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# Hunting for Sustainability in Tropical Forests

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# *Sustainability of Aché Hunting in the Mbaracayu Reserve, Paraguay*

KIM HILL AND JONATHAN PADWE

An understanding of native hunting and its impact on faunal density is critical for biodiversity conservation in the neotropics because more forested habitat is designated as indigenous reserve than all other types of conservation units combined (Rylands 1991; IUCN 1992; DaSilva and Sites 1995; Peres and Terborgh 1995). Despite a good deal of information on the overall structure of native game harvest in the neotropics (Beckerman and Sussenbach 1983; Vickers 1984; Redford and Robinson 1987) little is known about the way that harvest impacts animal populations through time and space. Some studies have suggested that hunted areas are depleted of game relative to nonhunted areas (see Hill et al. 1997 for review and discussion), but often these studies are based on census methods that are problematic. Specifically, many hunting impact studies to date (a) fail to distinguish changes in encounter rates due to evasive prey behavior from changes in animal density; (b) fail to control for the effects of variables other than hunting that also might be associated with differences in animal density; (c) do not provide independent measures of human hunting activity in areas assumed to be hunted; (d) 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; (e) are based on repeated transects in the same location, but inappropriately assume statistical independence of data and extrapolate to unsampled areas. We recently developed a procedure to measure the impact of human hunting on animal density that eliminates many of these problems (Hill et al. 1997). Nevertheless, other problems remain. Most importantly, many human hunting studies do not examine the relationship between hunting and animal densities over an adequate spatial scale to draw relevant conservation conclusions about the impact of hunting on the true *unit stock* of a prey population. The unit stock is the

population unit affected by harvesting. It consists of a collection of animals that interbreed, experience a common set of mortality and fertility parameters (from common causes), and show high intraunit migration relative to interunit migration. Most unit stocks of neotropical game inhabit vastly larger areas than are examined in most hunting studies; thus the scale of many hunting studies is inappropriate for use in wildlife management. Humans, like all central place foragers, are likely to deplete prey near their residential base. But how that depletion is manifested through space and time, and whether large unharvested prey populations are able to replenish depleted areas and maintain population viability, is a key issue that has not been adequately addressed.

*Source-sink* (SS) models are designed to examine population dynamics over a large spatial scale. SS models consider situations in which large populations are divided into subpopulations that experience negative and positive growth through time (Pulliam 1988; Pulliam and Danielson 1991). Sink areas experience annual population loss through mortality and emigration in excess of population gains through fertility. In source areas this relationship is reversed. Thus, in order for a sink population to be stable, annual immigration from a source must balance the net annual population loss. In theory, SS models can be used to determine if predator-prey relationships are stable in geographic regions larger than the observed prey catchment basin. However, because density-dependent effects on fertility, mortality, and dispersal are not well studied, SS models currently serve as more of a theoretical construct than a tool for empirical studies of harvest sustainability by predators. This concept is rarely acknowledged explicitly in prior neotropical hunting studies, but is implicit in some that examine hunted areas and protected areas together. In this chapter, we show that most hunting by our study population is performed in a 6-km radius from a permanent village site (the potential sink). We assume that the source population boundaries for the prey hunted in that zone are located at a point between the study population and other neighboring hunting populations that exploit the same prey. This assumption allows us to estimate harvest sustainability in a defined area that is biologically relevant.

The implications of game source and sink areas for determining harvest sustainability have not yet been fully appreciated by conservationists. For example, Robinson and Redford (1994b) reviewed five indices typically used as measures of game harvest sustainability:

1. Comparison of densities between harvested and unharvested locations
2. Change in animal density through time at a single location
3. Comparison of hunting yields in more and less harvested areas
4. Comparison of hunting yields through time
5. Comparison of age structure of prey populations in harvested and unharvested areas

Only the second and fourth of these points represent valid measures of sustainability when sink and source populations of prey exist. Spatial heterogeneity in animal density or age structure is expected but does not directly address the question of sustainability. Likewise, Bodmer (1994) has correctly noted that a comparison of harvest rate to reproductive rate can be used to estimate whether

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## BACKGROUND

### *The Mbaracay*

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harvests are likely to be sustainable. However, this is only true if the prey population in a potential source area is included in the production calculation and if the prey response to density-dependent effects on life history characteristics is known (because fertility and mortality are often density dependent).

Biological resource management often has relied on equilibrium population models to determine sustainable harvest rates for commercially and recreationally exploited species. Analyses of sustainability in this chapter are based on assuming a *surplus production model* of harvestable biomass where the change in biomass through time is the difference between net production and harvest, with net production defined by the logistic growth equation. The SS modeling approach complements this model by specifying the true unit stock. These models in combination with measured demographic parameters at different population densities can be used to define a harvest rate that will not deplete the prey population through time, as well as the maximum sustainable harvest rate, and a variety of other equilibrium harvest parameters under specified harvest effort (Walters 1986). In practice, however, the use of equilibrium management methods has been problematic. Not infrequently, unforeseen circumstances (i.e., parameters and relationships not in the model) cause temporary prey depletion that can eliminate the unit stock from a geographical area or lead to dangerously low populations that cannot withstand harvest at the theoretically calculated (and sometimes legally mandated) rates. The inability of population models to capture fully all aspects of population dynamics has led to an alternative viewpoint on management. This viewpoint, termed *adaptive management*, emphasizes the need for continual monitoring and appropriate adjustments in harvest regulation to accompany any steady-state population management policy (e.g., Walters 1986; Christensen et al. 1996).

In this chapter, we examine harvest sustainability by the Aché native population in the Mbaracayu Reserve based on equilibrium assumptions. The results can be used as a guideline for guessing whether current harvest rates will be sustainable over several years, but should be complemented with monitoring and adaptive management to ensure that steady-state harvest models do not result in prey population decline due to factors unforeseen in the models. The current analysis suggests that Aché hunting does not threaten the population of any important game species in Mbaracayu. This is true despite the fact that localized depletion near the Aché settlement can be shown for some species (Hill et al. 1997). A 5-year monitoring project begun in 1994 will allow us to assess whether projections from equilibrium SS modeling are useful and whether they fully capture the dynamics between Aché predators and their prey in the Mbaracayu Reserve.

