
Impact of Hunting on Large Vertebrates in the Mbaracayu Reserve, Paraguay

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Abstract: *Over 1,400,000 m of line transect data were collected in collaboration with Ache Indians to determine encounter rates with all large vertebrates in the Mbaracayu Reserve Paraguay. The data were analyzed using logistic regression in order to determine the impact of human hunting on animal encounter rates in the reserve. The method controlled for effects of season, weather, time of day, and habitat in order to statistically isolate the human predation effect. Encounters with the animals themselves as well as fresh signs of their activity allowed us to determine whether lower encounter rates in hunted zones are simply due to increased wariness by target species. Our results show that areas near hunters are hunted more frequently, and that *Dasypus novemcinctus*, *Cebus apella*, *Tapirus terrestris*, and *Mazama spp.* are all encountered at lower rates in those areas than in unhunted zones. We were unable to show that encounter rates with other important game species have been affected by human hunting. Demonstration of local depletion by central place foragers is expected, however, and cannot be used to conclude that prey species are in danger of regional extirpation.*

Impacto de la Captura de Vertebrados Mayores en la Reserva de Mbaracayu, Paraguay

Resumen: *Datos de mas de 1,400,000 m de transectos en linea fueron colectados en colaboración con los indios Ache para determinar las tasas de encuentro con vertebrados mayores en la reserva Mbaracayu del Paraguay. Los datos fueron analizados usando regresión logística para determinar el impacto de la cacería sobre la tasa de encuentros en la reserva. El método fue controlado para aislar el efecto de la depredación humana de los efectos de la estación, el clima, la hora del día y el tipo de habitat. Los encuentros con animales, así como marcas frescas de su actividad nos permitieron determinar si las tasas bajas de encuentros en las zonas de caza son simplemente debidas al incremento en la alerta de las especies blanco. Nuestros resultados muestran que las áreas cercanas a los cazadores son utilizadas mas frecuentemente y que *Dasypus novemcinctus*, *Cebus apella*, *tapirus terrestris* y *Mazama spp.* se encuentran todos en menor proporción que en las áreas no utilizadas para la cacería. No pudimos demostrar que las tasas de encuentros con otras especies de caza importantes han sido afectadas por la caza humana. Esperamos una disminución local debida a la presencia de forrajeros centrales, aunque esto no puede ser utilizado para concluir que las especies de presas se encuentran en peligro de una extirpación regional.*

Introduction

In the Amazon basin more natural habitat is designated as indigenous reserve, than the total protected in all other conservation units (Rylands 1991; IUCN 1992; da Silva & Sites 1995; Peres & Terborgh 1995). In addition,

many federal and state conservation units currently allow extractive activities by native populations. This means the study of native resource use patterns is a critical enterprise in Neotropical conservation.

Recent studies suggest that hunted areas are depleted of game relative to non-hunted areas (Freese et al. 1982; Bodmer et al. 1988, 1994; Peres 1990; Fragoso 1991; Glanz 1991; Silva & Strahl 1991; Vickers 1991; Alvard 1993, 1995), but many of these studies are based on cen-

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sus methods that are problematic. Specifically, most hunting impact studies to date (1) fail to distinguish changes in encounter rates due to evasive prey behavior from changes in animal density; (2) fail to control for the effects of variables other than hunting that might also be associated with differences in animal density; (3) fail to provide independent measures of human hunting activity in areas assumed to be hunted; (4) are based on data collected exclusively on established trails that animals either avoid or use extensively depending on the amount of human activity in the study area; and (5) are based on repeated transects in the same location, but inappropriately assume statistical independence of data and extrapolate to unsampled areas.

The Mbaracayu Reserve is located in the center of the traditional home range of Ache hunter-gatherers who were removed from the reserve area in the 1970s. The Ache have exceptional knowledge of the Paraguayan forest because they lived completely off wild resources until recently and most adults have spent most of their lives in the forest (Hill & Hurtado 1989). The challenge to us was to harness that knowledge in a scientifically useful way and provide precise quantitative information on the density patterns of large vertebrates inside the reserve. The two major goals were to acquire baseline large vertebrate density information in the reserve and to measure the impact of legal and illegal hunting inside the reserve. We described animal densities in the reserve previously (Hill et al. 1996); here we examine the impact of hunting on animal encounter rates. We developed a method of assessing hunting impact that requires little time input from expensive staff and uses multivariate log linear statistical techniques to isolate hunting from other factors that affect vertebrate encounter rates.

The Mbaracayu Reserve

The 60,000-ha Mbaracayu nature reserve and the surrounding quarter million hectare upper Jejui watershed is the largest tract of undisturbed forest in eastern Paraguay and the second largest (after the combined reserve areas in Brazil and Argentina around Yguazu falls) forested area of the Alto Parana formation of the Atlantic Rainforest. The reserve is located at approximately 55° west and 24° south in an area drained to the west by the Paraguay River. Most of the area is between 150–300 m elevation. Rainfall totals about 1800 mm per year on average and is characterized by extreme unpredictability in monthly pattern from year to year but with a statistical dry season from May to September (Sanchez 1973; FMB unpublished data). Temperature fluctuations mark seasonality, with average daily low-high temperatures of 14–25°C in July and 22–34°C in January.

Although the area was sparsely inhabited by horticultural Guarani Indians until the Jesuit missions and slave raids of the 17th century, historical documents suggest

that only nomadic Ache foragers inhabited the area after the Jesuit expulsion (Hill & Hurtado 1996; Reed 1995). In 1990 the reserve was purchased by The Nature Conservancy in conjunction with the Fundacion Moises Bertoni (FMB) a Paraguayan conservationist organization. In 1991 the reserve was granted legal status as a national forest reserve by the Paraguayan congress.

The Mbaracayu reserve contains about 90% of the Paraguayan species classified as rare and endangered (FMB 1992) and was chosen as the top priority conservation site in eastern Paraguay using vegetation analysis (Keel et al. 1993). It includes a remarkable ecozone diversity of forests, rivers, mountains, caves, grasslands and wetlands and within the 60,000-ha reserve there are areas of mature terra firme tropical forest, cerrado (ranging from campo sucio to cerradao), grassland, palm dominated swamps, bamboo (*Guadua*) forests, riparian flood forests, and a low drier forest type referred to as "kaati" by native Guarani speakers.

The Mbaracayu reserve is also one of the most important endemic bird centers in South America. Over 400 species of birds have been recorded in the reserve in the past 2 years (Madroño & Esquivel 1995 and personal communication). The mammalian fauna in eastern Paraguay has been the subject of many inventory studies, but no studies to determine absolute or relative densities of the entire array of large mammals. Myers et al. (1996) have recently summarized published and unpublished sources of information and reports 124 mammal species verified in eastern Paraguay. In the Mbaracayu reserve to date we have observed (but not vouchered) 93 species of mammals. A provisional list of mammals is published in Hill et al. (1996). Comparisons with other Neotropical sites such as Manu Park, Peru show relatively low species diversity in Mbaracayu, however, more species of the following families are found in Mbaracayu than in Manu Park (cf. Pacheco et al. 1993): Dasypodidae, Erethizontidae, Cavidae, Myocastoridae, Canidae, Mustilidae, Felidae, and Cervidae.

The law that created the Mbaracayu reserve as a legal entity in 1991 states in part: "*these groups [Ache] will be permitted to continue subsistence hunting and gathering in the area of the Nature Reserve, as long as they employ traditional methods... The participation of the local Ache community in the protection and administration of the reserve will be encouraged, and they [the Ache] will be offered permanent employment that comes about as a result of the development of scientific studies, recreation, and tourism, in the reserve and the protected areas around it.*" (Ley 112/91, Article 13). Because of this law, studies of Ache resource use patterns are critical to conservation planning for Mbaracayu.

The Ache

Since the 1970s the Ache have been "settled" on mission reservations but continue frequent forest treks that may

last weeks or months. The Ache economy is centered around hunting mammalian game with bow and arrow, extracting wild honey, and exploiting palm starch and insect larvae. Meat contributes about 60% of the calories in the diet (Hill et al. 1984) and eight species of mammals contribute 95% of the meat in the Ache diet by weight (nine-banded armadillo [*Dasybus novemcinctus*], paca [*Agouti paca*], capuchin monkey [*Cebus apella*], white-lipped peccary [*Tayassu pecari*], tapir [*Tapirus terrestris*], coatimundi [*Nasua nasua*], brocket deer [*Mazama* spp.], collared peccary [*Tayassu tajacu*], listed in order of importance by weight). The list of all vertebrates killed during periods of observation between 1980–1995 is shown in Table 1. The data were collected by direct observation or interviews with hunters after they returned from a trip to the forest. The data suggest a prey composition that is different from that reported at

any other South American site (Robinson & Redford 1987). Because eight species of mammal make up 95% of the biomass hunted by the Ache, we focus on those species throughout this paper.

