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# Hunting-Related Changes in Game Encounter Rates from 1994 to 2001 in the Mbaracayu Reserve, Paraguay

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**Abstract:** *This longitudinal study examines the impact of native hunting on the populations of 10 important game species in the Mbaracayu Reserve, Paraguay. From July 1994 to July 2001, native Ache research assistants surveyed 7,535 km of diurnal random transects in the reserve. Analyses of data from these transects and harvest-rate data from 5,526 Ache hunter days suggest that the hunting return rate declined significantly for one species. Nonsignificant declines were observed for 6 of the other 9 species. Native harvest percentages of the stock population appear sustainable for 10 major prey species, but rates of harvest from nonindigenous poaching could not be determined. Crude encounter rates for all 10 species declined over time, but only 2 of these were statistically significant in a univariate model. Multivariate logistic regression controlling for habitat type and location in the reserve showed significant declines in encounter rates over time for 4 species, but the effect of interaction between time and hunting pressure failed to confirm that declines in encounter rates were steeper in more-hunted versus less-hunted areas of the reserve. This may mean that other factors unrelated to hunting pressure are responsible for some of the declines in game encounter rates.*

Cambios Relacionados con la Cacería en las Tasas de Encuentro de Especies Cinegéticas de 1994 a 2001 en la Reserva Mbaracayu, Paraguay

**Resumen:** *Este estudio longitudinal examina el impacto de la cacería por nativos sobre las poblaciones de especies cinegéticas importantes en la Reserva Mbaracayu, Paraguay. De julio 1994 a julio 2001, nativos Ache asistentes de investigación examinaron 7,535 km de transectos diurnos aleatorios en la reserva. El análisis de los datos de estos transectos y de los datos de las tasas de captura de 5,526 días de cacería de cazadores Ache sugiere que la tasa de retorno de la caza declinó significativamente para una especie. Se observaron cambios no significativos para 6 de las otras 9 especies. Los porcentajes de captura de la población existente por nativos parecen ser sustentables para las 10 especies más importantes, pero no se pudieron determinar las tasas de cacería furtiva por no nativos. Las tasas crudas de encuentro con las 10 especies declinaron en el tiempo, pero solo dos de ellas fueron estadísticamente significativas en un modelo univariado. La regresión logística multivariada controlando el tipo de hábitat y localización en la reserva mostró declinaciones significativas en las tasas de encuentro para 4 especies, pero el efecto de interacción del "tiempo por presión de cacería" no confirmó que las declinaciones de las tasas de encuentro fueran más pronunciadas en las áreas de la reserva más cazadas versus menos cazadas. Esto puede significar que otros factores, no relacionados con la presión de cacería, son responsables de algunas de las declinaciones en las tasas de encuentro de especies cinegéticas.*

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## Introduction

Wild faunas have always been an important component of the diet of traditional societies of the Neotropics. And numerous studies have been carried out to examine whether human hunting depletes animal populations in Neotropical forest reserves (e.g., Freese et al. 1982; Bodmer et al. 1988, 1994; Peres 1990; Glanz 1990; Fragoso 1991; Silva & Strahl 1991; Vickers 1991; Alvard 1993, 1995; Robinson & Bennett 2000). Despite this large database, contrasting conclusions about human hunting have been presented. For example, Schwartzman et al. (2000*a*, 2000*b*) suggest that “the data are too sparse to judge the effects of forest peoples on large forest animals,” whereas others (e.g., Redford & Sanderson 2000; Terborgh 2000) conclude that in recent times “depletion has been the norm.”

Most Neotropical hunting studies have the primary goal of determining whether human predation represents a threat to biodiversity in designated conservation units (Bennett & Robinson 2000). But, despite that goal, many studies fail to adequately address the question of whether observed hunting is sustainable for three reasons. First, many researchers use methods that are capable of demonstrating only localized depletion caused by hunting. But localized depletion is an expected outcome whenever predator activities are concentrated in areas smaller than the entire catchment, and the formation of “sink” and “source” areas caused by such depletion does not always imply that harvest patterns are unsustainable (Hart 2000; Hill & Padwe 2000; Novaro et al. 2000).

Second, the temporal declines in hunted animal densities reported in some studies may be due to natural factors. Spatial and temporal analyses of density data on vertebrates suggest that most populations experience local crests and troughs of density over time (e.g., Bohning-Gaese et al. 1995; Brown et al. 2001*a*). These temporal fluctuations are spatially complex, consisting of moving, localized density peaks (waves) of different amplitude and wavelength caused by many different sources. The fluctuations are initially caused by localized resource abundance, fluctuating predator densities, fortuitous fluctuations in predator success rates, variations in reproductive rates, and differential pathogen effects, and then they spread in a manner determined by the migration patterns of each species. Detecting fluctuations in abundance caused by human hunting activity is complicated under such conditions. Any study that monitors a large number of species across only two time periods or two geographical regions will almost always find some species that are lower in density in one region or time period. Because many researchers have looked at only two zones (near and far from hunters) or only two time periods, natural density fluctuations may have given the illusion of depletion caused by hunting.

Finally, sustainability estimates in many studies are

based on equilibrium population models that assume that the maximum sustainable harvest rate is determined primarily by the density-independent rate of increase ( $r_{\max}$ ) of the species in question (Robinson 2000). Although the theoretical basis for the maximal harvest assumption is sound, many erratic and poorly understood population processes can lead to extirpation even when annual harvest rate is well below the calculated maximum sustainable level. Many species in a bounded ecosystem go extinct in relatively short time periods through completely natural processes (e.g., Brown et al. 2001*b*). This realization has led many conservation biologists to advocate flexible “adaptive management” (e.g., Walters 1986; Christensen et al. 1996) to regulate harvest according to real year-to-year fluctuations in the standing stock rather than setting a yearly harvest that is theoretically sustainable.