## BACKGROUND

### *The Mbaracayu Reserve*

The 60,000-hectare (ha) Mbaracayu Nature Reserve is the largest tract of undisturbed forest in eastern Paraguay. The Reserve is located at approximately 55° west and 24° south in an area that drains west to the Paraguay river. It is an area

characterized by gently rolling hills composed of soft sedimentary rock. Soils are sandy, heavily leached, and of low fertility. The hills are covered with subtropical broad-leaf semi-deciduous forest, whereas some low flat valleys are filled with tall broad-blade grasses. Most of the area is at an elevation of 150 to 300 m. Rainfall totals about 1800 mm/yr on average and is characterized by extreme unpredictability in monthly pattern from year to year but with a statistical dry season from May to August (Sanchez 1973). Temperature fluctuations mark seasonality, with average daily low-high temperatures of 14 to 25°C in July and 22 to 34°C in January. Temperature extremes are approximately 41°C and -3°C, with several days of hard frost each year, which often kills the leaves on many exposed trees and shrubs.

The Reserve was purchased by The Nature Conservancy (TNC), in conjunction with the Fundación Moisés Bertoni (FMB), a Paraguayan conservation NGO. In 1991, the Reserve was granted legal status as a national forest reserve by the Paraguayan congress. It was included on TNC's 1991 list of "last great places on earth" and is the home of a variety of rare and endangered animal and plant species. A crude map of vegetation zones was commissioned by the FMB in 1992 (figure 5-1).

The Mbaracayu Reserve contains about 90% of the Paraguayan animal and plant 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). The Reserve includes a remarkable diversity of forests, rivers, mountains, caves, grasslands, and wetlands. Indeed, the most striking feature of the Reserve is its pronounced microregional diversity. 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.

Although there are many distinguishable plant communities that form separate habitats in Mbaracayu (Hill et al. 1997), only the high forest has been systematically described. This forest type covers approximately 50% of the land surface surveyed by our research team (Hill et al. 1997). In 1987, a team of four botanists and two Aché assistants led by A. Gentry recorded all plants greater than 2.5 cm diameter at breast height (dbh) on transects that added up to a total area of 1000 m<sup>2</sup> in mature high forest of the north east corner of the Mbaracayu Reserve (Keel 1987). The basal area of tree species >10 cm dbh is 39 m<sup>2</sup>/ha in this sample. The five species with highest species importance values (SIV-sum of relative frequency, relative density, and relative dominance) (Keel et al. 1993) are *Sorocea bonplandii*, *Campomanesia xanthocarpa*, *Chrysophyllum gonocarpum*, *Myrciaria baporeti*, and *Balfourodendron riedelianum*.

Common emergents in the high forest include *Tabebuia heptaphylla*, *Astronium* spp., *Aspidosperma polyneuron*, *Albizzia hasleri*, *Anadenanthera* spp., *Enterolobium contortisiliquum*, *Peltoporum dubium*, *Cedrela fissilis*, *Patagonula americana*, and *Balfourodendron riedelianum*. The maturity of the forest is indicated by the high density (103 specimens in 1000 m<sup>2</sup>) of lianas >2.5 cm dbh, including many examples of lianas >10 cm dbh. Despite the presence of many valuable timber species

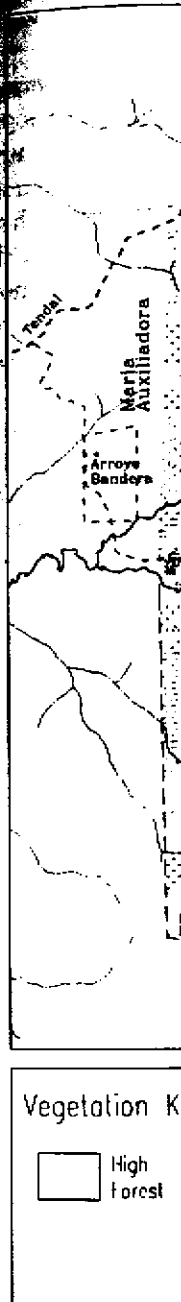


Figure 5-1. Mbaracayu Reserve, Fundación Moisés Bertoni (Arroyo Banderas, Moris Auxiliadora, Tendal, etc., labeled).

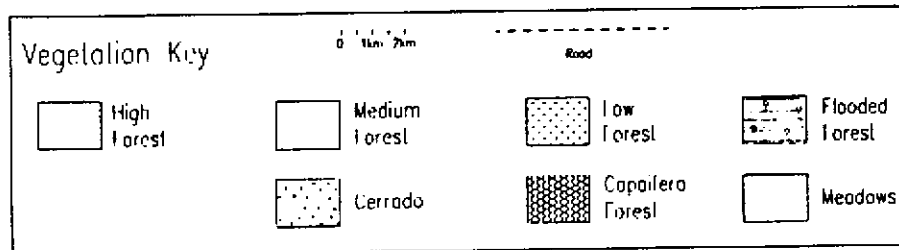
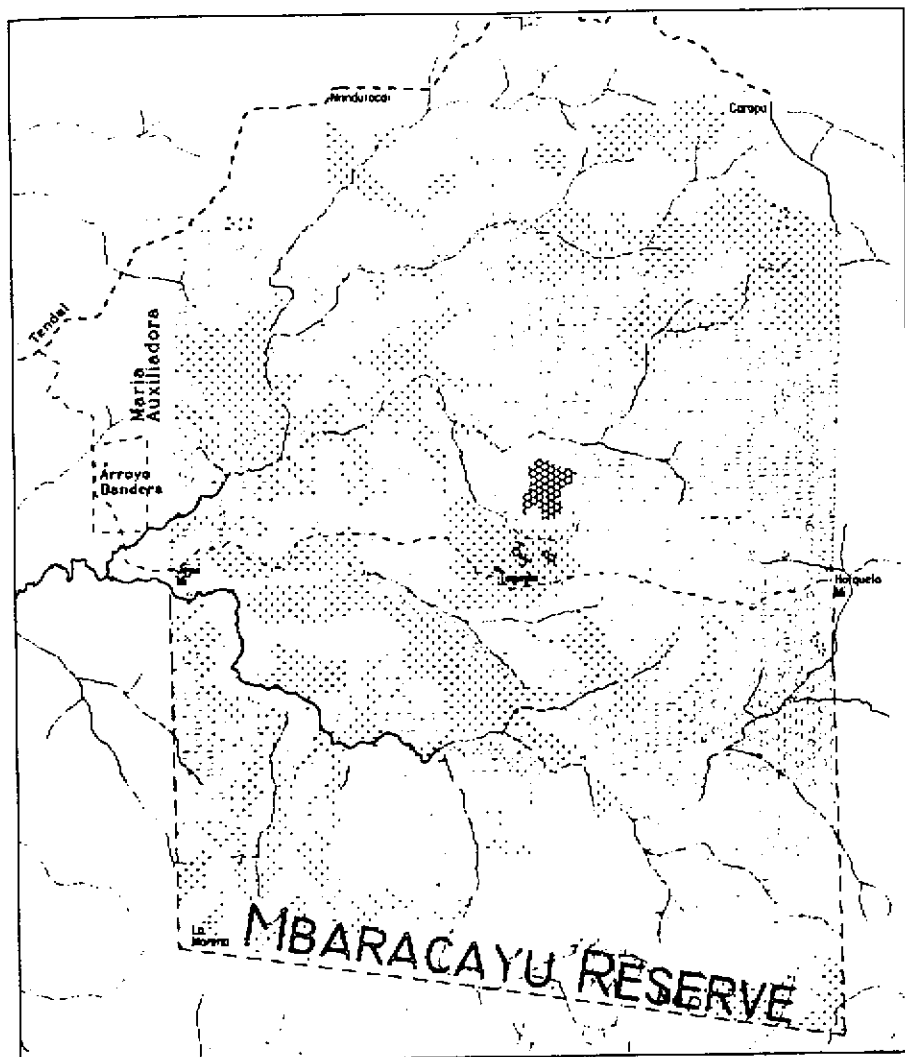