Hunting in the Mbaracayu Reserve

Both Ache and non-Ache hunters hunt in some sections of the Mbaracayu reserve. The Mbaracayu administration has placed guards at each of five guard stations around the periphery of the reserve to control the entry of non-Ache hunters. Although park guards have been effective at eliminating illegal timber extraction and establishment of swiddens within the reserve, they have not been able to completely eliminate poaching by non-Ache hunters.

Table 1. Vertebrates (listed in rank order of biomass) killed by Ache hunters during observation periods from 1980–1996.

Important species	Common name	No. killed	Killed ^a (kg)	Proportion harvest biomass ^b			
				1980	1981–85	1994–95	1995–96
<i>Dasybus novemcinctus</i>	nine-banded armadillo	1223	4688.5	0.135	0.239	0.405	0.443
<i>Agouti paca</i>	paca	332	2239.0	0.108	0.131	0.163	0.206
<i>Cebus apella</i>	capuchin monkey	849	1941.4	0.207	0.206	0.094	0.089
<i>Tayassu pecari</i>	white-lipped peccary	54	1345.9	0.228	0.156	0.052	0.018
<i>Tapirus terrestris</i>	tapir	7	1239.0	0.000	0.000	0.165	0.130
<i>Nasua nasua</i>	coatimundi	250	864.6	0.150	0.065	0.038	0.035
<i>Mazama</i> spp.	brocket deer	29	748.2	0.106	0.081	0.024	0.031
<i>Tayassu tajacu</i>	collared peccary	25	408.0	0.022	0.056	0.027	0.012
			sum	0.955	0.933	0.967	0.964
Other species							
<i>Tupinambis teguixin</i>	tegu lizard	64	148.6				
<i>Cabassous tatouay</i>	naked-tailed armadillo	18	97.2				
<i>Dasyprocta azarae</i>	agouti	24	64.8				
<i>Tamandua tetradactyla</i>	collared anteater	8	40.0				
<i>Bothrops</i> spp.	bushmaster snake	34	34.0				
<i>Penelope superciliaris</i>	Rusty-margined Guan	39	31.7				
<i>Myrmecophaga tridactyla</i>	giant anteater	1	30.5				
Unidentified birds	birds	43	30.1				
<i>Caiman latirostris</i>	caiman	5	25.0				
<i>Speothos venaticus</i>	bushdog	4	22.0				
<i>Coragyps atratus</i>	black vulture	9	18.0				
<i>Panthera onca</i>	jaugar	1	15.0				
<i>Euphractus sexcinctus</i>	yellow armadillo	3	15.0				
<i>Allouatta caraya</i>	black howler monkey	2	11.6				
Unident. <i>Didelphidae</i>	opossums	3	9.6				
<i>Sarcoramphus papa</i>	King Vulture	3	9.0				
<i>Odontophorus capueira</i>	Wood-Quail	6	6.0				
<i>Tinamidae</i>	tinamous	5	5.0				
<i>Rhampastidae</i>	tucans	3	3.0				
<i>Felis tigrinis</i>	oncilla	1	2.2				
<i>Sylvilagus brasiliensis</i>	rabbit	2	1.8				
<i>Didelphis</i> spp.	opossum	2	3.0				
<i>Geochelone</i> sp.	tortoise	1	1.0				
<i>Ara chloroptera</i>	Scarlet Macaw	1	1.0				
Unidentified <i>Muridae</i>	mice	1	0.3				
Total sample (kg)			14101.6				

^aMean weight in kilograms is taken from a sample of Ache prey or Eisenberg and Redford (1994) in order to standardize weights for years when only number of individuals were recorded.

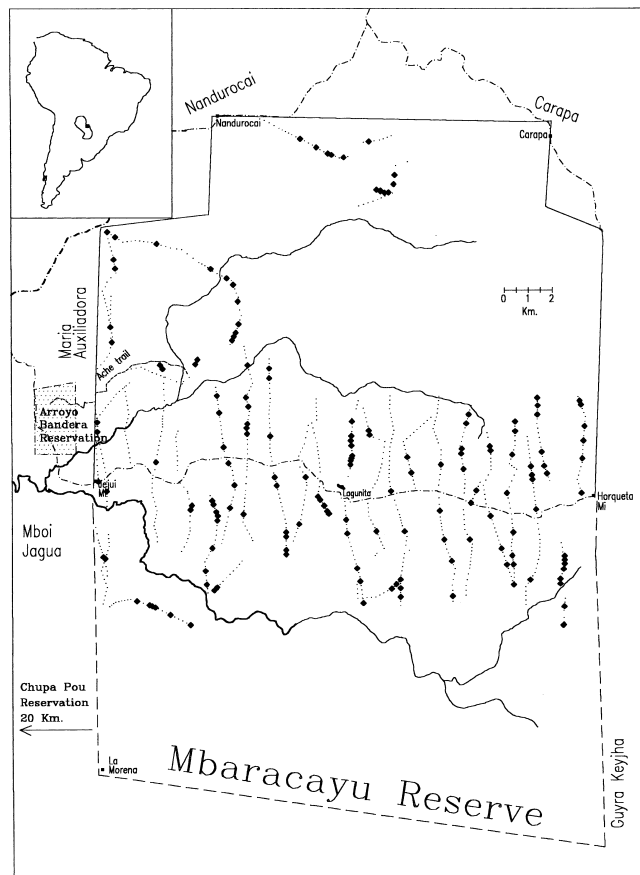
^bSample sizes are 1980, 2191 kg; 1981–85, 3513 kg; 1994–95, 4301 kg; 1995–96, 4096 kg.

The Ache have been hunting in the Mbaracayu area for at least a century and began intensively hunting the northwest portion of the reserve when the Arroyo Bandera reservation, with 90 residents, was established near that area around 1980 (Fig. 1). Ache from the more distant and larger Chupa Pou reservation (about 420 residents) occasionally hunt in the southwest portion of the reserve. The Ache hunt with bows and arrows or by hand during day hunts that originate from their reservation. They also go on extended treks inside the reserve that generally last 3–5 days but can last up to a month.

Non-Ache hunters in the reserve include Paraguayan and Brazilian peasants as well as Guarani horticultural Indians. We refer to all these groups as “Paraguayans.” Peasant settlements with hunters include Nandurocai

(40 families), Maria Auxiliadora (80 families), Carapa (10 families), Mboi Jagua (50 families), and Guyra Kejha (80 families). Survey data (unpublished) suggest that only a few hunters enter the reserve from each settlement. Peasants usually engage in tree stand hunting at night with shotguns and target tapir, deer, paca, and agouti under fruiting trees, at mud licks, or in areas baited with corn. Occasionally peasants engage in diurnal hunting in the reserve using dogs and primarily target both species of peccary and armadillos.

Much of the analyses we present employs distance from the point at which Ache or peasant hunters enter the reserve as an independent variable to explain variation in animal encounter rates. Ache hunters nearly always enter the reserve along a single trail from their village, which lies about 2.5 km from the western boundary of the reserve (Fig. 1). Once Ache hunters reach the reserve boundaries they leave the trail and begin hunting. Thus, the distance from Ache hunters is calculated from the point where their trail enters the reserve. Peasant hunters enter the reserve all along the colonized zones. Distance to peasant hunters is therefore calculated as the nearest distance to a reserve border except in the area of the Ache reservation where no Paraguayan hunters enter. We call the distance from Ache or Paraguayan hunting access point the Ache or Paraguayan DNAP (distance to nearest access point), respectively.



*Figure 1. Map of the Mbaracayu Reserve, showing the road bisecting the reserve (dashed line), the guard stations around the periphery of the reserve (squares), and the hunting populations outside the reserve. The first 54 transects are shown (dotted lines) and locations of all direct encounters with *Dasypus novemcinctus* on those transects (diamonds). Transects 55–91 sampled the same area as well as greater coverage in southern and northern portions of the reserve and the zone near the Arroyo Bandera Reservation and the Maria Auxiliadora Settlement.*

Methods

The Study Area

Ache assistants reported over 80 terms for vegetation type during the course of our data collection. Several of the terms were equivalent (synonymous), but 66 were considered independent and distinguishable as patches of vegetational subcommunities within larger vegetational classes. We aggregated these into eight major vegetational classes. These classes are easily recognized by any Ache forager and K.H. We do not claim they represent the best way to subdivide the Mbaracayu floral communities, but they are relevant to Ache hunters. These eight categories, listed in order from driest to wettest, were (1) low forest; (2) forest dominated by vines and lianas; (3) large bamboo forest; (4) small bamboo forest; (5) high forest; (6) riparian forest; (7) meadow or grassland; and (8) swamp.