We present the results from 7 years of monthly monitoring of hunting and vertebrate densities in the Mbaracayu Forest Reserve (MFR), Paraguay. Analyses after the second year of the project allowed us to determine that Ache hunters depleted some game animal populations near their residence site (Hill et al. 1997) but that annual Ache harvest rates of the total catchment area seemed well below the theoretical maximum harvest rates for all major game species (Hill & Padwe 2000). However, we were not able to assess the level of impact due to illegal poaching in the MFR by non-Ache hunters. The 7-year data set allowed us to examine whether Ache hunting is sustainable and whether the effects of poaching have led to a decline in game populations. Our analyses also provide deeper insights into the population dynamics of some important South American game species.

## Background

The 65,000-ha MFR (approximately lat. 24°S, long. 55°W) is the largest tract of interior Atlantic forest in Paraguay. It is an area characterized by gently rolling hills covered with subtropical, semideciduous forest and low flat valleys filled with tall grasses. Rainfall totals about 2000 mm per year on average and is characterized by high unpredictability in monthly pattern from year to year but with a statistical dry season from May to August. Seasonal temperature fluctuations are more consistent, with temperature extremes ranging between 39° C and 0° C. The cold season often includes a few days of hard frost each year, which kill the leaves on many exposed trees and shrubs. Both yearly rainfall and mean temperature fluctuated considerably during the 7-year study period. In particular, the 1996–1997 and 1997–1998 El Niño years received almost twice as much rainfall as the warmer dry 1999–2000 La Niña year.

In 1991 the MFR was granted legal status as a national forest reserve by the Paraguayan congress, and in 2000

the reserve and surrounding forested areas of the Jejui watershed were declared a biosphere reserve of the United Nations Educational, Scientific, and Cultural Organization (UNESCO). The 1991 decree creating the MFR gives Ache natives, who once freely roamed the Mbaracayu area, permanent hunting and collecting rights inside the reserve (Hill et al. 1997).

The MFR contains about 90% of the Paraguayan animal and plant species classified as rare and endangered and was chosen as the top-priority conservation site in eastern Paraguay based on vegetation analysis (Keel et al. 1993). Within the MFR there are areas of mature terra firme tropical forest (described in Hill & Padwe 2000), cerrado, grassland, palm-dominated swamps, bamboo forests, riparian flood forests, and a low drier forest type referred to as "kaati" by Guarani speakers.

The MFR is an important endemic bird center with over 400 species of birds recorded in the past few years. (Madroño & Esquivel 1995). A provisional list of the mammalian fauna in the MFR includes 99 species of mammals identified by various methods (Hill & Padwe 2000).

Although Guarani horticulturalists and Ache hunter-gatherers probably both inhabited the MFR in pre-Columbian and early colonial times, by the twentieth century the Ache were the only people living in the forested portions of the area now encompassed by the UNESCO biosphere reserve. Since the 1970s the Ache have been "settled" on reservations but continue frequent treks into the forested areas of their traditional homeland. Now, three Ache communities totaling about 550 individuals are within walking distance of the MFR.

The Ache economy is traditionally centered on hunting vertebrate game with bow and arrow, extracting wild honey, and exploiting palm starch and insect larvae. Numerous fruits are also exploited seasonally, but they constitute only a small fraction of the energy in the yearly diet (Hill et al. 1984; Kaplan et al. 2000). Ache men, who reside at the reservation settlements, now hunt daily in the MFR, returning to the reservation at night. In addition, multifamily groups including men, women, and children sometimes go on extended treks inside the reserve that last about 5–7 days but can sometimes last a month or longer.

Both Ache and non-Ache hunters hunt in some sections of the Mbaracayu Reserve, creating locally depleted sinks for some animal species (Hill & Padwe 2000). Guarani Indians hunt with traps or dogs and mainly kill armadillos and tegu lizards (scientific names are listed in Table 1). Paraguayan peasants usually engage in night tree-stand hunting with shotguns and target tapir, deer, and paca under fruiting trees, at mud licks, or in areas that have been baited with corn. Peasants also engage in diurnal hunting in the reserve and use dogs to target peccaries, armadillos, and large cracid birds.

## Methods

### Data Collection

We estimated animal densities and encounter rates from diurnal line-transect data collected by Ache research assistants. Transects were usually walked 5 days in a row twice each month. After camping at night, each day's transect began 200–400 m from the previous day's stopping point. Researchers did not walk on cut trails; rather, they proceeded through whatever vegetation they encountered. They generally covered about 5 km per day, walking at a rate of about 1 km/hour. The starting point for the first transect of each 5-day trip was selected randomly without replacement from each possible 0.5-km point along the road bisecting the reserve, or from accessible reserve-boundary roads and trails. Transects were established to follow a straight compass bearing (N,S,E,W) for the first day and to continue in the same direction on successive days. If continuing straight would have taken the team out of the reserve, the path was bent 90°. After 5 days the team returned home to recharge battery packs and restock supplies. Transects covered all areas of the reserve, although areas close to human settlements were more frequently sampled to increase the power of statistical comparisons of hunted and unhunted areas.

While walking transects, the team of five researchers spread out about 50 m apart, walking in parallel and communicating by radio. To ensure independence of observations, animals encountered by more than one researcher were counted only for the nearest person to the encounter. This truncates the maximum possible distance of encounter for those walking in the three middle positions. Researchers walked together for 200 m and then stopped to report by radio to a single data collector, who carried a global positioning system receiver and measured elapsed distance with a string box. Radio communication took place about once every 12 minutes and was not audible beyond about 15 m. Complete details of the transect methods are given by Hill et al. (1997). Encounters with all vertebrates of >0.5 kg mean body weight were recorded. The total list of encountered species included 32 native mammals, five reptiles, and 26 birds (some of which were slightly smaller than 0.5 kg). The transect team also encountered Ache and non-Ache hunters and a few domestic animals (mainly pigs and hunting dogs) inside the reserve.

Direct encounters were categorized into one of three types: animal seen, animal heard, or animal in burrow. The presence of animals encountered in burrows was verified by introducing a stick or vine until the animal moved or made a noise. We lumped all direct encounters (seen, heard, in burrow; Table 2) for statistical analyses.