Figure 5-1. Major vegetation zones in the Mbaracayu Reserve as mapped by the Fundación Moises Bertoni (FMB 1992). The location of the Aché research team (Arroyo Bandera), as well as three small Paraguayan communities (Maria Auxiliadora, Tendal, and Guyra Kehja) are shown. Permanent forest guard posts are also labeled.

throughout most of the Reserve, some portions of the Reserve were selectively logged for lapacho (*Tabebuia heptaphylla*) and peroba (*Aspidosperma polyneuron*) in the 1970s and 1980s.

The most important palms in Mbaracayu are *Syagrus (Arrecastrum) romanzoffiana* and *Acromia totai (sclerocarpa)*, which produce edible fiber, growing shoots, fruits, and nuts. We have counted *Syagrus* palms at a density of approximately 0.8/ha in dry forest and about 20/ha in poorly drained forest using ground transects and aerial surveys. Another extremely common species that might have important effects on the high forest animal community is *Citrus aurantium*, the common orange. This is a species of domestic origin that has spread throughout the forests of eastern Paraguay (Gade 1976) in the 450 years since it was introduced to the region by the Jesuits. It is an important food item of *Agouti*, *Cebus*, and *Tayassu* as well as numerous birds.

The Mbaracayu Reserve is 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 and Esquivel 1995 and personal communication). The mammalian fauna of eastern Paraguay has been the subject of many inventory studies, but no studies to determine absolute or relative densities of mammals. Myers et al. (1995) have recently summarized available data and report 124 mammal species verified in eastern Paraguay. In the Mbaracayu Reserve to date, we have listed 99 species of mammals identified by visiting inventory teams or ourselves. Because these data come from several sources, and some identifications are based on single sightings, it should be considered provisional. Bats make up 23 species on this provisional list, with nonvolant mammals comprising 76 species. A provisional list of Mbaracayu mammals excluding marsupials, bats, and small rodents (< 500 g body weight) is shown in table 5-1.

### *The Aché*

The law that created the Mbaracayu Reserve as a legal entity in 1991 states in part:

In recognition of the prior use of the forest by the Aché indigenous community, these groups will be permitted to continue subsistence hunting and gathering in the area of the Nature Reserve, as long as they employ traditional methods, and according to that which is allowed in the administrative plan of the reserve. The participation of the local Aché community in the protection and administration of the reserve will be encouraged, and they (the Aché) 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)

For this reason, studies of Aché resource use patterns are critical to conservation planning for Mbaracayu.

Archeological data suggest that foraging peoples might have inhabited the forested areas of eastern Paraguay for at least 10,000 years. The Aché were described by early Jesuit explorers, but historical evidence shows that the Aché experienced no peaceful contact with outsiders (either Indian or peasant colonists)

Table 5-1. Provisional List of Mammals Sighted or Trapped in the Mbaracayu Reserve, 1970-1996

Scientific Name	Common Name
<b>Edentates</b>	<b>(8 Species)</b>
<i>Tamandua tetradactyla</i>	Collared anteater
<i>Mymecophaga tridactyla</i>	Giant anteater
<i>Dasybus novemcinctus</i>	Nine-banded armadillo
<i>Dasybus septemcinctus</i>	Seven-banded armadillo
<i>Euphractus sexcinctus</i>	Yellow armadillo
<i>Cabassous tatouay</i>	Naked-tailed armadillo
<i>Priodontes maximus</i>	Giant armadillo
<i>Tolypeutes</i> spp.	Three-banded armadillo
<b>Primates</b>	<b>(2 species)</b>
<i>Cebus apella</i>	Brown capuchin monkey
<i>Alouatta caraya</i>	Black howler monkey
<b>Lagomorphs</b>	<b>(1 species)</b>
<i>Sylvilagus brasiliensis</i>	Rabbit
<b>Large rodents</b>	<b>(7 species)</b>
<i>Sphiggurus spinosus</i>	Porcupine
<i>Coendou paraguayensis</i>	Paraguay porcupine
<i>Dasyprocta azarae</i>	Agouti
<i>Agouti paca</i>	Paca
<i>Cavia aperea</i>	Guinea pig
<i>Hydrochaeris hydrochaeris</i>	Capybara
<i>Myocastor coypus</i>	Nutria
<b>Perissodactyls</b>	<b>(1 species)</b>
<i>Tapirus terrestris</i>	Tapir
<b>Carnivores</b>	<b>(17 species)</b>
<i>Cerdocyon thous</i>	Crab-eating fox
<i>Dusicyon gymnocerus</i>	South American fox
<i>Chrysocyon brachyurus</i>	Maned wolf
<i>Speotbaeus venaticus</i>	Bush dog
<i>Galictis cuja</i>	Grison
<i>Eira barbara</i>	Tayra
<i>Conepatus chinga</i>	Hog-nosed skunk
<i>Procyon cancrivorus</i>	Crab-eating raccoon
<i>Nasua nasua</i>	Coati
<i>Lutra longicaudis</i>	Southern river otter
<i>Pteronura brasiliensis</i>	Giant otter
<i>Panthera onca</i>	Jaguar
<i>Felis pardalis</i>	Ocelot
<i>Felis wiedii</i>	Margay
<i>Felis tigrina</i>	Oncilla
<i>Felis yagouaroundi</i>	Jaguarundi
<i>Felis concolor</i>	Puma
<b>Artiodactyls</b>	<b>(5 species)</b>
<i>Tayassu pecari</i>	White-lipped peccary
<i>Tayassu tajacu</i>	Collared peccary
<i>Mazama americana</i>	Red brocket deer
<i>Mazama gouazoubira</i>	Grey brocket deer
<i>Mazama rufina</i>	Dwarf red brocket deer

This list does not include marsupials, bats, or rodents with body weights of less than 500 g.



between the Spanish conquest in the 1500s and recent incursions into their territory in the 1970s (Hill and Hurtado 1996). Since the 1970s, the Aché have been "settled" on government/mission reservations but continue frequent forest treks that may last weeks or even months. The population currently consists of about 700 people living in five settlements. Previous anthropological studies of the Aché have focused on a wide variety of economic topics (see Hill and Hurtado 1989 for review) and Aché life history patterns (Hill and Hurtado 1996).