Low forests are found on flat dry tableland high above stream drainages and characterized by trees <15 m high and usually with a dbh <10 cm and none with dbh >25 cm. Ground cover is dominated by bromeliads. Medium to high liana forest is found in high flat interfluvial regions far from standing or running water. Ground cover is sparse, but lianas density is high. Medium forests with large bamboo include few large trees and an

abundance of *Guadua angustifolia* bamboo. Medium forests with small bamboo understory are generally 15–25 m high with an abundance of small diameter *Merostachys claussoni* bamboo at ground level which may grow 1–3 m high and at times can be dense. High forest is the most common vegetation community in the Mbaracayu reserve and is described in detail in Hill et al. (1996). It is found at intermediate elevations above the water table on gently sloping ground. The basal area of tree species >10 cm dbh is 39 m²/ha in high forest (Keel 1987). Ground cover in high forest is generally sparse including low ferns and heliconias or bromeliads. The forest on the downslope near streams and rivers is generally richer in fruit species, higher, and even easier to walk through. We treated these riparian forests as a separate forest type (and so do the Ache). Grasslands are areas of open meadow with patches of cerrado vegetation. They are usually wet during part of the year and are characterized by poor drainage and a layer of black organic matter overlaying white sandy soils. Swamps are sparsely forested areas that are wet throughout the year with standing water up to 0.5 m deep during some parts of the year.

Field Procedures

The field method of game censusing consisted of a stratified random sample of diurnal walking transects through the Mbaracayu reserve. Most starting points were subsampled from locations along the dirt road running east-west and bisecting the reserve, but about 10% of transect sample days commenced in the middle of the reserve after camping overnight. In the second year of the study we carried out 5 days of transect censusing in the forest belonging to the two Ache reservations. Transect directions were generally restricted to north, south, east, or west in order to limit transect overlap. All absolute locations during the study were determined using a Trimble Pathfinder Pro Global Positioning System (GPS) receiver. Relative walking distance along a transect, however, was measured using a string box and is considerably more accurate.

Transects were walked by a team of five native assistants and a data recorder. All researchers walked in parallel along a single transect line. Four native assistants spaced themselves at approximately 25 and 50 m on either side perpendicular to the transect line, and one walked directly on the transect line about 5 m ahead of the data recorder. In essence five parallel transects were walked simultaneously on each day with about 25 m spacing between them. Each assistant carried a VHF radio to communicate with the data recorder. The data recorder coordinated the team movement along the transect by radio and carried the GPS unit and a string box which was used to measure progress along the transect with a readout to the nearest centimeter. Each transect began at the specified GPS location and proceeded toward a specified compass bearing throughout

the day. Transects passed through whatever vegetation was encountered but were temporarily suspended in water deeper than 0.5 m. They continued on the far side of whatever body of water (swamps, streams, rivers, etc.) had to be crossed.

After receiving a radio signal from the data recorder each native assistant began walking along the transect or parallel to it depending on position. Team members walked at a rate of about 1 km per hour (verified by time entries and string box distance measures). Native assistants were occasionally veered a few meters each side of the transect in order to verify that burrows they encountered were occupied. When the data recorder reached 200 m, as measured on the string box, he instructed the field assistants to stop and report encounter data. Assistants, in sequence, reported over the radio: (1) vegetation type at stop point; (2) all encounters during the previous 200 m with all large vertebrates or their fresh signs; (3) distance perpendicular to the progression line for each encounter; and (4) whether or not the encounter would have led to a hunting opportunity and a variety of other information relevant to an ongoing study of economic decisions of local hunters. The data recorder made progressive entries concerning time of day, weather, and landmarks. The data recorder took an averaged GPS reading every 600 to 800 m along the transect to estimate the absolute location of the transect within the study area for later analyses. Absolute location between GPS readings was estimated by interpolation. (The locations of the first 54 transects are shown in Fig. 1.)

Native research assistants from the Ache tribe were trained for 1 week prior to beginning data collection. All had extensive experience hunting in the area and were born inside the study area. They practiced radio use, learned basic concepts of mapping, compass, and GPS use, and practiced distance measurement and verification using a rangefinder, metal tape, and stringbox. Assistants were familiar with the western numbering system prior to the study but could not read or write. Transects generally began between 0700 and 0900 and lasted until rain forced a termination of work or around 1200 hours. After a break, work resumed for 1–2 more hours. Researchers covered between 2–5 km per day depending on weather, forest conditions, and number of obstructions (swamps, rivers, etc.). Some transects began as early in the day as light would permit and some started later in the day and ran until dark.

Encounters with target species were recorded for all mammal, bird, and reptile species that native assistants judged to be larger than 0.5 kg mean body weight. Two types of encounters were recorded: (1) animal seen, heard, or found in burrow and (2) fresh signs of the animal or fresh feces encountered. All encounters of the first type were lumped together for analyses into a category we referred to as “direct encounters.” This category was considered equivalent to an “encounter” in

most other studies, with little doubt that noises made by certain animals, in combination with fresh tracks, allowed for positive identification even when the animal was not visually observed. Occupied terrestrial burrows were also included in this category. Assistants confirmed presence of an animal in its burrow by flushing it or by introducing a long vine and getting the animal to move inside. In a few cases Ache assistants insisted an animal was inside (by certain signs, smell, etc.) even when they could not get direct confirmation, and we counted these instances.

Encounters of the second type were aggregated for analyses into a category we called "indirect encounters." Fresh signs of an animal were only reported if Ache assistants estimated the signs to be less than 24 hours old. These signs included tracks, feeding disturbance, territorial markers, beds and nests, urine, scent, body excretions, etc. The time cutoff at 24 hours led to some ambiguities but in general our researchers were in agreement with each other about which signs did or did not meet that criteria. Human signs within the study area were recorded if judged to be less than 1 year old. These included tracks, broken or cut vegetation, hunting blinds, camps, refuse, traps, and tracks of horses. Ache researchers claimed to be able to distinguish signs of their own people from those of non-Ache by a variety of clues.

Because of the way transects were walked, multiple encounters with the same animal were possible. For statistical analyses, however, encounters were only scored for the individual closest to the animal. This means that direct encounters are statistically independent. Tracks from the same animal discovered in adjacent 200 m units were reported in each unit; thus, for animals that cover large distances, track encounters were not always independent. It is nearly impossible to remedy this problem because it would require all five assistants to recognize individual animals whose tracks had been seen by any of the others in the previous 200-m unit. Statistical analyses of every other risk unit, however, can alleviate this problem when the sample size is large.

Analytical Methods

We considered each 200 m of our line transects as a unit during which observers were at risk of encountering a variety of animal species. Thus, our statistical analysis aimed to estimate the probability of a specified encounter in a 200-m "risk unit" under specified conditions. This approach has the advantage that it does not require any absolute animal density estimate. It thus avoids the use of transform methods that are commonly but inappropriately used to estimate densities of animals that move rapidly away from observers (Burnham et al. 1980). Although our data were analyzed as rates of encounter, there are methods for estimating total area sampled for each species, thus we can produce absolute density estimates equivalent to those in other studies

(Hill et al. 1996). Here we assume that encounter rate per 200 m is a monotonically increasing function of density, thus statistical conclusions drawn from encounter rate data are likely to apply to density patterns as well.

Hazards models (Kalbfleish & Prentice 1980; Allison 1984; Tuma & Hannan 1984; Blossfeld et al. 1989) are designed to statistically isolate the effects of certain variables on the probability of specified events taking place during a specified risk unit. Because encounter rates on line transects are the most convenient way to monitor resources in large areas, hazard rate analyses are highly appropriate.

We used logistic regression (Aldrich & Nelson 1984) to model association with a two-state dependent variable (encounter or no encounter). The risk unit for a potential event was a 200-m segment of the transect line. The statistical technique is therefore equivalent to discrete time logistic regression (Allison 1982; Blossfeld et al. 1989) except that our risk unit is a discrete distance category.

This analytic technique allows us to assess the impact of categorical variables (e.g., forest type A or B) and continuous variables (e.g., distance from a human population) on the probability of an event happening (e.g., an encounter with a deer). Most importantly for this type of study, hazards models can be multivariate so that one can eliminate (control for) the effects of variables that might affect encounter rates with particular animals (such as weather, habitat type, season, year, time of day, observer, position in the transect formation, etc.) in order to isolate the impact of human use patterns on game encounter rates.