Annual harvest rates and daily hunting success rate for each species were determined by systematic interviews

with all hunters in the Arroyo Bandera Ache community. Because of its proximity to the reserve and greater dedication to a nomadic hunting lifestyle, we estimated that this community harvested >90% of all game harvested by the Ache in the MFR. Systematic interviews with hunters in the Kuetuvy community from 2000 through 2001 confirmed that estimate. One native researcher interviewed all hunters in the community every few days and recorded the species, sex, and age category of each animal killed by each hunter on each day and the total number of days hunted, whether successful or not, for each hunter. The harvest of non-Ache poachers was not measured, but we estimated (based on the population size of the non-Ache people and rumors about hunting activity) that there were about 20–30 active poachers in the northwestern section of the MFR during most of the study and perhaps 50 active poachers in the southeastern corner of the reserve during the final 4 years of the study. This is about equal to the total number of Ache hunters that used the MFR during the study period.

### Analytical Methods

Initially we used the Distance software program (Laake et al. 1994) to convert transect-encounter rates and perpendicular distances to encounters into absolute densities for equilibrium analyses of sustainability of harvest. Encounters were truncated to eliminate the most distant 5% of all encounters. We assumed a “hazard” detection function (Buckland et al. 1993) for all animals analyzed here. This function includes a variety of possible expansion terms (simple polynomial, cosine, hermite polynomial). To get the best estimate of the shape of the detection function, we adopted the hazard function that included whichever expansion terms gave the highest value of Akaike’s information criterion. Mean number of individuals per group encountered was estimated based on a few surveyed groups and the opinion of Ache hunters concerning typical group sizes for prey species.

We modeled the effect of hunting on animal populations and the statistical assessment of their decline over time with logistic regression (see Hill et al. 1997). The dependent variable for these models was the probability of an encounter with the designated species per 200-m unit of transect. We chose this distance because it was unlikely that the probability of encounter with a target species would be dependent on whether or not an encounter had taken place 200 m away for most species (this is not true for white-lipped peccaries, so *p* values for that species should be ignored). Encounters in sequential 200-m units may not be perfectly independent for any species with large, nonoverlapping territories (likewise, the encounters for those walking 50 m apart may not be perfectly independent). Because of this, our final assessment of sustainability considers multiple in-

dependent measures of population fluctuations through time for each species.

Although changes in crude encounter rates are instructive, each yearly set of transects was a random sample drawn from the entire MFR. Some yearly samples in our study contained more total kilometers of transect in favorable or unfavorable habitats or in heavily versus lightly hunted areas. Thus, we developed logistic multiple-regression models with the probability of encounter with each species as the dependent variable and “elapsed time since study began” as the predictor variable in each regression. Hunting pressure and six forest types were entered as control variables in each regression. Each regression was based on 37,673 risk units (200-m lengths of transect). In multiple regressions, we defined hunting pressure as the total number of hunter signs observed in an area (e.g., tracks, camps, direct encounters) divided by total transect distance walked in that area. Some sections of the MFR showed 0 signs of hunters per 100 km of transect, and other 5 × 5 km squares had almost 50 encounters with signs of hunters per 100 km of transect walked in that square (Fig. 1). Vegetation type was initially recorded in the Ache language for all 200-m segments of transect. Later we combined the over 80 vegetation terms into six major forest types—high primary forest, low bromeliad forest, gallery forest, low liana forest, small bamboo forest, large bamboo forest, meadow-swamp—and entered them as covariates in the multiple regression.

## Results

### Changes in Daily Rate of Hunting Return

The harvest composition of all large vertebrates killed by Ache hunters in the MFR from August 1994 to January 2000 showed that only 10 species comprised at least 1% of the number of individuals killed or at least 1% of the total biomass harvested (Table 1). These species com-

7.3	10.8	7.1	7.9
14.7	1.6	0.4	2.7
17.3*	3.5	2.0	4.6
7.7	0.5	4.6	4.4
0.7	0.0	1.4	12.5
8.9	13.5	24.6	41.8

Figure 1. Encounters with signs of hunters/100 km in each 25-km<sup>2</sup> area of the Mbaracayu Reserve. Squares are arranged as in geographical space with north at the top. Square with an asterisk is the area adjacent to the Arroyo Bandera reservation and is most heavily hunted by the Ache.

**Table 1.** Important vertebrate species harvested by Ache hunters 1994–2000.

Common name	Scientific name	Individuals killed (%)	Total kg (%)
Nine-banded armadillo*	<i>Dasyopus novemcintus</i>	2,863 (57.9)	10,879 (46.4)
Capuchin monkey*	<i>Cebus apella</i>	668 (13.5)	1,536 (6.6)
Paca*	<i>Agouti paca</i>	651 (13.2)	4,362 (18.6)
Coatimundi*	<i>Nasua nasua</i>	192 (3.9)	672 (2.9)
Tegu lizard*	<i>Tupinambis merianae</i>	146 (3.0)	336 (1.4)
Rusty-margined guan*	<i>Penelope superciliaris</i>	63 (1.3)	50 (0.2)
White-lipped peccary*	<i>Tayassu pecari</i>	50 (1.0)	1,245 (5.3)
Agouti	<i>Dasyprocta azarae</i>	35 (0.7)	95 (0.4)
Naked-tailed armadillo	<i>Cabassous tatouay</i>	32 (0.6)	173 (0.7)
Yellow armadillo	<i>Euphractus sexcintus</i>	30 (0.6)	150 (0.6)
Collared peccary*	<i>Tayassu tajacu</i>	29 (0.6)	473 (2.0)
Red brocket deer*	<i>Mazama americana</i>	25 (0.5)	645 (2.8)
Solitary tinamou	<i>Tinamus solitarius</i>	23 (0.5)	23 (0.1)
Collared anteater	<i>Tamandua tetradactyla</i>	19 (0.4)	95 (0.4)
Black Vulture	<i>Coragypus atratus</i>	19 (0.4)	38 (0.2)
Tapir*	<i>Tapirus terrestris</i>	13 (0.3)	2,301 (9.8)
Caiman	<i>Caiman latirostris</i>	12 (0.2)	60 (0.3)
Tayra	<i>Eira barbara</i>	7 (0.1)	21 (0.1)
Boa constrictor	<i>Boa constrictor</i>	6 (0.1)	90 (0.4)
Rabbit	<i>Sylvilagus brasiliensis</i>	6 (0.1)	5 (0.0)
Crab-eating fox	<i>Cerdocyon thous</i>	6 (0.1)	24 (0.1)
Porcupine	<i>Sphiggurus spinosus</i>	5 (0.1)	15 (0.1)
Black-front Piping Guan	<i>Pipile yukutinga</i>	5 (0.1)	4 (0.0)
All other vertebrates		36 (0.7)	144 (0.6)
Total		4,941	23,436