During the first half of the twentieth century, the Northern Aché inhabited a 20,000-km<sup>2</sup> area of eastern Paraguay centered in the upper Jejui watershed, which is now the Mbaracayu Reserve. At a population density of only 0.03 person/km<sup>2</sup> the Aché probably had little impact on animal densities prior to their reduction on reservation settlements. During the 1970s, Aché bands were tracked down, brought out to passable roads, and transported on missionary or military trucks to a few reservations, where they were expected to remain (Hill and Hurtado 1996, Chapter 2). Reservations consisted of only a few thousand hectares, and despite the fact that outsiders began teaching the Aché to farm, most individuals reentered the forest frequently on long foraging treks because reservation resources were inadequate to feed the population. The last of the uncontacted Aché bands took refuge in the northern section of the Mbaracayu Reserve until 1978, when they too were contacted and transported to a nearby reservation.

At this writing, two Aché reservations totaling about 500 individuals are within walking distance of the Mbaracayu Reserve, and the Aché have begun to recognize the long-term impact of their economic activities on the natural resources of the shrinking forested areas near their reservations. The Aché economy is traditionally centered around hunting mammalian 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). The current reservation economy also includes swidden agriculture (mainly manioc and maize) and some domestic animals (chickens and pigs), which have been introduced in the past 15 years. Younger Aché also have become increasingly involved in seasonal wage labor at nearby farms.

### *Hunting in the Mbaracayu Reserve*

Both Aché and non-Aché hunters hunt in some sections of the Mbaracayu Reserve. The Mbaracayu administration has placed two guards at each of five guard stations around the periphery of the Reserve to control the entry of non-Aché hunters, and the road that bisects the Reserve is blocked by a locked gate at both ends. A three-person team of roving guards monitors illegal activity throughout the Reserve. Although park guards have been effective at eliminating large-scale disturbance (illegal timber extraction and establishment of swiddens), within the Reserve they have not been able to eliminate poaching by non-Aché hunters. Because we have no reliable data on poaching, we will examine only Aché hunting practices in this chapter. However, we do assume that regions hunted by

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### METHODS

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The non-Aché hunters include Paraguayan and Brazilian frontiersmen—peasants as well as Guaraní horticultural Indians. Guaraní Indians have lived in the Mboi Jagua reservation about 7 km from the western border of the Reserve for about 30 years (and in nearby traditional villages before that) and rarely hunt in the Reserve. When they do, they usually carry only a machete and target armadillos (*Dasyus*) or tegu lizards (*Tupinambis*). Most Paraguayan and Brazilian peasants are recent arrivals to the Mbaracayu area. The Maria Auxiliadora settlement along the northern section of the western border of the Reserve has only existed for about 3 years and consists of about 80 families who are close enough to hunt in the Reserve. Recent survey data (P. Garfer, personal communication) suggest that only a small fraction of this peasant population hunts, and that number has diminished over time. However, a new settlement, Guyra Kejha, has just been established near the southeastern corner of the Reserve, and preliminary data from 1996 suggest extensive peasant hunting in that area. Peasants usually engage in night tree stand hunting with shotguns. They target tapir, deer, paca, and agouti under fruiting trees, at mud licks, or in areas that have been baited with corn. Occasionally, peasants engage in diurnal hunting in the Reserve using dogs, and they primarily target both species of peccary, armadillos, and the three species of large cracid birds found in the Reserve.

The Aché have been hunting in the Mbaracayu area for at least a century, and they began intensively hunting the northwestern portion of the Reserve when the Arroyo Bandera reservation was established near that area around 1980. Aché from the more distant Chupa Pou reservation occasionally hunt in the southwestern portion of the Reserve. The Aché 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 to 5 days but can sometimes last much longer.

## METHODS

### *Aché Game Harvest Patterns*

Harvest rates for individual game species were determined from two data sets covering a span of 15 years. From 1980 to 1985, one of us (K.H.) recorded the species and weights of all game killed each day by Aché hunters on treks in the forest during trips in which we accompanied the Aché (see Hawkes et al. 1982 for details). This sample, taken from three field sessions, was not randomly distributed through the year, but does cover most months of the yearly cycle. It consists of 185 observation days in the forest, which comprised 2087 man hunting days. From August 1994 to the present, another of us (F.J.) has recorded all animals killed by members of the Arroyo Bandera reservation and (since August 1995) all man days spent hunting in the forest regardless of success. Because the observer

(FJ.) lives full time at the Arroyo Bandera reservation, and all houses are within view, with sharing of game widespread, it is unlikely that a significant number of harvested animals were unrecorded. The data from August 1994 through December 1996 cover 869 observation days. The community consisted of an average of 90 individuals, 28 of whom were potential hunters (men at least 17 years old) and 83 of whom were consumers (> 3 years old). To convert number of animals harvested of each species into biomass, we have used mean weights from our own observations or those reported by Redford and Eisenberg (1992).

### *Animal Densities*

Game densities were estimated using a stratified sample of diurnal line transects through the Mbaracayu Reserve. Details of the field method have been reported elsewhere (Hill et al. 1997). Line transect methods are the most widely used technique to census large neotropical mammals and birds (Cant 1977; Glanz 1982; Emmons 1984; Robinson and Redford 1986b; Bodmer et al. 1988a; Peres 1990; Glanz 1991; Silva and Strahl 1991; Bodmer et al. 1994). Properly collected transect data used in conjunction with widely available analytical software can provide robust estimates of average density in an appropriately sampled area if all targets on the line are detected (Buckland et al. 1993; Laake et al. 1993).

In our study, line transect starting points were drawn without replacement from the set of all locations along the dirt road running east-west and bisecting the Reserve. About 10% of transect sample days commenced off the road, after camping overnight in the forest. Absolute locations during the study were determined using a Trimble Pathfinder Pro Global Positioning System (GPS) receiver, whereas relative distance along a transect was measured using a string box.

