (<i>Didelphis sp.</i>)	5
Coati (<i>Nasua narica</i>)	2
Curassow (<i>Crax rubra</i>)	38
Ocellated Turkey (<i>Meleagris ocellata</i>)	29
Crested Guan (<i>Penelope purpescens</i>)	1
Other bird	1

Table 2-2. Comparative captures from remote triggered cameras in upland forest of Tikal National Park vs Rio Azul/Dos Lagunas, Guatemala, 2001.

Species	Tikal ¹	Rio Azul/Dos Lagunas
Jaguar (<i>Panthera onca</i>)	1	16 (4 individuals)
Puma (<i>Puma concolor</i>)	5	30
Ocelot (<i>Leopardus pardalis</i>)	6	8
Margay (<i>Leopardus wiedii</i>)	6	0
Brocket Deer (<i>Mazama sp.</i>)	2	4
White-tailed deer (<i>Odocoileus virginianus</i>)	5	0
Collared Peccary (<i>Tayassu tajacu</i>)	3	1
White-lipped peccary (<i>Tayassu pecari</i>)	0	8
Tapir (<i>Tapirus bairdii</i>)	1	9
Camera nights ²	574	585
Number of trap stations	18	27
Season	Mar-May 1994	Mar-Jul 2001

¹ After (Kaewanishi, 1995)

² 2 cameras = 1 night, 1 camera = .5 night

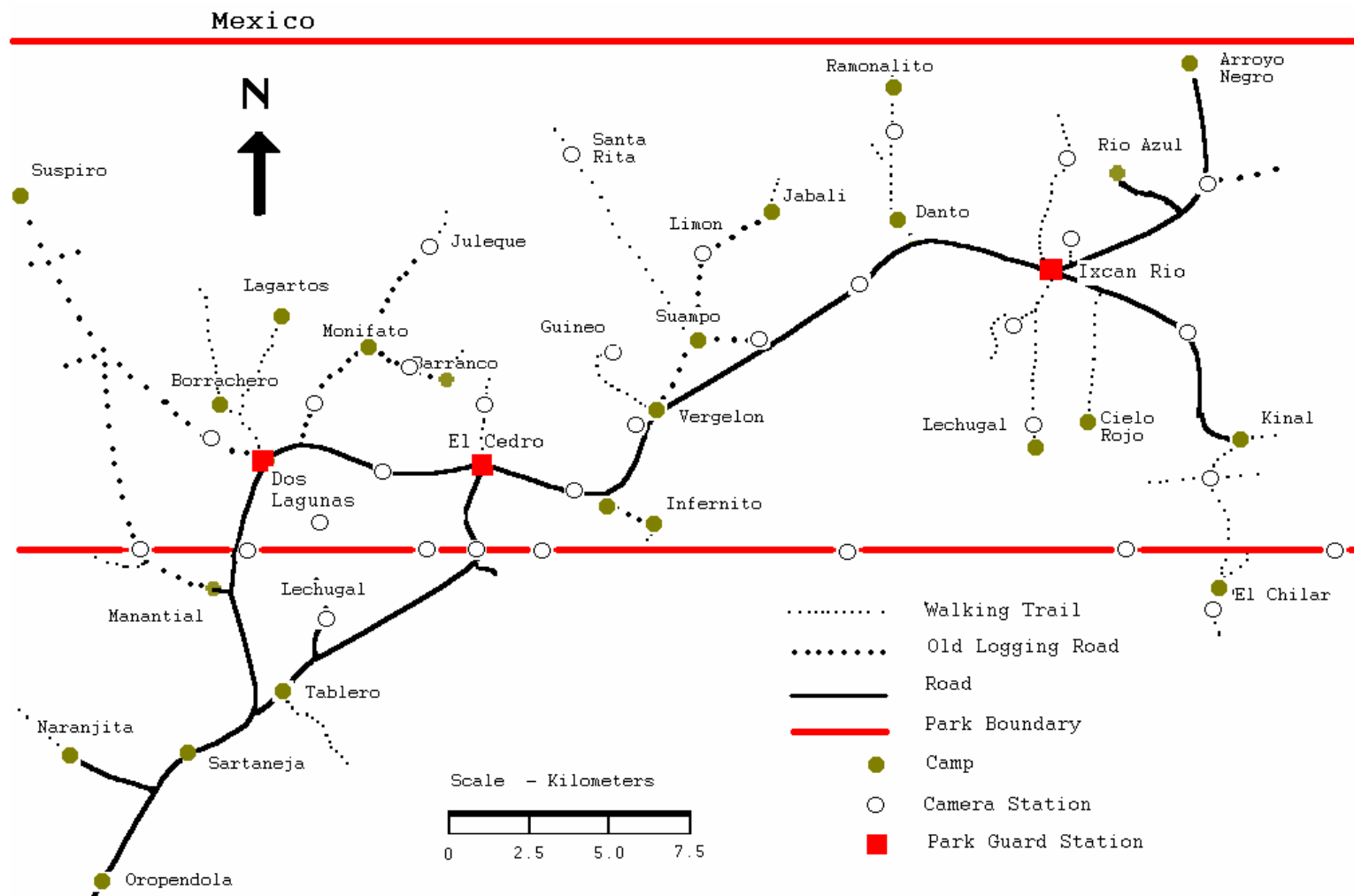


Figure 2-1. Map of camera-trap locations, roads and trails within Rio Azul/El Mirador National Park and Biotope Dos Lagunas, Guatemala, 2001.