Results

Encounter Rates

The first 91 days of field work between June 1994 and January 1996 resulted in a total of 1,426,000 m of line transect data or 7130 risk units of 200 m each. The set of all large mammals and selected birds and reptiles that are important in the Ache diet and were encountered during transect censusing is shown in Table 2. The table illustrates the importance of collecting data on indirect manifestations of a species presence rather than on direct encounters only. Eight species of mammals were encountered directly more than 10 times, and eight additional species were encountered directly at least once. However, we registered indirect encounters with 12 mammalian species for which no direct encounter took place. Thus, nearly one half of the total mammalian species encountered were recorded only because of the collection of data on recent signs and feces. Finally, there were at least 10 species of large mammals for whom no encounter was recorded during our sample period (Hill et al. 1996) despite the fact that we observed all these species or their signs while hunting during recent years.

Table 2. Large vertebrates encountered in the first 91 transects from June 1994–January 1996.

Scientific name ^a	English name	Number of encounters		
		Direct	Indirect	Average encounter distance ^b
Xenartha				
<i>Tamandua tetradactyla</i>	collared anteater	1	7	5.0
<i>Myrmecophaga tridactyla</i>	giant anteater	0	1	
<i>Dasybus novemcintus</i>	nine-banded armadillo	254	5105	2.1
<i>Dasybus septemcintus</i>	seven-banded armadillo	0	9	
<i>Cabassous tatouay</i>	naked-tailed armadillo	2	59	0.3
Primates				
<i>Cebus apella</i>	brown capuchin monkey	81	115	45.7
<i>Allouatta caraya</i>	black howler monkey	1	0	800.0
Carnivora				
<i>Cerdocyon thous</i>	crab-eating fox			
or		1	111	300.0
<i>Dusicyon gymnocerus</i>	South American fox			
<i>Chrysocyon brachyurus</i>	maned wolf	0	1	
<i>Speotbos venaticus</i>	bush dog	0	3	
<i>Panthera onca</i>	jaguar	4	42	106.3
<i>Felis pardalis</i>	ocelot			
or		0	4	
<i>Felis wiedii</i>	margay			
<i>Felis tigrina</i>	oncilla	1	23	3.0
<i>Puma concolor</i>	puma	3	7	40.0
<i>Procyon cancrivorus</i>	crab-eating raccoon	0	20	
<i>Nasua nasua</i>	coati	14	60	46.2
<i>Lutra longicaudis</i>	southern river otter	0	4	
<i>Eira barbara</i>	tayra	0	9	
Artiodactyla				
<i>Tayassu pecari</i>	white-lipped peccary	2	24	107.5
<i>Tayassu tajacu</i>	collared peccary	10	740	16.0
<i>Mazama americana</i>	red brocket deer			
or		75	1916	8.2
<i>Mazama gouazoubira</i>	grey brocket deer			
Perissodactyla				
<i>Tapirus terrestris</i>	tapir	31	1350	29.8
Rodenta				
<i>Dasyprocta azarae</i>	agouti	34	366	9.3
<i>Agouti paca</i>	paca	29	802	1.3
<i>Hydrochaeris hydrochaeris</i>	capybara	0	4	
<i>Cavia aperea</i>	guinea pig	0	2	
<i>Myocaster coypu</i>	nutria	0	1	
Other				
<i>Sus. sp.</i>	domestic pig	0	2	
Selected aves				
<i>Crypturellus obsoletus</i>	Common Tinamou	46	3	5.9
<i>Tinamus solitarius</i>	Solitary Tinamou	18	0	8.6
<i>Crypturellus tataupa</i>	Tataupa Tinamou	51	0	6.1
<i>Crypturellus undulatus</i>	Undulated Tinamou	44	2	5.7
<i>Sarcorambus papa</i>	King Vulture	2	0	47.5
<i>Cathartes sp.</i>	Turkey Vulture	8	0	11.4
<i>Coragyps atratus</i>	Black Vulture	6	0	26.2
<i>Ara chloroptera</i>	Red and Green Macaw	20	0	210.2
<i>Ramphastos toco</i>	Toco Toucan	28	1	53.4
<i>Pipile jakutinga</i>	Black-fronted Piping Guan	33	4	7.8
<i>Penelope supercilialis</i>	Rusty-margined Guan	142	14	8.8
<i>Odontophorus capueira</i>	Spot-winged Wood-Quail	52	0	6.8
<i>Columba cayannensis</i>	Pale-vented Pigeon	12	0	9.0
Reptiles				
<i>Bothrops spp.</i>	bushmaster snake	3	0	0.8
<i>Crotalus durissus</i>	rattlesnake	1	0	0.0
<i>Tupinambis teguixin</i>	tegu lizard	32	2	5.5
<i>Boa constrictor</i>	boa	4	0	2.0
<i>Caiman latirostris</i>	Paraguayan caiman	0	2	

^aSpecies separated by "or" are not always distinguished in the Ache language and were often recorded together.^bMean perpendicular distance from direct encounters to transect.

Hunting Activity and Covariance with Other Factors

The data base generated by the transect censuses can be used to map all encounters throughout the reserve for any species. Some apparent effects of hunting can be visually detected. For example, there were few encounters of *Dasypus* on transects near the Ache reservation relative to the number encountered in the remote areas of the reserve (Fig. 1). To determine whether these patterns are associated with human hunting, however, one must first ascertain whether hunting activity is more prevalent in areas near human settlements. Second, one must statistically control for other variables that might affect animal encounter rates and could confound the interpretation of the hunting impact on encounter rates.

The probability of encountering signs of hunters in the reserve drops rapidly and is nearly zero at distances greater than 10 km from the nearest access point into the reserve (Fig. 2). Although our data demonstrate that distance from nearest access point (DNAP) for a hunting population is a good measure of hunting pressure, many other factors we recorded during our study also covary with DNAP. We examined effects of four non-hunting variables that we recorded systematically on every transect and expected to affect animal encounter rates. Those variables are season of the year (dry in May–September), whether the wind was blowing when the data was collected, time of day (morning, 0500–0900; midday, 0900–1400; afternoon, 1400–1800), and habitat type (defined in the methods section). We divided all transect areas into five categories: (1) the Ache reservations; (2) zones close only to the Ache (<3 km Ache DNAP, but \geq 3 km Paraguayan DNAP); (3) zones only close to Paraguayans (<3 km Paraguayan DNAP, but \geq 3 km Ache DNAP); (4) zones close to both Ache and Paraguayans; and

(5) zones distant from both Ache and Paraguayan hunters (\geq 3 km Paraguayan DNAP and \geq 3 km Ache DNAP).

The encounter rates with hunters were higher in the zones nearest them (Table 3). For example, signs of Ache hunters were reported in 17.8% of all risk units on Ache reservation land, compared to only 0.7% of all risk units more than 3 km DNAP from either Ache or Paraguayan hunters. Likewise signs of Paraguayan hunters were more common in the zones near only to them (5.5%) than on Ache reservations (0%) or zones distant from both Ache and Paraguayan hunters (0.6%). Many of the important game animals were more likely to be encountered in zones distant from hunters than in the zones nearest to Ache and Paraguayan hunters (Table 3). Encounters with signs of *Dasypus* took place in only 31.9% of risk units on the Ache reservations but steadily increased to 74.8% of all risk units in the zones most distant from all hunters. These results cannot be used to assess hunting impact, however, because other variables that probably affect game encounter rates also covary with hunting zone.

The four non-hunting variables we examined were not equally distributed among the hunting zones of our sample (Table 3). For example, none of the reservation risk units were sampled in the dry season despite the fact that 55.9% of the risk units in zones distant from hunters were sampled in the dry season. Likewise, the area close to Ache hunters was sampled when the wind was blowing more often than in other zones and is also characterized by very little small bamboo forest and an abundance of high forest and swamp relative to zones distant from hunters. The area nearest to Paraguayan hunters is characterized by an abundance of large bamboo and was sampled in the afternoon more often than other zones. If these variables affected game encounter rates, those effects must be statistically controlled in order to isolate the impact of hunting activity on animal encounter rates.

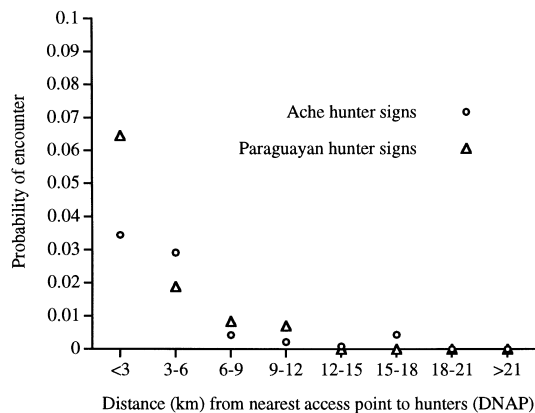


Figure 2. The probability of encounter with signs of Ache or Paraguayan hunters in each 200 m of line transect as a function of distance intervals from the nearest point at which each group of hunters enters the Mbaracayu Reserve.