Transects were initially walked by a team of five native assistants and a data recorder. After the first year, native assistants recorded all data without outside help. Observers walked in parallel along a central transect line. The four native assistants spaced themselves at approximately 25 and 50 m on either side and perpendicular to the center line, and one walked directly on the center line about 5 m ahead of the data recorder. Each assistant carried a VHF radio to communicate with the data recorder. Each transect began at the specified GPS location and proceeded toward a specified compass bearing throughout the day. No transects were performed on trails, but instead the team walked through whatever vegetation was encountered.

After receiving a radio signal from the data recorder, each native observer began walking along the center transect line or parallel to it. Team members walked at a rate of about 1 km/hr. Native assistants were allowed to veer a few meters each side of the transect to verify that burrows they encountered were indeed 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 for that 200-m unit. Observers, in sequence, reported over the radio all encounters during the previous 200 m with all species (including humans) and the encounter type (defined below). The data recorder took an averaged GPS reading every 600

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to 800 m along the transect in order to estimate the absolute location of the transect within the study area for later analyses. Location between GPS readings was estimated by interpolation using string box measurements. The locations of transects from June 1994 to June 1996 are shown in figure 5-2.

Native Aché research assistants were trained for 1 week prior to beginning data collection and went through periodic retraining and distance verification sessions. 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 range-finder, metal tape, and string box. Assistants were familiar with the western numbering system but could not read or write. Their ability to estimate distance in the forest was good. Verification of reported distances to specified points in the forest shows a regression coefficient between actual and estimated distance of 0.84 ( $n = 113$  trials between 3 and 80 m actual distance,  $r = 0.94$ ). Thus, Aché distance estimates were on average about 84% of the true distance and did not show much deviation from the actual distance. However, Aché assistants generally reported distance to the nearest animal of a social group rather than to its center. This means that absolute density estimates of animals that live in dispersed groups will be too high if the data are taken at face value (but this error can be corrected if the mean diameter of social groups is known).

Aché men insisted on working in teams to avoid forest dangers. Therefore, the method that we use generates a great deal of data per field day. However, walking simultaneous parallel transects through uncut vegetation with radio communication every 200 m is undoubtedly noisier than the standard method of a single observer walking on a cleared trail and noting encounters silently. We believe that this is not a serious problem, but empirical verification would be useful, by doing single observer transects on cut trails in the same area. Native observers are quite skilled and might detect many animals that would not be detected by observers who have not lived their whole lives in the forest. Aché observers insisted that most target species do not flee until they have direct confirmation of a predator visually or by smell. Such a response should be common in many prey species where the costs of unnecessary flight are high. Thus, we assume that noises of walking through vegetation did not spook most target species until they were near enough that they could be detected (by an Aché) when fleeing the area. The Aché concurred with this conclusion based on reading animal tracks, which suggested that few animals fled completely undetected just before observers arrived. Aché assistants also report that quiet radio conversation does not spook most target species. In any case, radio conversation was not audible to us at distances greater than 15 m, and communications took place only once every 15 minutes on average. Thus, we provisionally conclude that although there might be problems with the noise made by our transect team, these are outweighed by the multiple disadvantages of typical line transect studies that use observers who have not grown up in the survey area walking repeatedly on a few trails that are not randomly placed in the study area (see Hill et al. 1997 for discussion).

Encounters were recorded for all mammal, bird, and reptile species that are

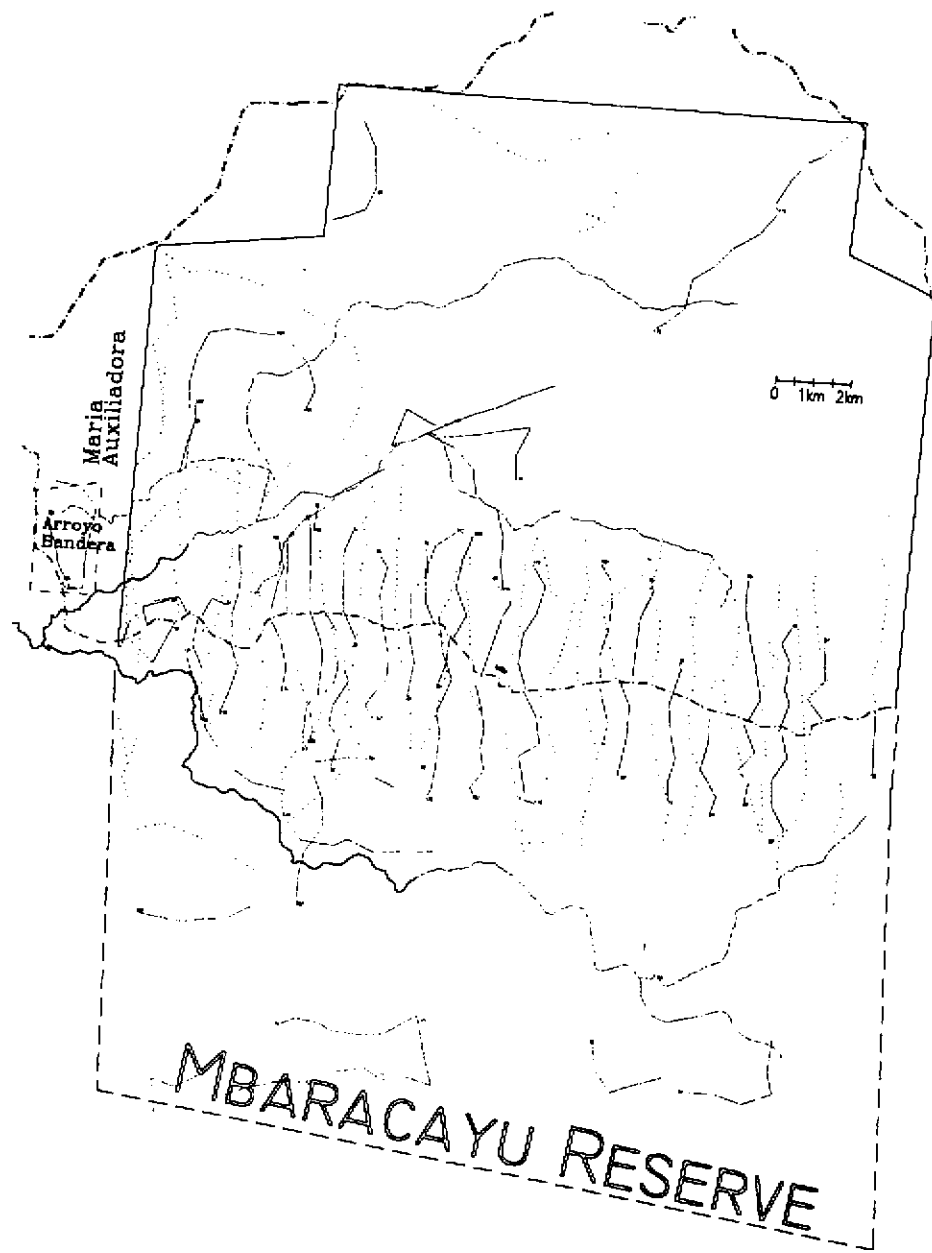


Figure 5-2. The location of diurnal transects performed in the Mbaracayu Reserve by the Aché research team. Dotted lines show transects from May 1994 to May 1995, solid numbered lines show transects from June 1995 to June 1996. A total of 123 different transects were performed inside the Reserve and three on the Arroyo Bandera and Chupa Pou (not shown) reservations. Most transects began from the road (*dashed line*) bisecting the Reserve east—west. The northwest corner was sampled frequently in order to monitor the extent of poaching by peasants in that zone.