\* These species contribute >1% of the total number of animals harvested or >1% of the total biomass harvested.

bined made up 95% of all individuals and 96% of the biomass harvested. They were the focus of our subsequent analyses. Data on Ache hunting days from September 1995 to January 2000 (5526 hunter days) allowed us to determine whether there were changes in harvest success rates through time.

Seasonal and yearly fluctuations in harvest rates were discernible for some species (Fig. 2a–2e). For example, nine-banded armadillo harvest rates generally peaked from May to August each year, and tegu lizards were only harvested from September to December, when they are active above ground. Despite short-term fluctuations, the analyses also showed a tendency toward decreasing harvest rates over time for most species, but the decrease was significant for only 1 of the 10 species, *C. apella* ( $F = 4.71$ ,  $p = 0.035$ ,  $r^2 = 0.8$ ). The lack of statistical significance in the trend for most species was due to high variability in the monthly harvest rate across the sample period. Three species—red brocket deer and both species of peccary—showed nonsignificant increases in hunting success rate through the study period.

### Harvest Percentage of Stock Population

During the first 7 years of this study, the Ache research team walked a total of 7535 km of diurnal line transect. The total number of encounters for each species each

year and kilometers of transect walked are shown in Table 2. Analyses with Distance software provided estimates of the densities and lower 95% confidence limits of those densities for the 10 most-hunted mammal and bird species in the Ache diet. These ranged from a high of about 26 individuals/km<sup>2</sup> for nine-banded armadillos and capuchin monkeys to a low of about 1 individual/km<sup>2</sup> for tapirs (Table 3). Multiplying the density by 600 km<sup>2</sup> gave an estimate of the total stock population for each species. Again, nine-banded armadillos and capuchin monkeys had the highest stock populations, with over 16,000 individuals in the MFR, whereas the tapir population contained only about 650 individuals. We compared the mean number of individuals harvested per year for each species (Table 1) with the estimate of the stock population to estimate the annual harvest percentage in the MFR. We calculated an estimate of the maximum annual harvest percentage by dividing the yearly harvest by the lower 95% confidence interval for the density of each species. All species had an annual harvest of <5% of the standing stock, and 6 of the 10 species had maximum harvest rates estimates below 1% per year (Table 3). Finally, we estimated the maximum sustainable harvest rate for each species, and compared this to the observed harvest rate. Maximum sustainable harvest rate is estimated as  $0.4\lambda_{\max}$  (Robinson 2000), where  $\lambda_{\max}$  is the density-independent maximum population

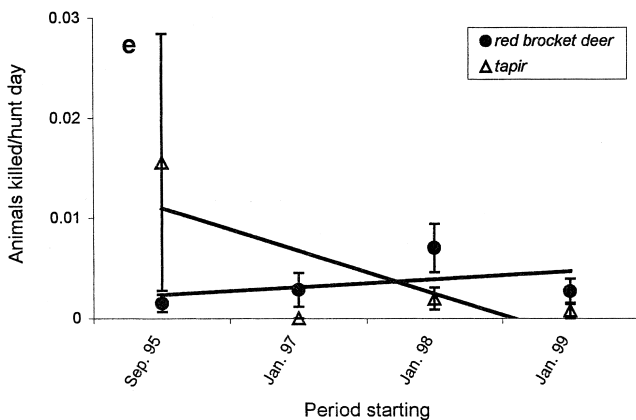
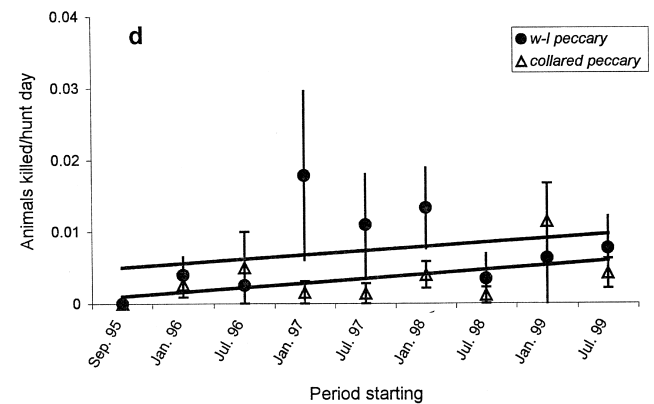
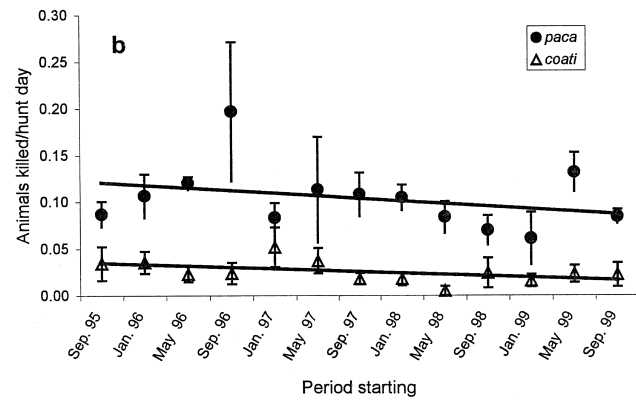
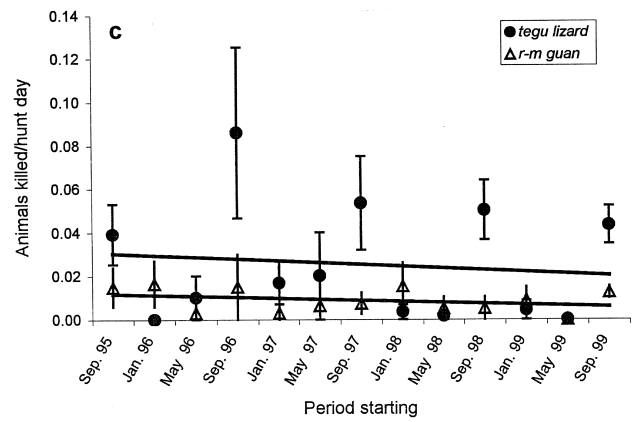
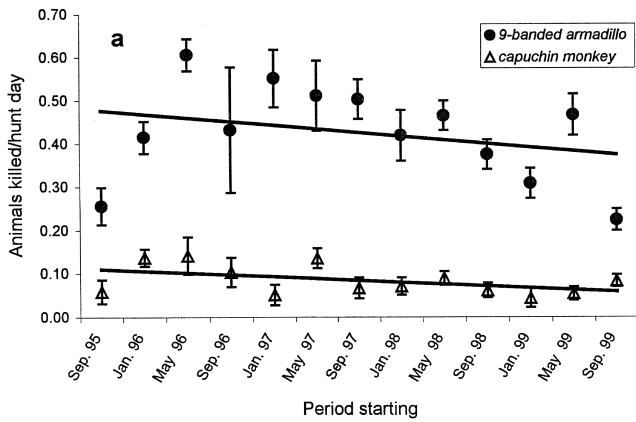