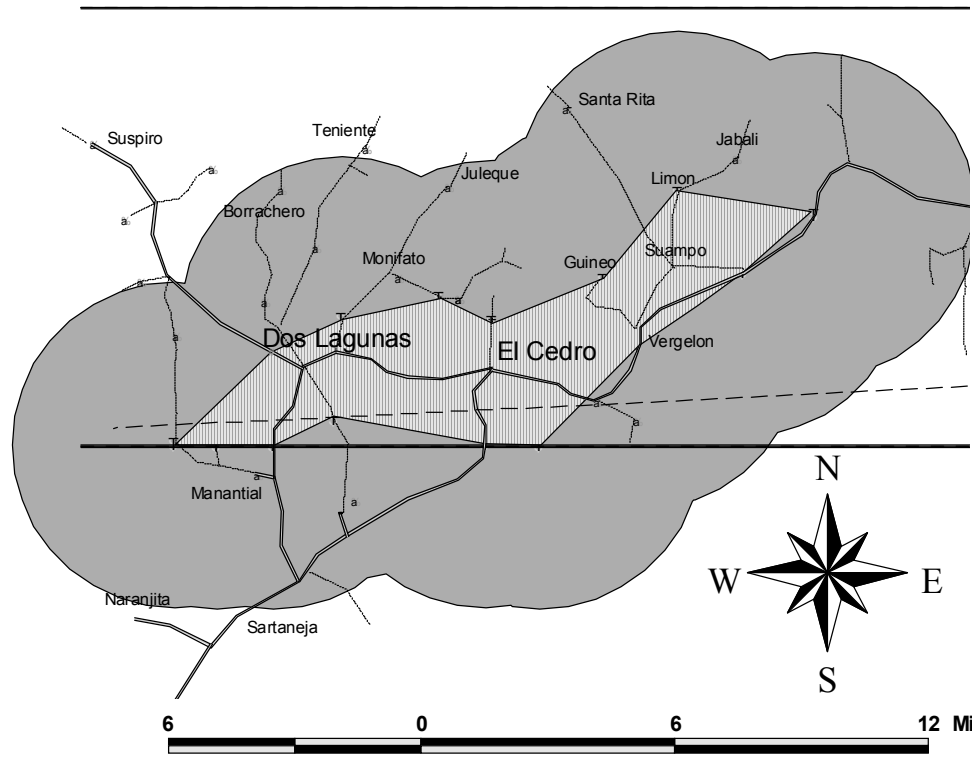


Figure 2-2. Map of polygon and surrounding buffer area surveyed with camera-traps.

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BIOGRAPHICAL SKETCH

I was raised the oldest son of an officer in the U.S. Air Force. My father's occupation meant a life of continuous relocation. Every three years, he would be reassigned and we would move to a new place. My travels took me from Ohio and Illinois, to Germany and Spain.

My ambition to work in wildlife conservation began at a very young age. Camping and fishing trips were my most memorable experiences from before entering elementary school. When we first learned to use the school library, I repeatedly checked out books about nature and wild animals. The Time Life book *Bears and Other Carnivores* was always my boyhood favorite.

As a freshman in high school, my direction in life was solidified after making my first major book purchase, a hardback book entitled *The Doomsday Book of Animals* by David Day. This book contained a plentiful supply of illustrations. Each picture was a beautifully vivid, artistic rendition of an animal species that had gone extinct such as Stellar's sea cow, Atlas lion, Bali tiger, quagga and dodo. Besides the pictures, each animal had a brief excerpt about the reasons for its extinction. Every description told the same story. Mankind was directly to blame, sometimes in a very brutal and callous manner, for the ultimate disappearance of every species of animal in that book. Beauty destroyed without forethought by stupidity and greed. I did not understand at the time how civilized, adult man could be so despicable. Then and there, I firmly resolved to work against the further addition of animals to that long list of extinctions.

In 1992, after finishing high school and community college in Germany, I fulfilled a longstanding ambition by arriving at the University of Florida to be fully immersed in classes about wildlife, ecology and conservation. At the University of Florida, I was actively involved in the student body, served on student council and was the student chapter vice president of the Wildlife Society. I graduated from the University of Florida in August 1994 with a Bachelor of Science in Forest Resource Conservation.

After leaving the University, I worked at various seasonal jobs; I evaluated the effects of forest management and fire regimes upon wood thrush in central Georgia, then censused birds, amphibians and small mammals on industrial timberlands in Washington state. I greatly enjoyed working in the field but felt that my knowledge and abilities could be better utilized elsewhere.

The Peace Corps provided a perfect opportunity for service to my country and to the world at large. Since I had knowledge and an education that was in scarce supply outside of the U.S. and Europe, it was my belief that I could make a bigger difference working in a third world nation as compared one more developed. Consequently, I finished the long application process and headed off with high ideals, aspirations and a backpack full of books.

I served in Honduras for three and a half years where most serve for only two. During that time I proposed, implemented and administered a mammal inventory within a Honduran national park; developed, planned and facilitated a hunter education course; trained Honduran counterparts in the areas of wildlife management and participatory community analysis; facilitated the development of a management plan for Sierra de Agalta National Park; and organized and directed a community in the construction of an aqueduct system with water coming from within the confines of the national park. During my final three months, I supervised and provided support to over 15 Peace Corps volunteers working in the natural resources sector.

I gained real experience in the difficulties posed by working in underdeveloped nations. What I learned was that communities and government agencies must work together to conserve the natural resources and that communities must perceive some direct benefit from their protection. Also, I realized how vitally important it is to strengthen local capacity and collaborate with professionals from the host country. In Guatemala, for example, it is Guatemalans who will, over the long term, contribute the most to the conservation of natural resources in that country.