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larger than 0.5 kg mean body weight. Two types of encounters were recorded: (a) animal seen, heard, or found in burrow; and (b) fresh signs of the animal or fresh feces encountered. All encounters of the first type are lumped together for analyses into a category that we refer to as *direct encounters*. When multiple observers detected the same animal, only the observation of the closest observer was used for analyses. We generally required observers to confirm the presence of an animal in an occupied burrow by flushing it, or by introducing a long vine and getting the animal to move inside. In a few cases, Aché assistants insisted that there was an animal inside (by certain signs, smell, etc.), even when they could not get direct confirmation, and we recorded those burrows as occupied.

Encounters of the second type are aggregated for analyses into a category that we term *indirect encounters*. These signs included tracks, feeding disturbance, territorial markers, beds and nests, urine, scent, body excretions, etc. that were judged to be less than 24 hours old. Indirect encounter patterns have been reported elsewhere (Hill et al. 1997) and are not analyzed here.

To estimate effective strip width of our line transects, and the densities of target animal species, we analyzed our data using the DISTANCE statistical package (Laake et al. 1993). This package uses a variety of transforms to estimate the shape of the detection probability function with perpendicular distance from the transect line. Detection probability is assumed to be 100% for target species located on the transect line. The integral of the best fit detection function is the estimated strip width for a species. In order to obtain a good fit for the detection function, our encounter distance data were truncated so that 5% of the observations at greatest detection distance were eliminated from the sample. Additional truncation was introduced by our field methods in which parallel transects were performed simultaneously.

Because many prey species are detected at distances greater than half the mean distance between our transect observers (12.5 m), multiple observers often detected the same animal. For these species, each observer's transect width was truncated at the mid-point between observers, and only the encounter with the closest observer was recorded. Because *D. novemcinctus* and *A. paca* were encountered in their burrows and almost never encountered at a distance of greater than 12.5 m from the transect line, the effective strip width for those species was estimated directly from the encounter frequency distribution as described above. For all other species, the effective strip width was estimated from a detection frequency distribution that was generally truncated at 12.5 m for observers not on the outside of the transect formation.

The DISTANCE program produces confidence intervals by assessing strip width and encounter variance between transects. Because our field team walked in parallel and synchronously, we aggregated the data from all five men on each day into a single transect. This led to a sample of 126 independent transects covering 2054.85 person-km. Some transects were removed from the sample for certain species when encounters with those species were reported without a perpendicular distance estimate (this happened early in the study for some species).

For social groups, the encounter rate with groups must be multiplied by the

mean group size to estimate accurately the density of individuals. No data exist on group size for social animals in the Mbaracayu Reserve, and our attempts to census groups met with limited success because prey flee or adopt evasive tactics when humans are detected. Nevertheless, Aché forest knowledge and conversations with researchers at a nearby site in Yguazu Park, Argentina, and Brazil provided us with the following rough estimates of mean group size: *Cebus*,  $n = 18$ ; *Nasua*,  $n = 8$ ; *Tayassu pecari*,  $n = 80$ ; *T. tajacu*,  $n = 1.5$ . Unfortunately, we have no variance measure around these estimates, so confidence intervals can only be estimated for group encounter rates and then multiplied by group size to produce a rough estimate of the confidence interval for density of individual animals. Encounters with other species reported in this chapter are assumed to be with individual animals, so confidence intervals and densities can be estimated directly.

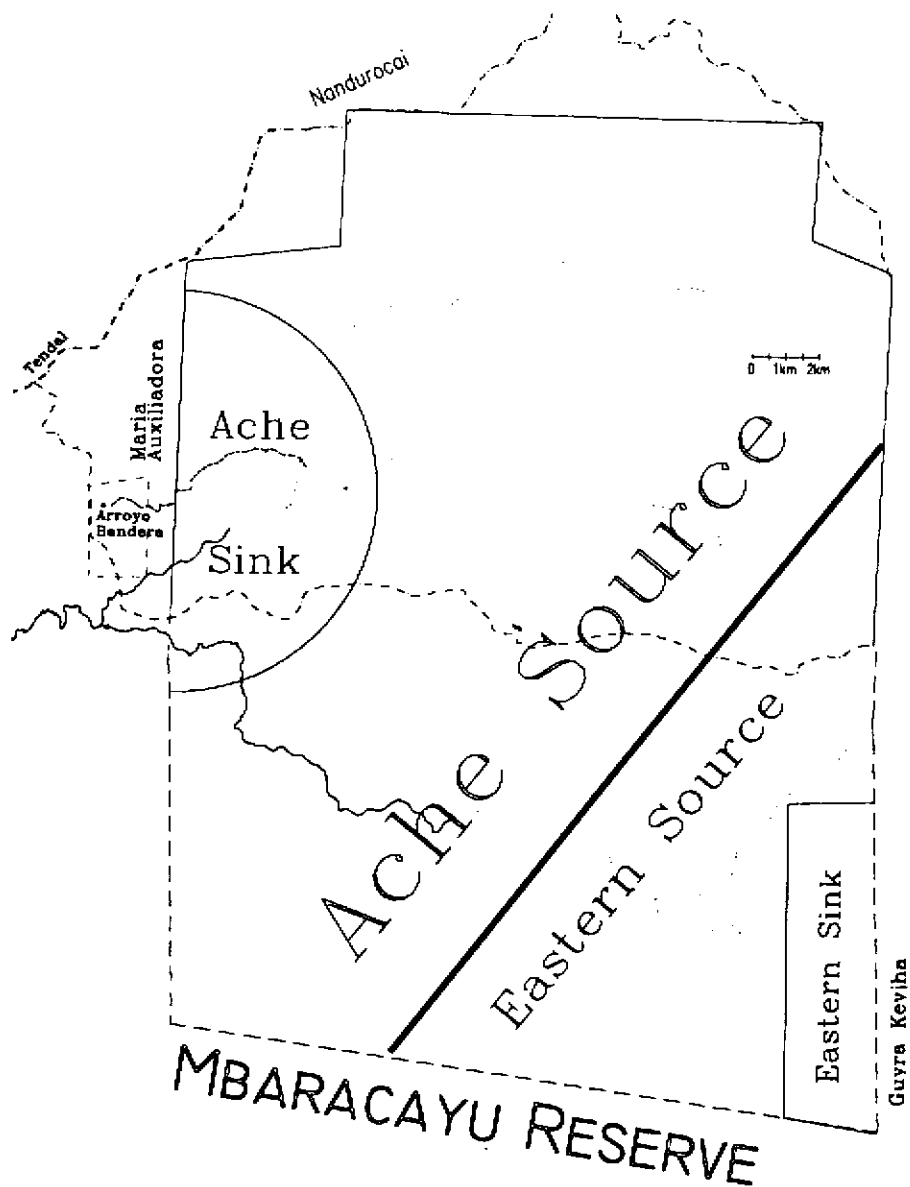
### *Size of Hypothesized Sinks and Sources*