Figure 2. Monthly mean number of animals killed per hunter day of each species during each time segment of specified length. Labels on the x-axis show the starting date for each time segment. Rates on the y-axis are calculated by summing all individuals reported killed and dividing by all days hunted during each month and then averaging over all months in that segment. Bars show  $\pm 1$  SE of the mean monthly rates. Lines show linear regression fits to the data. Most commonly killed animals were (a) nine-banded armadillo and cebus monkey, followed by (b) paca and coati. Animals sometimes killed included (c) tegu lizards and rusty-margined guan. Animals rarely killed were (d) collared and white-lipped peccaries. Very rarely killed animals were (e) red brocket deer and tapir.

growth rate. The estimated maximum observed annual harvest percentages (using the lower 95% confidence interval for animal density) were well under the estimated maximum sustainable harvest rates for all target species.

**Animal Encounter Rates over Time**

Analyses of yearly crude encounter rates per 100 km of transect for each species in the study suggested long-

term declines in crude encounter rates for all species except red brocket deer (Fig. 3). These declines were statistically significant only for nine-banded armadillos and rusty-margined guans ( $p = 0.018$ ,  $p = 0.012$ , respectively).

The mean reported perpendicular distance from the transect line to the encountered item also decreased over time for some species (Table 2), especially those originally reported as encountered at large distances

**Table 2.** Species encounters (enc.) and mean encounter distance (mean dist.) from 7 years of transect data.\*

Species	1994		1995		1996		1997		1998		1999		2000	
	no. enc.	mean dist.	no. enc.	mean dist.	no. enc.	mean dist.	no. enc.	mean dist.	no. enc.	mean dist.	no. enc.	mean dist.	no. enc.	mean dist.
Nine-banded armadillo	170	1.9	255	2.1	283	2.0	251	1.8	77	1.4	129	2.1	57	2.2
Capuchin monkey	55	31.2	55	22.8	79	23.8	89	19.4	26	15.2	80	11.2	27	11.5
Coatimundi	11	26.3	7	24.8	1	3.0	3	7.7	2	2.8	2	4.0	2	2.0
Collared peccary	6	6.4	9	6.3	15	8.0	21	4.8	2	7.4	8	2.9	0	
Rusty-margined guan	93	8.4	89	6.3	121	5.7	129	3.9	29	3.0	76	3.7	42	5.3
Paca	17	1.0	42	2.0	43	2.1	39	1.6	8	1.3	38	1.6	10	2.0
Tegu lizard	17	4.4	15	3.7	18	2.8	23	2.8	4	1.8	24	1.9	10	4.2
Red brocket deer	43	7.7	53	7.2	48	6.3	64	4.1	33	4.0	63	5.5	25	4.9
White-lipped peccary	2	15.0	1	32.0	2	7.0	4	9.7	0	6.3	4	4.5	0	
Tapir	21	26.1	18	20.1	28	13.8	15	9.4	4	6.0	26	4.2	9	21
Kilometers transect	961		1089		1511		1428		460		1393		693	

\* Years beginning in July. Mean encounter distance is mean perpendicular distance in meters from transect to encountered item.

(monkeys, coatis, both peccaries). Native researchers were probably initially confused about this measure and may have sometimes recorded distance to encounter (from themselves) rather than perpendicular distance from the transect line. Later training corrected this problem, and mean reported distance to encounter thus decreased for these species.

To isolate the relationship between elapsed time (since study began) and encounter rates, we performed multiple logistic regression, controlling for hunting pressure and habitat type in 200-m risk units. We also included the interaction variable of elapsed time  $\times$  hunting pressure to determine whether more heavily hunted areas were characterized by steeper declines in encounter rate over time than unhunted areas. This interaction effect was the key variable that tested whether

hunting was responsible for observed declines in encounter rate.

Encounter rates of 4 of the 10 species declined significantly over time with hunting pressure and habitat type controlled (Table 4). Three additional species declined that were not statistically significant. One species (paca) showed a significant increase in encounter rate over time. Encounter rates of only 5 of the 10 species declined in areas with higher hunting pressure, and the effect was statistically significant for only one of those species (nine-banded armadillo). The only species that showed a significant interaction effect between elapsed time and hunting pressure was the red brocket deer. The encounter rate with this deer species decreased significantly and more steeply in areas with higher hunting pressure than in those with lower hunting pressure.