Covariates of Animal Encounter Rates

To determine whether non-hunting variables are partially or totally responsible for differences in animal encounter rates in different hunting zones, we examined the effects of the four non-hunting variables described above on animal encounter rates.

The odds ratio for the association between each non-hunting variable and encounter rate with signs of hunters or one of the eight species analyzed is the ratio of the odds of an event when the independent variable takes its two categorical states (Table 4). For rare events the odds ratio is approximately the same as the ratio of the probabilities of an event under the two conditions. When a categorical variable takes more than two states, the odds ratios are calculated against one state which is the control. For example, the data in Table 4 shows that *Mazama* is 2.273 times as likely to be encountered in

Table 3. Mean values of independent variables in each sample zone* and the encounter rate with signs of hunters and the most important game species.

Variables	Min.	Max.	Ache	Ache close	Both close	Parag. close	Neither close
			reservation n = 135 mean	n = 151 mean	n = 265 mean	n = 454 mean	n = 6132 mean
Independent							
Ache DNAP	-1	23.53	-1.000	2.182	1.810	11.467	11.663
Parag. DNAP	-1	23.43	-1.000	5.324	1.014	1.604	10.983
Dry season	0	1	0.000	0.603	0.393	0.532	0.559
Wind blowing	0	1	0.111	0.430	0.321	0.374	0.348
Morning	0	1	0.200	0.046	0.000	0.035	0.094
Mid-day	0	1	0.763	0.755	0.814	0.576	0.702
Afternoon	0	1	0.037	0.199	0.186	0.388	0.204
Meadow	0	1	0.000	0.053	0.032	0.031	0.029
Low forest	0	1	0.000	0.073	0.111	0.025	0.030
Liana forest	0	1	0.156	0.013	0.086	0.071	0.090
Large bamboo	0	1	0.000	0.000	0.168	0.104	0.011
Small bamboo	0	1	0.126	0.046	0.093	0.154	0.253
High forest	0	1	0.615	0.623	0.368	0.511	0.479
Riparian forest	0	1	0.074	0.086	0.079	0.063	0.067
Swamp	0	1	0.030	0.106	0.064	0.040	0.040
Dependent							
Ache indirect	0	1	0.178	0.073	0.011	0.007	0.007
Paraguayan indirect	0	1	0.000	0.033	0.094	0.055	0.006
<i>Dasybus</i> direct	0	1	0.015	0.007	0.011	0.026	0.038
<i>Dasybus</i> indirect	0	1	0.319	0.318	0.396	0.685	0.748
<i>Agouti</i> direct	0	1	0.000	0.007	0.000	0.004	0.004
<i>Agouti</i> indirect	0	1	0.015	0.179	0.068	0.110	0.115
<i>Cebus</i> direct	0	1	0.000	0.000	0.008	0.013	0.012
<i>Cebus</i> indirect	0	1	0.000	0.013	0.000	0.009	0.018
<i>Tayassu p.</i> direct	0	1	0.000	0.000	0.000	0.000	0.000
<i>Tayassu p.</i> indirect	0	1	0.000	0.000	0.000	0.010	0.003
<i>Tapirus</i> direct	0	1	0.000	0.000	0.000	0.002	0.005
<i>Tapirus</i> indirect	0	1	0.000	0.258	0.068	0.100	0.206
<i>Nasua</i> direct	0	1	0.000	0.000	0.004	0.002	0.002
<i>Nasua</i> indirect	0	1	0.007	0.026	0.008	0.007	0.008
<i>Mazama</i> direct	0	1	0.015	0.007	0.011	0.017	0.010
<i>Mazama</i> indirect	0	1	0.407	0.305	0.139	0.265	0.272
<i>Tayassu t.</i> direct	0	1	0.000	0.000	0.000	0.002	0.001
<i>Tayassu t.</i> indirect	0	1	0.193	0.119	0.075	0.084	0.104

*Sample zones are Ache Reservation; Ache close (<3 km Ache DNAP, >3 km Paraguayan DNAP); both close (<3 km Ache DNAP, <3 km Paraguayan DNAP); Paraguayan close (>3 km Ache DNAP, <3 km Paraguayan DNAP); neither close (>3 km Ache DNAP, >3 km Parag. DNAP). DNAP is the distance from the nearest access point where hunters of each population enter the reserve.

the dry season as in the wet season, signs of *Cebus* are 1.987 times as likely to be encountered in the morning as during mid-day, and *Tapirus* is 4.89 times as likely to be encountered in a risk unit of low forest as in a risk unit of high forest. It should also be noted that the maximum likelihood model sometimes failed to converge when the number of events for any categorical independent variable is very small.

The analyses show that season, weather, time, and habitat variables are all significantly associated with encounter rates for some animals, and that the encounter of all eight species as well as human hunters are all associated with at least one of the four non-hunting variables. Signs or encounters with *Tapirus*, *Mazama*, *Cebus*, *Nasua*, and *Agouti* are all more common in the dry season. These could indicate different seasonal activity

patterns for these species, or the abundance of signs in a particular season could simply be due to easier detection of tracks and signs under certain weather conditions. Additionally, encounter rates were lower during the warm-wet (fruiting) season for all the vertebrates we examined except *Dasybus*. Perhaps frugivorous species rapidly satiate with fruit during that season and then spend their time resting, which makes them difficult to encounter and more likely to hear approaching humans and adopt avoidance tactics.

Whether the wind was blowing was also associated with encounter rates for some animals and their signs. It should be mentioned that the wind blows more frequently in Paraguay during the dry season and especially on cold days, so this variable may show association patterns not simply attributable to wind. But Ache hunters

Table 4. Univariate effects of independent variables on the probability of encounter with game animals or hunters.*

Variable	Dasypus				Agouti				Cebus				Tayassu p.				Ache	
	Direct odds	p	Indirect odds	p	Direct odds	p	Indirect odds	p	Direct odds	p	Indirect odds	p	Direct odds	p	Indirect odds	p	Direct odds	p
Dry season	1.208		0.667	**	0.788		1.459	**	1.369		2.633	**	nc		0.660		0.823	
Wind blowing	1.535	**	1.163	*	1.675		1.020		0.761		1.507	?	nc		nc		0.687	
Morning	0.715		1.373	**	1.324		0.906		1.546		1.987	**	nc		nc		3.300	**
Mid-day	control		control		control		control		control		control		control		control		control	
Afternoon	1.191		0.810	**	1.168		0.810	*	1.494		0.945		nc		nc		1.445	
Meadow	0.373	?	0.339	**	nc		2.037	**	0.459		0.285		nc		nc		1.103	
Low forest	0.563		0.570	**	2.433		1.527	*	nc		0.515		nc		nc		0.657	
Liana forest	0.723		1.046		nc		0.215	**	0.777		0.777		nc		1.439		0.493	
Large bamboo	0.487		0.364	**	nc		0.572	?	2.434	?	1.127		nc		nc		nc	
Small bamboo	1.303	?	1.100		1.903		0.791	*	1.305		1.377		2.070		0.108	*	0.514	*
High forest	control		control		control		control		control		control		control		control		control	
Riparian forest	0.778		0.713	*	1.783		3.236	**	2.687	**	0.632		nc		nc		2.470	**
Swamp	0.531		0.443	**	0.953		3.411	**	0.324		1.231		nc		nc		0.517	

Variable	Tapirus				Nasua				Mazama				Tayassu t.				Paraguayan	
	Direct odds	p	Indirect odds	p	Direct odds	p	Indirect odds	p	Direct odds	p	Indirect odds	p	Direct odds	p	Indirect odds	p	Direct odds	p
Dry season	1.088		1.535	**	5.086	*	1.387		2.273	**	1.300	**	0.563		0.948		0.663	?
Wind blowing	1.295		1.370	**	0.731		0.504		1.855	**	1.220	**	nc		1.152	?	0.981	
Morning	0.308		1.173		nc		2.171	*	1.104		1.808	**	1.340		1.007		0.622	
Mid-day	control		control		control		control		control		control		control		control		control	
Afternoon	0.633		1.175	*	nc		1.269		1.213		0.969		1.650		0.830	?	0.993	
Meadow	1.799		2.449	**	2.315		nc		0.348		0.191	**	nc		0.571	?	nc	
Low forest	4.890	*	1.491	*	nc		0.536		nc		0.211	**	nc		0.786		0.287	
Liana forest	2.433		0.528	**	0.779		1.214		0.828		0.966		0.779		0.787		0.324	?
Large bamboo	nc		0.331	**	3.011		0.776		1.846		0.758		nc		0.621		5.356	**
Small bamboo	2.722	*	1.088		0.887		1.074		0.492	*	0.502	**	0.591		1.337	**	0.534	*
High forest	control		control		control		control		control		control		control		control		control	
Riparian forest	2.379		1.109		1.016		1.588		0.615		0.735	**	nc		1.328	?	1.578	
Swamp	nc		2.254	**	nc		1.273		0.994		0.246	**	nc		1.466	*	0.683	

*The odds of the event with the effect of the independent variable divided by the odds of the event without the independent variable effect, n.c. = no convergence of the maximum likelihood model. Probabilities are **, $p < 0.01$; *, $p < 0.05$; ?, $p < 0.1$.

did suggest that terrestrial animals are encountered more frequently in the wind because they sleep during the day and cannot hear hunters approaching, whereas arboreal animals are more difficult to encounter when the wind is blowing because hunters cannot hear them foraging.