The hunting zone that we hypothesize as the Aché sink is used by both Aché and Paraguayan hunters. The catchment area of hunting for the Arroyo Bandera reservation is considered to be a semicircular area 6 km in radius from the point at which the Aché enter the Reserve (figure 5-3). There is only one trail from the Arroyo Bandera village to the Reserve, with the border of the Reserve about 2.5 km from the village. Because women and children rarely walk more than 2 km per day off trails in the forest, and men do not participate in multi-day hunts without women and children, very few Aché hunts ever take place more than about 6 km inside the Reserve. We estimate this core hunting area to be about 56.5 km<sup>2</sup>. Data support our impression of the location of the core Aché hunting zone. The encounter rate with signs of Aché hunters on random transects is 17 times higher in the 6-km radius catchment area than in the areas more distant. This catchment area also overlaps with the Maria Auxiliadora peasant hunting zone; encounter rates with signs of Paraguayan hunters were ten times higher in this zone than elsewhere in the Reserve.

The eastern hunting zone that we also hypothesize as a sink is harder to delineate and has been hunted only by Paraguayan poachers since 1995. As far as we can tell from hunter signs, it is a strip about 10 km long and 3 km wide along the far southeastern boundary of the Reserve. If the area is extensively hunted, this might be a sink of some 30 km<sup>2</sup> that competes for immigrants with the Aché hunting catchment area. Because the area is remote from our base of operations, not enough data are available to characterize hunting intensity in this area relative to other areas of the Reserve.

The potential source area for immigration into hunting zone sinks is the entire Mbaracayu Reserve, minus the western and eastern hunting zones (figure 5-3). This area shows a density of hunter signs more than an order of magnitude higher than in the area hypothesized to be the Aché sink (Hill et al. 1997). The total area is approximately 513.5 km<sup>2</sup>. However, some of this area must serve as the source for the eastern hunting zone if poachers continue to operate in that area. We thus eliminate the entire southeastern quarter of the Reserve as a potential source for

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**Figure 5-3.** Areas defined in this study as potential hunting sinks and sources. The Aché sink begins where the Aché village trail (*dashed line*) enters the Reserve. The frequently hunted zone is a half circle of radius 6 km from that point. Most hunting by peasants from Maria Auxiliadora takes place in the same sink. The Guyra Kejha peasant population hunts in the eastern sink, which is about 10 km long and 3 km wide. The two potential source areas for the hunting sinks are the southeastern quarter of the Reserve and the remainder of the Reserve. The eastern source also extends to a large forested block outside the southern boundary of the Reserve.



prey species that immigrate into the Aché sink, leaving about 393.5 km<sup>2</sup> as the potential source area for species depleted in the Aché sink. The eastern source area includes 120 km<sup>2</sup> inside the Reserve and another 100 to 200 km<sup>2</sup> of forest outside the southern boundary of the Reserve. These estimates are admittedly crude but will have to suffice until better data are available.

## RESULTS

### *Aché Game Harvest Patterns*

The list of all vertebrates killed during sample periods between 1980 and 1995 is shown in table 5-2 in descending order of biomass. Nine species of vertebrates contribute about 95% of the meat in the Aché diet by weight (table 5-3). Less than 2% of the biomass in table 5-2 was taken using a shotgun; the remainder was killed with bow and arrow or by hand. Similarly, little of the game was taken with the use of dogs. The list of prey species in table 5-2 can be compared with the list of all mammals in Mbaracayu (table 5-1) to get an idea of Aché prey selectivity for mammals. A chronological trend toward an increasing importance of small hand-hunted game (*D. novemcinctus* and *A. paca*) is evident from table 5-3 and is related to the decreasing use of bow and arrow by young hunters. The increasing importance of *T. terrestris* is due to the introduction of metal-tipped arrows in the early 1990s.

### *Importance of Aché Hunting*

The economic importance of Aché hunting is clear from table 5-2. From 1994 through 1996, Arroyo Bandera Aché obtained a mean of 12.5 kg of live game per day, which would yield about 10 kg of edible meat. This is 122 g of meat per consumer day. At local market prices it would require about \$25 per day to purchase this amount of beef, well above the combined mean daily income for the entire Arroyo Bandera population. Thus, wild game could not currently be replaced by domestic meat, even if all available income were spent only on meat purchases.

The cultural importance of Aché hunting is more difficult to specify. Although the Aché have generally been willing to substitute meat from domestic animals for wild game, hunting remains important for three reasons. First, Aché children must be given a name from an animal that their mother prepares for consumption during pregnancy. Aché leaders have emphasized the importance of wild animal names in several recent tribal meetings, and there is general consensus that even rare and endangered animals must be hunted occasionally in order that important Aché names not be lost. This belief is strongly tied to an Aché mythology that sees all animals as they originally derived from Aché ancestors, and a belief that the essence of an Aché person is formed by consuming these animals. Aché names are an important link to past ancestors.