**Table 3.** Analysis of total stock population and annual harvest percentage for important prey.

Species	Measured in Mbaracayu						Theoretical <sup>a</sup>
	group encounter		assumed <sup>b</sup> group size	estimated stock population	estimated annual harvest	estimated maximum harvest 95% CI	estimated maximum % sustainable harvest
	density (no/km <sup>2</sup> )	lower 95% CI					
Nine-banded armadillo	25.92	22.71	1.05	16,329.6	536.0	3.7	40
Capuchin monkey	1.51	1.28	18.00	16,320.0	122.0	0.9	3
Coatimundi	1.71	0.79	8.00	8,208.0	35.0	0.9	?
Collared peccary	3.03	1.81	4.00	7,272.0	5.1	0.1	50
Rusty-margined Guan	6.28	5.18	1.05	3,956.4	11.0	0.3	9
Paca	4.61	3.77	1.05	2,904.3	115.0	4.8	19
Tegu lizard <sup>c</sup>	3.36	2.36	1.00	2,016.0	27.5	1.9	?
Red brocket deer	3.08	2.42	1.00	1,848.0	4.5	0.3	20
White-lipped peccary <sup>d</sup>	0.03	0.02	80.00	1,507.5	8.3	1.1	26
Tapir	1.09	0.78	1.00	654.0	2.6	0.6	12

<sup>a</sup> Based on Robinson (2000) and Alvard (1993).

<sup>b</sup> Based on occasional censuses of encountered groups and Ache opinion.

<sup>c</sup> Based on the encounter rate in October of each year.

<sup>d</sup> There were too few encounters with T. peccari to get a stable estimate of the detection function. The density is estimated by assuming that all groups within 100 m on either side of the 5 people were encountered during the 5 years. The minimum density estimate is one-half that number.

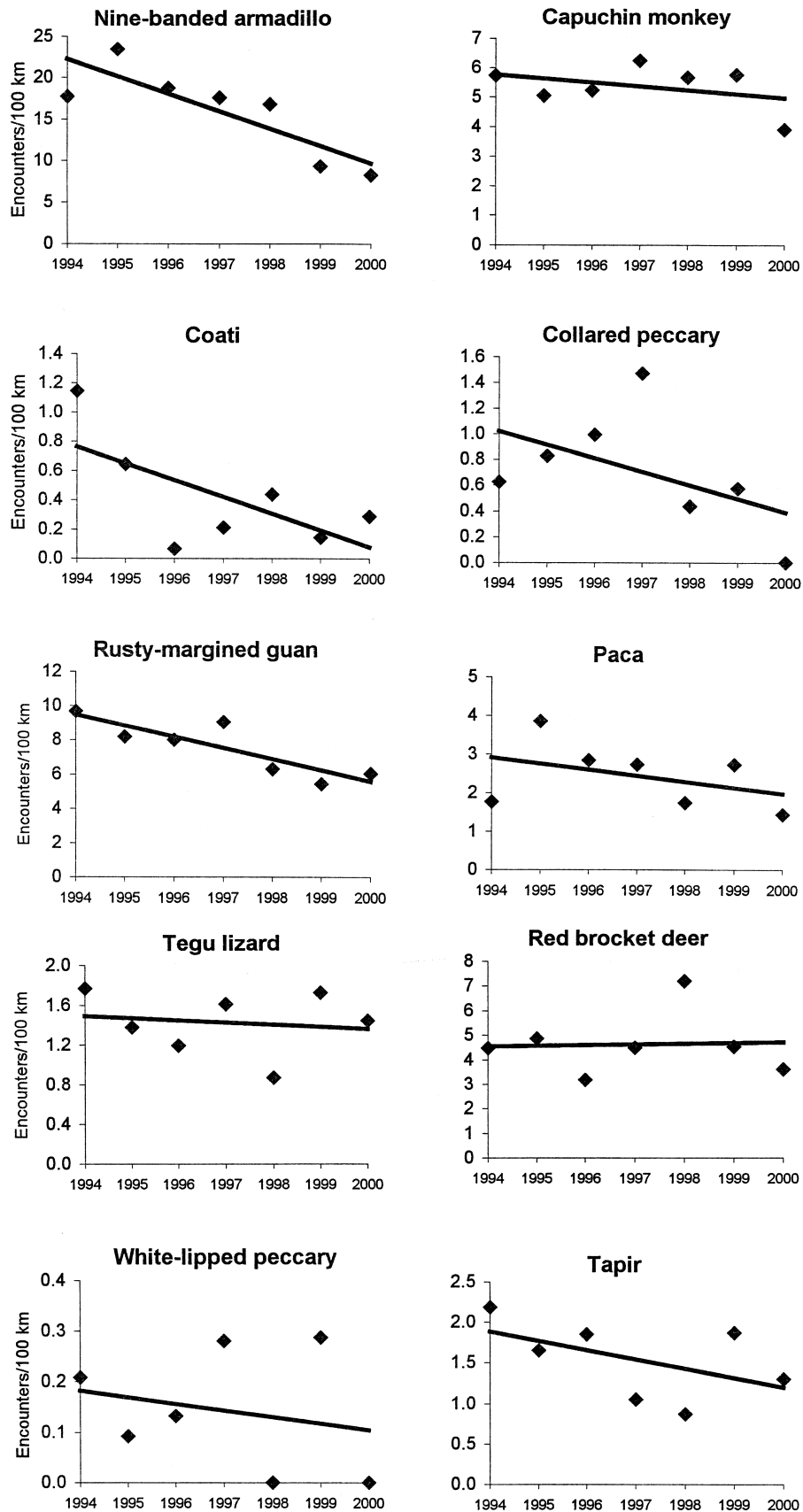


Figure 3. Crude encounter rates/100 km of 10 important hunted species. Encounter rates were calculated as total encounters divided by total kilometers of transect walked in each 12-month period of the study.