There were no significant associations between time of day and direct encounter rate with any of the main game animals. Several species were, however, characterized by an increase in the encounter with fresh signs in the morning relative to mid-day. Finally, all animals but *Nasua* (which was encountered very few times) appear to show significant habitat preferences. These cannot be simply due to the preference of hunters because the same habitat preferences are seen in un hunted zones of the reserve. Human hunters also show some habitat associations but most of these are explained by the proximity of certain forest types in abundance near human settlements (Table 3). Ache hunters, however, show an apparent preference for hunting in riparian forest even though it is not abundant near their settlement. This agrees with informant statements suggesting the favorite

Ache hunting strategy is to walk along one side of a watercourse for some distance and then back along the other side.

Our data appear to confirm several aspects of Ache forest lore. For example, the Ache state and our data agree that *Cabassous* inhabits low forest (data available from author), whereas *Dasypus* lives in high forest and avoids meadows and large bamboo; *Cebus* and *Nasua* show the same vegetational preferences for riparian forest and large bamboo; and *Tapirus* and *Agouti* are especially common near water but this is not true for *Mazama* or *Dasyprocta*. The data strongly suggest that vegetational community is a variable that should be controlled in order to characterize the impact on human activities on animal encounter rates.

Multivariate Hazard Models of Encounter Probability

Multivariate logistic regression including DNAP and the four non-hunting variables can be employed to isolate the relationship between hunting zones or distance

from the point at which Ache hunters enter the reserve and the encounter rate of target species in this study even when other variables significantly affect encounter rates. Results (Table 5) suggest that *Tapirus*, *Mazama*, *Dasyopus*, and *Cebus* are all probably depleted near in zones hunted frequently by Ache hunters. The odds ratio in the close zone versus far is significantly less than 1.0 for signs of *Tapirus*, *Mazama*, and *Dasyopus*, and direct encounters with *Dasyopus*. The zones Ache reservation, Ache close, or both close show significantly lower encounter rates with signs of *Mazama*, *Dasyopus*, and *Agouti*, and direct encounters with *Dasyopus*. There were no direct encounters with *Tapirus* on the reservation or in the zones close to the Ache, thus that maximum likelihood model failed to converge. Finally, the slope of the regression (determined by the sign of the parameter estimate) of encounter rate by the continuous variable "Ache DNAP" is positive for direct encounters

with *Tapirus*, *Dasyopus*, and *Cebus*, and signs of *Tapirus*, *Mazama*, and *Dasyopus*.

No species showed a decrease in direct encounter rate in hunted area without a decrease in indirect encounters in the same area (Table 5). This suggests that decreased encounters with game in hunted areas is due to animal absence not just an increase in wariness or flight distance. Additionally, only two species in this list, *Tapirus*, and *Dasyopus*, show significantly lower encounter rates in zones that are only near Paraguayan hunters. *Tapirus* is the only species that shows lower encounter rates in zones only near Paraguayan hunters than in zones only near the Ache. Third, Ache reservations show significantly higher encounter rates with signs of *Mazama* and *Tayassu t.* than are found in zones distant from all hunters. This is true despite the fact that signs of Ache hunters are 30 times more common on the reservation than in the distant zones of the reserve.

Table 5. Probability of encounter by hunting zones, Ache DNAP, and transect number, when all significant variables from Table 4 are controlled.^a

Variable	Dasyopus				Agouti				Cebus				Tayassu p.				Ache	
	Direct odds	p	Indirect odds	p	Direct odds	p	Indirect odds	p	Direct odds	p	Indirect odds	p	Direct odds	p	Indirect odds	p	Indirect odds	p
Categorical ^b																		
Ache DNAP																		
<3 km	0.239	**	0.205	**	nc		0.814		0.395		0.315	?	nc		nc		3.773	**
Reservation	0.406		0.104	**	nc		0.136	**	nc		nc		nc		nc		29.788	**
Ache close	0.151	?	0.151	**	nc		1.300		nc		nc		nc		nc		12.256	**
Both close	0.283	*	0.210	**	nc		0.507		nc		nc		nc		nc		1.878	
Paraguayan close	0.705		0.756	*	nc		1.020		nc		nc		nc		nc		1.096	
Neither close	control parameter		control parameter		control parameter		control parameter		control parameter		control parameter		control parameter		control parameter		control parameter	
Continuous ^c																		
Ache DNAP	0.033	**	0.111	**	nc		0.004		0.039	*	0.008		0.009		0.025		-0.309	**
Transect number	-0.014		0.021	**	nc		0.002		-0.002		0.009	*	-0.062		-0.007		0.007	
Variable	Tapirus				Nasua				Mazama				Tayassu t.				Paraguayan	
	Direct odds	p	Indirect odds	p	Direct odds	p	Indirect odds	p	Direct odds	p	Indirect odds	p	Direct odds	p	Indirect odds	p	Indirect odds	p
Categorical ^b																		
Ache DNAP																		
<3 km	nc		0.615	**	1.400		2.025	?	0.831		0.739	*	nc		0.944		6.595	**
Reservation	nc		nc		nc		0.857		2.623		1.837	**	nc		2.237	**	nc	
Ache close	nc		1.178		nc		3.604	*	0.529		1.250		nc		1.258		nc	
Both close	nc		0.291	**	nc		1.057		1.098		0.494	**	nc		0.755		nc	
Paraguayan close	nc		0.446	**	nc		0.891		1.576		0.935		nc		0.772		nc	
Neither close	control parameter		control parameter		control parameter		control parameter		control parameter		control parameter		control parameter		control parameter		control parameter	
Continuous ^c																		
Ache DNAP	0.071	*	0.023	**	0.046		-0.051	*	0.030		0.024	**	-0.031		0.012	?	-0.096	**
Transect number	0.004		0.006	**	0.001		-0.021	**	0.005		0.007	**	0.018		0.002		0.010	*

^aThe odds ratio is the odds of the event with the effect of the independent variable divided by the odds of the event without the independent variable effect. Probabilities are **, p < 0.01; *, p < 0.05; ?, p < 0.1. nc = no convergence of the model.

^bHunting zones are defined the same as for Table 3.

^cContinuous variables show the parameter estimate for the slope of the relationship between the variable and the logit of the event.

Finally, in order to examine the *shape* of the relationship between encounter rate and Ache DNAP we repeated the analyses with DNAP aggregated in 3-km intervals for the four species that appeared to be depleted near the Ache. Encounter rates with signs of all four species suggest depletion only in the region closer than 6 km DNAP (Fig. 3a-d). Encounter rates with signs of all four species seem to asymptote in the region further than 6 km DNAP. The same pattern is seen for direct encounters of *Dasypus*, *Cebus*, and *Tapirus*. Hunting seems only to decrease encounter rates in zones closer than 6 km DNAP. Direct encounters with *Mazama*, however, show no clear spatial pattern, and suggest that factors other than those entered in the model are associated with a good deal of variation in *Mazama* encounter rates.

Discussion

When potential confounding variables were controlled statistically, only *Dasypus*, *Cebus*, *Tapirus*, *Mazama*,

among the most hunted game animals, showed statistically significant increases in encounter rates as DNAP increased. Peaks and valleys in the encounter rate by DNAP curve, as well as rather large confidence intervals, suggest there is still much to be learned about the determinants of animal densities inside the reserve (e.g., *Mazama*, Fig. 3d).

Several important lessons from this study could apply to other projects that attempt to measure the impact of hunting on animal densities. First, the encounter rate with all species in our study covaried significantly with some non-hunting variables, suggesting that statistical analyses must include controls for potentially confounding variables. Second, a quantitative demonstration that some zones are more hunted than others is required in order to assess causality. In our study signs of human hunters decreased rapidly with distance from the point at which they enter the Mbaracayu reserve, allowing us to quantitatively assess hunting activity in comparison zones.