Seven of the 10 species also showed significant habitat associations when compared with species in the control type of high forest. These habitat associations indicated higher encounter rates for species with a positive parameter estimate and lower encounter rates for species with a negative parameter estimate. Large bamboo forest was the more distinct habitat type when compared with high forest. On the other hand, encounter rates in gallery forest were indistinguishable from those in high forest for all species.

## Discussion

Mean daily harvest rates for all but three species (red brocket deer and both species of peccaries) declined slightly over time, but the decline was statistically significant only for capuchin monkeys. These results are consistent with the Ache view that some game species have become increasingly scarce through time. However, Ache harvest rates of the two peccary species increased during the study period, so it is possible that the decline in capuchin monkey harvest rates was due to a change in hunting strategy rather than prey density. If Ache hunters began to focus more on following peccary trails as the study period progressed, they might be expected to have harvested fewer monkeys per day simply through their own choices of game search patterns.

Ache harvest rates for all-important game species were well below the maximum theoretically sustainable harvest rates. In fact, none of the important species in the Ache diet were harvested at more than one-third the estimated maximum sustainable harvest rate, and most were harvested at less than one-tenth that rate. But this does not indicate that all species are safe from extirpation or that hunting is not responsible for declines in animal encounter rates in the MFR. Considerable poaching by non-Ache hunters also takes place in the reserve, and we had no way to measure the size of that harvest. Indirect evidence suggests that the poaching harvest could be quite large, because rates of encounter with signs of hunters in two 25-km<sup>2</sup> blocks in the southeast corner of the MFR were higher than in the block directly adjacent to the Ache reservation, where most Ache hunting takes place (Fig. 1).

Crude encounter-rate data also show declines through time for all species except red brocket deer. These declines were not to the result of increased wariness of target species because mean encounter distances did not increase for any of the 10 species examined (Table 2). However, the declines in crude encounter rates were statistically significant only for the nine-banded armadillo and rusty-margined guan. The logistic multiple regression allowed us to examine three independent questions: (1) Did encounter rates decrease over time for

any species when other factors affecting encounter rates were controlled? (2) Were heavily hunted areas characterized by a lower encounter rate than lightly hunted areas? (3) Were declines in encounters over time steeper in more heavily hunted areas?

The logistic multiple-regression analyses did show statistically significant declines in encounter rate over time for four species: nine-banded armadillo, coati, rusty-margined guan, tapir. Three species—capuchin monkey, collared peccary, tegu lizard—showed a nonsignificant but negative association between elapsed time in the study and encounter rates. The confidence interval around the odds ratio of encounter rate by elapsed time for capuchin monkeys was small (between 1.04 and 0.89), suggesting that the null hypothesis (no change in encounter rate through time) can be accepted for that species. But the regressions for the collared peccary and tegu lizard showed larger confidence intervals for the odds ratio (the lower limit was below 0.8). This means, for example, that given the observed variance, encounter rates with them could have dropped as low as 20% of the original values over the 7-year observation period ( $0.8^7 = 0.2$ ), and the trend would not have been statistically significant. Thus, we cannot draw any strong conclusion about those species.

Finally, three other species, red brocket deer, white-lipped peccary, and paca, did not decline in encounter rate over time (they showed positive parameter estimates for the association). The confidence intervals around the odds ratio estimates for red brocket deer and paca were small, and the lower limit was close to or above unity (1.14 and 0.97, respectively). Thus, we can be confident there was no decline for these species. The confidence interval around the odds-ratio estimate for the white-lipped peccary was considerably larger (the lower limit is 0.69). Thus, we cannot place much confidence in our assessment that the encounter rates for that species did not decline through time.

Interestingly, half the species in our study did not decrease in density with higher hunting pressure, and only encounter rates of nine-banded armadillos were significantly lower in areas with greater hunting activity. Equal densities in hunted and unhunted areas for some of these same species have also been reported in other studies (e.g., Bodmer et al. 1997). Perhaps rapid prey migration into low-density regions eliminated the local impacts of hunting for many species. Finally, the decline in encounter rate through time was not steeper in more heavily hunted areas for any species except red brocket deer. Again, this effect may be due to migrational patterns (if deer are exceptionally wary of hunters) rather than localized excess mortality.

Our findings give cause for concern about the large vertebrate community of the MFR. Encounter rates seem to be declining for many species according to several different measures. But there is still little evidence that

**Table 4.** Logistic regression on probability of encounter with important game species.

Species	Elapsed time (years)	Elapsed time odds ratio	Hunting pressure	Interaction time × hunting pressure			
	High forest	Low forest bromeliad	Gallery forest	Low forest lianas	Small bamboo	Large bamboo	Meadow swamp
Nine-banded armadillo	-0.145 <sup>a</sup>	0.86	-0.295 <sup>b</sup>				
Capuchin monkey	-0.041	0.96	-0.113				
Coatimundi	-0.374 <sup>c</sup>	0.68	0.105	0.002			
Collared peccary	-0.058	0.94	0.331	-0.156			
Rusty-margined Guan	-0.102 <sup>b</sup>	0.90	-0.222	0.001			
Paca	0.227 <sup>a</sup>	1.26	0.154	-0.026			
Tegu lizard	-0.158	0.85	-0.268	0.124			
Red brocket deer	0.056	1.05	0.202	-0.087 <sup>c</sup>			
White-lipped peccary	0.049	1.05	0.679				
Tapir	-0.166 <sup>c</sup>	0.85	-0.513	0.143			
Nine-banded armadillo	control			-0.349 <sup>b</sup>	0.161 <sup>b</sup>		-0.43 <sup>a</sup>
Capuchin monkey	control					0.440 <sup>a</sup>	-0.643 <sup>a</sup>
Coatimundi	control					1.287 <sup>a</sup>	
Collared peccary	control						
Rusty-margined Guan	control	0.484 <sup>a</sup>		0.716 <sup>c</sup>			
Paca	control			-1.403 <sup>c</sup>		-0.972 <sup>a</sup>	
Tegu lizard	control						
Red brocket deer	control	-1.581 <sup>a</sup>			-0.387 <sup>a</sup>	0.405 <sup>a</sup>	
White-lipped peccary	control						
Tapir	control	1.173 <sup>b</sup>		0.689 <sup>a</sup>	0.651 <sup>b</sup>	0.779 <sup>a</sup>	