Third, the use of indirect encounter data to complement what is learned from direct encounters seems use-

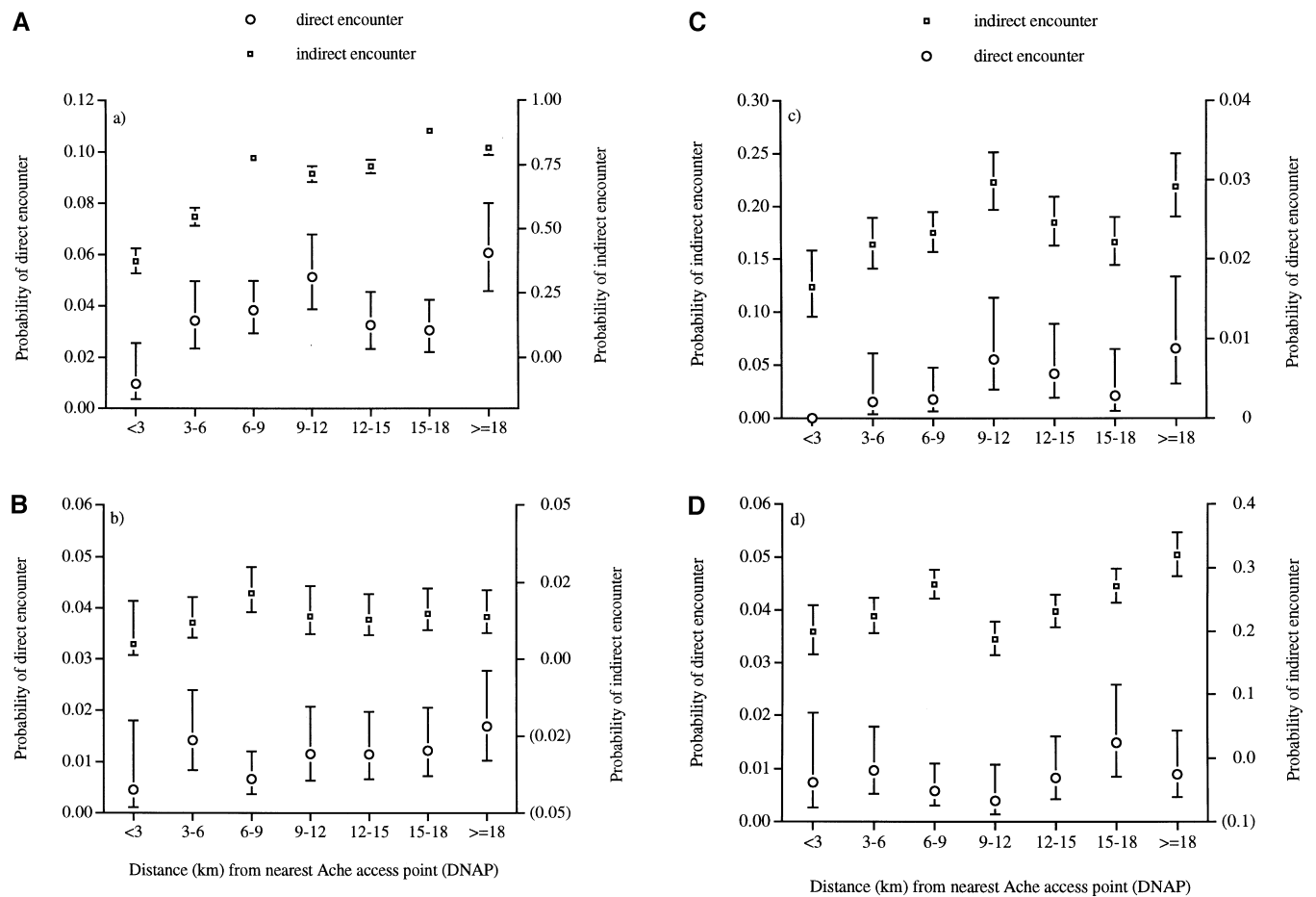


Figure 3. Encounter rates (and 95% confidence intervals) with *Dasypus novemcinctus* (a), *Cebus apella* (b), *Tapirus terrestris* (c), *Mazama spp.* (d) as a function of distance interval from the point at which Ache hunters enter the reserve.

ful. Native skills at recognition of animal signs allowed us to use indirect evidence of species presence, thus eliminating the possibility that encounter rates were lower in hunted zones only because of avoidance tactics by species of interest. The use of animal signs is complicated, however, by the fact that activity patterns and the types of signs that animals leave may differ considerably between habitat types. Also, the visibility of animal signs probably varies across some of the habitat types we examined. This means that changes in the encounter rate with animal signs can only be interpreted if habitat effects are statistically controlled.

Fourth, logistic regression appears to be a powerful tool for isolating the variables that affect encounter rate. This method has some advantages and some disadvantages when compared to distance sampling density estimates. Logistic regression is well designed for multivariate analysis and the examination of effects by continuous variables, whereas distance sampling techniques are not. Logistic regression, for example, can easily be used to examine simultaneously the effects of season, habitat, and hunting activity on animal encounter rates. No statistical method we have seen used in distance sampling could analyze simultaneously these effects on animal density. Current distance sampling density methods cannot be used in regression without adopting variance components analysis, which is somewhat complex. Logistic regression allows for analysis of factors that affect detection probability on the line, whereas distance sampling techniques assume that probability is always one. This is especially important if an unknown proportion of animals move away from the line without being detected. Finally, logistic regression produces information on encounter rates with target species, which is critical for many models of human predation behavior.

Distance sampling methods to assess density have several advantages over the analysis of encounter rates. Most importantly they are not affected by most causes of variation in animal encounter rates and they essentially correct for detection variation (at distances away from the line) regardless of the cause, in order to produce robust density estimates (Buckland et al. 1993). They are characterized by clearly defined variance and confidence intervals that allow for direct comparison among a small number of strata if the sample size of transects is adequate. Additionally, there are rapidly developing statistical techniques for use with density data that may soon overcome most of the disadvantages (K. Burnham, personal communication). Finally, they produce density estimates, which are of primary concern to most researchers.

The encounter rate analysis we employed can not determine if encounter *distance* for target species covaries with conditions of interest. If encounter distance does covary with distance from hunters or vegetation class, for example, we may find spurious changes in encounter rate when density is constant or apparently constant

encounter rates when density varies. We examined this possibility for our own data and found no significant differences in mean encounter distance between zones close and far from Ache hunters (data not shown). Because changes in direct encounter rates were mirrored by changes in indirect encounter rates in our study and because mean encounter distance did not differ across hunting zones, we conclude that differences in encounter rate as a function of distance from hunters (Table 5) are due to differences in animal densities.

We have been able to show that encounter rates are lower near human hunters for some species but not others; however, we did not address whether current hunting levels are sustainable. The changes in encounter rates with DNAP shown in Figs. 3a-d suggest that demonstrating depletion near hunters may be irrelevant to the question of sustainability because even depleted species seem to show normal densities at distances greater than 6 km from the point at which hunters enter the reserve. We estimated the proportion of each important game species that is harvested from the Mbaracayu reserve by Ache hunters. Those estimates ranged from 0.4% for *Tayassu p.* and *Mazama* to 7.6% for *Agouti* (Hill et al. 1996). Such rates are not likely to endanger any of these species within the Mbaracayu reserve. This conclusion is supported by analyses shown in Table 5. In the first 2 years of data collection we found no evidence of a decrease in the encounter rate as a function of transect date for any species, once distance from hunters and other non-hunting variables were controlled (Table 5, last row).

Some authors have recently asserted that conservation of a complete set of floral and faunal species requires areas inviolate to human use (e.g., Robinson 1992; Peres & Terborgh 1995), but this conclusion has not been supported with relevant data. The demonstration of some localized depletion due to human hunting is not sufficient to assert that species will be lost in a large protected area if humans are allowed to harvest food resources in that area at a low level. The fact that the species present today have coexisted with humans for at least 12,000 years and that humans have always been an active component of the current Neotropical milieu provides a strong argument to the contrary. As far as can be discerned, there were no uninhabited areas of the Neotropics at European contact (Denevan 1992), there have been no large uninhabited areas in the time since European arrival (Steward 1944-1949), and most areas that are now targeted for biodiversity conservation are currently or have been used recently by native people (Lizarralde 1993).

It should be emphasized that because the earliest native populations spread through the Neotropics prior to the terminal Pleistocene extinctions (Meggers 1982; Roosevelt 1994), the current set of Neotropical species has never existed as a "natural community" without hu-

man activity. Humans have acted as predators, competitors, and seed dispersers in the Neotropics for at least 12,000 years. They have disturbed and restructured forests through swidden agriculture for at least 5000 years (Balee 1994). Humans are a natural top predator of the Neotropics, their presence and activities, as practiced traditionally, are just as natural as those of jaguars, anacondas, or Harpy Eagles. The removal of top predators from any area is an ecological gamble, that may threaten biodiversity and result in a community structure that is anything but natural (Glanz 1990; Janson & Emmons 1990; Terborgh 1990). Conservationists should concern themselves with whether human hunting patterns in an area are sustainable rather than whether they can be shown to affect local densities of game species.