<sup>a</sup>  $p < 0.001$ .<sup>b</sup>  $p < 0.01$ .<sup>c</sup>  $p < 0.05$ .

hunting pressure was the main cause of the observed declines. Higher density of hunter signs was not associated with lower encounter rates for most species, and declines through time were just as steep in un hunted areas as in heavily hunted areas for all species except red brocket deer. And some species are declining drastically despite no evidence that hunting is the cause of that decline. For example, encounter rates for coatis dropped to 10% of their initial levels over the 7-year period, despite the fact that <1% of the stock population was harvested each year and coati encounter rates in heavily hunted areas were no lower than in un hunted areas. Only 1 of the 10 vertebrate species appears to have declined in density over time and shows lower encounter rates in heavily hunted areas: the nine-banded armadillo, an easily hunted animal and favorite food of Ache and Guarani Indians and Paraguayan peasants. However, because we estimated that only 3.5% of the reserve population is harvested by the Ache each year and because the population is still large (about 16,000 individuals) and the reproductive rate high, there is no danger of extirpation of this species in the near future.

Despite the results of statistical analyses, other species may be in greater danger. During our study period, tapir encounter rates declined to one-third of their initial rates. Spatial analysis of tapir encounters over time (not shown here) suggests that depletion is taking place

mainly in the zones most distant from Ache settlements. That depletion is due to Paraguayan poaching, but because tapirs harvested by poachers were not included in our assessment of whether the harvest is sustainable (Table 3), we cannot be sure whether the situation threatens the viability of the tapir population in Mbaracayu. However, because we estimated that there were only about 650 individuals in the entire reserve, that the reproductive rate of tapirs is fairly low, and that the population is declining at a significant rate through time, we would suggest that controlling tapir poaching in MFR should be a high priority.

Other important species in the Ache economy show no evidence of being endangered by current hunting activities or recent natural fluctuations in population density. However, the steep decline in the crude encounter rates for collared peccaries and the apparent small population of white-lipped peccaries in the reserve, along with the difficulty of obtaining accurate estimates (with low confidence intervals) of the population size for these species, should lead Mbaracayu managers to carefully monitor them as well. We cannot always afford to wait until declines are statistically significant before we act.

The most important lesson of this study is that Neotropical wildlife management requires a sophisticated view of population dynamics. Fluctuations in animal populations are complex even when humans are not an agent of

change. In circumscribed natural habitats, animal densities increase and decrease, species go extinct, and others colonize (Ernest & Brown 2000; Brown et al. 2001b). Much of this may be weather-related in ways that are not yet well understood for Neotropical forests. In Chile, the effects of El Niño oscillations on rodent populations have been extremely complex, with differential changes in both time and elevation for the same species (Lima et al. 1999). In Mbaracayu, the 2 years of extremely wet weather (1996–1998) followed by a drought year in 1999 produced erratic fruiting patterns. None of the six important fruits in the Ache diet was encountered in all study years, and some were extremely abundant in one year and totally failed in a subsequent year. Because many tropical prey species are frugivorous to some extent whereas others compete with frugivores, prey on frugivores, or are preyed upon by frugivore predators, it is impossible to speculate how these changes in food availability affected the game species we monitored. Only sophisticated research designs will isolate the effects of hunting versus those of other natural factors on the density of mammal species in the Neotropics.

Some authors strongly suggest that human hunting must be eliminated in Neotropical reserves to preserve natural ecosystems of high biodiversity and with an abundance of large vertebrates (Schwartzman et al. 2000a). These studies are sometimes based on flawed interpretations that localized hunting depletion indicates unsustainability of the human harvest. But they may also be dangerously naïve concerning the role of humans as top predators in the ecosystems we are trying to conserve.

Conservation biologists sometimes express concern for the effects of missing nonhuman top predators such as jaguars (*Panthera onca*), Harpy Eagles (*Harpia harpyja*), and anacondas (*Eunectes* sp.) (e.g., Miller et al. 2001) but voice no concern for the loss of humans as the natural top predator in post-Pleistocene Neotropical forest communities. The indirect effects of removing all activities of top predators are complex and unpredictable, and they could possibly lead to unwanted declines in many Neotropical species. Such effects are much better understood in modern fisheries, whose complexity does not approach that of Neotropical forests. Still, it is unclear how the elimination of top predators in those systems affects the densities of any particular prey species in either the short or long term (Yodanis 2001).

Until Neotropical ecosystems are much better understood, the most conservative management policy is probably to permit human predation at levels near those imposed by traditional native populations during the past 10,000 years. Along with permitted human hunting, the harvest patterns in those units should be carefully monitored over time. The current situation in the MFR suggests that a top priority should be to eliminate all poaching and monitor native hunting patterns carefully until declines in game-species populations cease.

## Conclusions

We draw three general conclusions from our 7-year study in the MFR that can be applied to the management of other Neotropical reserves.

- (1) Static equilibrium models of harvest sustainability are useful guides, but the adaptive-management approach of continuous population monitoring over long time periods provides the margin of safety needed when unforeseen factors or rare events may lead to the rapid decimation of a stock population.
- (2) Only detailed studies of ecological principals can untangle the complexities of fluctuations in population size and assign causality to human activity or natural factors.
- (3) Studies of population trends in sink and source areas of a stock population are required to assess the impact of human activities on the target species. Localized depletion due to hunting is commonly expected, but only when hunting can be shown as the cause of continuous decline in populations over time can it be considered unsustainable.

We believe that our study provides an illustration of the complicated nature of biological communities and the difficulties of determining whether human predation patterns in any particular area are sustainable or whether they are responsible for population fluctuations observed over short periods of time. Although faunal management in human-use areas may be more complicated than some researchers had hoped, complete and thorough studies of human predation and other population processes operating through time will allow us to reap large gains in overall knowledge of community ecology and wildlife management.

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