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Literature Cited

- Aldrich, J. H., and F. D. Nelson. 1984. Linear probability, logit and probit models. Sage University paper series on quantitative applications in the social sciences. Sage Publications, Beverly Hills.
- Allison, P. D. 1982. Discrete time methods for the analyses of event histories. Pages 61–98 in S. Leinhardt, editor. *Social methodology*. Jossey-Bass, San Francisco.
- Allison, P. D. 1984. Event history analyses: regression for longitudinal event data. Pages 7–46 in Sage University paper series on quantitative applications in the social sciences. Sage Publications, Beverly Hills.
- Alvard, M. 1993. Testing the “ecologically noble savage” hypothesis: interspecific prey choice by Piro hunters of Amazonian Peru. *Human Ecology* 21:355–387.
- Alvard, M. 1995. Conservation by native peoples: prey choice in a depleted habitat. *Human Nature* 5:127–154.
- Balee, W. 1994. Footprints of the forest: Kaapor ethnobotany—the historical ecology of plant utilization by an Amazonian people. Columbia University Press, New York.
- Blossfeld, H. P., A. Hamerle, and K. U. Mayer. 1989. *Event history analyses*. Lawrence Erlbaum Associates, Hillsdale, New Jersey.
- Bodmer, R. E., T. G. Fang, and L. Moya. 1988. Primates and ungulates: a comparison of susceptibility to hunting. *Primate Conservation* 9:79–83.
- Bodmer, R. E., T. G. Fang, L. Moya, and R. Gill. 1994. Managing wildlife to conserve Amazonian forests: population biology and economic considerations of game hunting. *Biological Conservation* 67:29–35.
- Burnham, K. P., D. R. Anderson, and J. L. Laake. 1980. Estimation of density from line transect sampling of biological populations. *Wildlife Monographs* 72.
- da Silva, N. J., and J. W. Sites. 1995. Patterns of diversity of neotropical *Squamate* reptile species with emphasis on the Brazilian Amazon and the conservation potential of indigenous reserves. *Conservation Biology* 9:873–901.
- Denevan, W. 1992. Native American populations in 1492: recent research and a revised hemispheric estimate. Pages XVII–XXXVIII in W. Denevan, editor. *The native population of the Americas in 1492*. 2nd edition. University of Wisconsin Press, Madison.
- FMB (Fundacion Moises Bertoni). 1992. *Reserva Natural Mbaracayu*. Plan operativa. Fundacion Moises Bertoni, Asuncion, Paraguay.
- Fragoso, J. M. 1991. The effect of hunting on tapirs in Belize. Pages 154–162 in J. Robinson and K. Redford, editors. *Neotropical wildlife use and conservation*. University of Chicago Press, Chicago.
- Freese, C. H., P. G. Heltne, N. Castro, and G. Whitesides. 1982. Patterns and determinants of monkey densities in Peru and Bolivia, with notes on distributions. *International Journal of Primatology* 3:53–90.
- Glantz, W. 1982. The terrestrial mammal fauna of Barro Colorado Island: censuses and long-term changes. Pages 455–468 in E. G. Leight, Jr., A. S. Rand, and D. M. Windsor, editors. *The ecology of a tropical forest*. Smithsonian Institution Press, Washington, D.C.
- Glantz, W. 1990. Neotropical mammal densities: how unusual is the community on Barro Colorado Island. Pages 287–313 in A. Gentry, editor. *Four neotropical rainforests*. Yale University Press, New Haven.
- Hill, K., H. Kaplan, K. Hawkes, and A. Hurtado. 1984. Seasonal variance in the diet of Ache hunter-gatherers of eastern Paraguay. *Human Ecology* 12:145–180.
- Hill, K., and A. Hurtado. 1989. Hunter-gatherers of the New World. *American Scientist* 77:436–443.
- Hill, K., and A. M. Hurtado. 1996. *Ache life history: the ecology and demography of a foraging people*. Aldine de Gruyter, New York.
- Hill, K., J. Padwe, C. Bejyvagi, A. Bepurangi, F. Jakugi, R. Tykuarangi, and T. Tykuarangi. In Press. Sustainability of Ache hunting in the Mbaracayu Reserve, Paraguay. In J. Robinson and E. Bennet, editors. *Hunting for sustainability in tropical forests*. Columbia University Press, New York.
- IUCN (World Conservation Monitoring Center). 1992. *Protected areas of the world: a review of national systems*. Volume 4. Nearctic and neotropics. IUCN, Cambridge, England.
- Janson, C., and L. Emmons. 1990. Ecological structure of the non-flying mammal community at Cocha Cashu biological station, Manu National Park, Peru. Pages 339–357 in A. Gentry, editor. *Four neotropical rainforests*. Yale University Press, New Haven.
- Kalbfleisch, J. D., and R. L. Prentice. 1980. *The statistical analyses of failure time data*. John Wiley, New York.
- Keel, S. 1987. Informe de viaje al terreno del Banco Mundial. Centro de Datos para la Conservacion, Asuncion, Paraguay.
- Keel, S., A. Gentry, and L. Spinzi. 1993. Using vegetation analysis to facilitate the selection of conservation sites in eastern Paraguay. *Conservation Biology* 7:66–75.
- Lizarralde, M. 1993. Indice y mapa de grupos ethnolingüísticos autóctonos de América del Sur. *Antropologica*, suplemento 5. Fundacion La Salle de Ciencias Naturales, Caracas, Venezuela.
- Madroño, N. A., and E. Z. Esquivel. 1995. Reserva Natural del Bosque Mbaracayu: su importancia en la conservación de aves amenazadas, cuasi-amenazadas y endémicas del Bosque Atlántico del Interior. *Cotinga* 4:52–57.
- Meggars, B. 1982. Archeological and ethnographic evidence compatible with the model of forest fragmentation. Pages 483–496 in G. Prance, editor. *Biological diversification in the tropics*. Columbia University Press, New York.
- Myers, P., A. Taber, and I. Gamarra de Fox. 1996. La mastozoología en Paraguay. In G. Caballos and J. Simonetti, editors. *Diversidad y Conservación de los Mamíferos Neotropicales*. In press.
- Pachecho, V., B. D. Patterson, J. L. Patton, L. H. Emmons, S. Solari, and C. F. Ascorra. 1993. List of mammal species known to occur in Manu Biosphere Reserve, Peru. Publicaciones del Museo de Historia Natural, Universidad de San Marcos, Lima.
- Peres, C. A. 1990. Effects of hunting on western Amazonian primate communities. *Biological Conservation* 54:47–59.
- Peres, C. A., and J. Terborgh. 1995. Amazonian nature reserves: an

- analysis of the defensibility status of existing conservation units and design criteria for the future. *Conservation Biology* 9:34-46.
- Reed, R. K. 1995. Prophets of agroforestry. University of Texas Press, Austin.
- Robinson, J. 1992. The limits to caring: sustainable living and the loss of biodiversity. *Conservation Biology* 7:20-28.
- Roosevelt, A. 1994. Strategy for a new synthesis. Pages 1-20 in A. Roosevelt, editor. *Amazonian Indians from prehistory to the present: anthropological perspectives*. University of Arizona Press, Tucson.
- Rylands, A. 1991. The status of conservation areas in the Brazilian Amazon. World Wildlife Fund, Washington, D.C.
- Sanchez, T. F. 1973. The climate of Paraguay. Pages 33-38 in J. R. Gorham, editor. *Paraguay: ecological essays*. Academy of the Arts and Sciences of the Americas, Miami.
- Silva, J. L., and S. D. Strahl. 1991. Human impact on populations of Chachalacas, Guans, and Curassows (Galliformes:Cricidae) in Venezuela. Pages 37-52 in J. Robinson and K. Redford, editors. *Neotropical wildlife use and conservation*. University of Chicago Press, Chicago.
- Steward, J., editor. 1944-1949. *Handbook of South American Indians*. Volume 1-7. Bureau of American Ethology Bulletin. U.S. Government Printing Office, Washington, D.C.
- Terborgh, J. 1990. An overview of research at Cocha Cashu Biological Station. Pages 48-59 in A. Gentry, editor. *Four neotropical rainforests*. Yale University Press, New Haven.
- Tuma, N. B., and M. T. Hannan. 1984. *Social dynamics*. Academic Press, Orlando, Florida.
- Vickers, W. T. 1991. Hunting yields and game composition over ten years in a Amazon Indian territory. Pages 53-81 in J. Robinson and K. Redford, editors. *Neotropical wildlife use and conservation*. University of Chicago Press, Chicago.