5-2. Vertebrate Sampling

Scientific Name
<i>D. novemcinctus</i>
<i>A. paca</i>
<i>C. apella</i>
<i>T. terrestris</i>
<i>P. pecari</i>
<i>M. nasua</i>
<i>M. spp.</i>
<i>M. tajacu</i>
<i>M. teguicini</i>
<i>M. tatouay</i>
<i>P. azarae</i>
<i>M. tetradactyla</i>
<i>P. sexcinctus</i>
<i>P. hydrochaeris</i>
<i>M. murinus</i>
<i>M. superciliaris</i>
<i>M. latirostris</i>
<i>M. spp.</i>
<i>M. tridactyla</i>
Unidentified birds
<i>M. caraya</i>
<i>M. venaticus</i>
<i>M. atratus</i>
<i>M. constrictor</i>
<i>M. onca</i>
<i>M. barbara</i>
<i>M. papua</i>
<i>M. solitarius</i>
<i>O. capueira</i>
<i>C. obsoletus</i>
<i>R. discolorus</i>
<i>F. tigrina</i>
<i>C. aura</i>
<i>C. fasciolata</i>
<i>S. brasiliensis</i>
<i>D. septemcinctus</i>
<i>D. spp.</i>
<i>G. spp.</i>
<i>A. chloroptera</i>
<i>P. yakutinga</i>
<i>C. lanatus</i>
<i>R. toko</i>
Unidentified Muridae
Sum

\*Mean weight (in kg) is for years when only a sr

Table 5-2. Vertebrates Harvested by Aché Hunters (in Rank Order of Biomass) during Sample Periods from 1980 to 1996

Scientific Name	Common Name	Number Killed	Mean Weight <sup>a</sup>	Total kg Killed	All Animals (%)	Total Biomass (%)
<i>Dasypus novemcinctus</i>	Nine-banded armadillo	1500	3.8	5750.4	42.8	35.2
<i>Agouti paca</i>	Paca	390	6.7	2630.1	11.1	16.1
<i>Cebus apella</i>	Brown capuchin monkey	889	2.3	2032.8	25.4	12.5
<i>Tapirus terrestris</i>	Tapir	9	177.0	1593.0	0.3	9.8
<i>Tayassu pecari</i>	White-lipped peccary	55	24.9	1370.8	1.6	8.4
<i>Nasua nasua</i>	Coati	261	3.5	902.6	7.5	5.5
<i>Mazama</i> spp.	Brocket deer	27	25.8	696.6	0.8	4.3
<i>Tayassu tajacu</i>	Collared peccary	27	16.3	440.6	0.8	2.7
<i>Tupinambis teguixin</i>	Tegu lizard	77	2.3	178.8	2.2	1.1
<i>Cabassous tatouay</i>	Naked-tailed armadillo	24	5.4	129.6	0.7	0.8
<i>Dasypus azarae</i>	Agouti	26	2.7	70.2	0.7	0.4
<i>Tamandua tetradactyla</i>	Collared anteater	11	5.0	55.0	0.3	0.3
<i>Euphractus sexcinctus</i>	Yellow armadillo	10	5.0	50.0	0.3	0.3
<i>Hydrochaeris hydrochaeris</i>	Capybara	1	45.0	45.0	0.0	0.3
<i>Eumeces murinus</i>	Anaconda	1	40.0	40.0	0.0	0.2
<i>Penelope superciliosus</i>	Rusty-margined guan	44	0.8	35.8	1.3	0.2
<i>Caiman latirostris</i>	Caiman	7	5.0	35.0	0.2	0.2
<i>Bothrops</i> spp.	Bushmaster snake	33	1.0	33.0	0.9	0.2
<i>Myrmecophaga tridactyla</i>	Giant anteater	1	30.5	30.5	0.0	0.2
Unidentified birds	Birds	43	0.7	30.1	1.2	0.2
<i>Alouatta caraya</i>	Black howler monkey	5	5.8	29.0	0.1	0.2
<i>Speothos venaticus</i>	Bush dog	4	5.5	22.0	0.1	0.1
<i>Coragyps atratus</i>	Black vulture	11	2.0	22.0	0.3	0.1
<i>Boa constrictor</i>	Boa constrictor	1	15.0	15.0	0.0	0.1
<i>Panthera onca</i>	Jaguar	1	15.0	15.0	0.0	0.1
<i>Eira barbara</i>	Tayra	3	4.0	12.0	0.1	0.1
<i>Sarcorampus papa</i>	King vulture	3	3.0	9.0	0.1	0.1
<i>Tinamus solitarius</i>	Solitary tinamou	8	1.0	8.0	0.2	0.0
<i>Odontophorus capueira</i>	Wood-quail	8	1.0	8.0	0.2	0.0
<i>Crypturellus obsoletus</i>	Tinamou	5	1.0	5.0	0.1	0.0
<i>Ramphastos discolorus</i>	Red-breasted toucan	3	1.0	3.0	0.1	0.0
<i>Felis tigrina</i>	Oncilla	1	2.2	2.2	0.0	0.0
<i>Cathartes aura</i>	Turkey vulture	1	2.0	2.0	0.0	0.0
<i>Crax fasciolata</i>	Bare-faced curassow	1	2.0	2.0	0.0	0.0
<i>Sylvilagus brasiliensis</i>	Rabbit	2	0.9	1.8	0.1	0.0
<i>Dasypus septemcinctus</i>	Seven-banded armadillo	1	1.6	1.6	0.0	0.0
<i>Didelphis</i> spp.	Opossum	1	1.5	1.5	0.0	0.0
<i>Geochelone</i> spp.	Tortoise	1	1.0	1.0	0.0	0.0
<i>Ara chloroptera</i>	Scarlet macaw	1	1.0	1.0	0.0	0.0
<i>Pipile yakutinga</i>	Black-fronted piping guan	1	1.0	1.0	0.0	0.0
<i>Caluromys lanatus</i>	Western woolly opossum	3	0.3	1.0	0.1	0.0
<i>Ramphastos toco</i>	Toco toucan	1	0.7	0.7	0.0	0.0
Unidentified Muridae	Mice	1	0.3	0.3	0.0	0.0
<b>Sum</b>		<b>3503</b>		<b>16,314.0</b>	<b>100.0</b>	<b>100.0</b>

<sup>a</sup>Mean weight (in kg) is taken from a sample of Aché prey, or Eisenberg and Redford (1994) in order to standardize weights for years when only a small number of individuals was recorded.

**Table 5-3. Vertebrates That Contributed More Than 1% of the Biomass Harvested by Aché Hunters from 1980 to 1996**

Important Species	Common Name	Proportion of All Vertebrate Biomass Harvested*				
		1980	1981-1985	1994-1995	1995-1996	All Years
<i>Dasyus novemcinctus</i>	Nine-banded armadillo	0.135	0.239	0.431	0.439	0.352
<i>Agouti paca</i>	Paca	0.108	0.130	0.182	0.183	0.161
<i>Cebus apella</i>	Capuchin monkey	0.207	0.206	0.095	0.064	0.125
<i>Tapirus terrestris</i>	Tapir	0.000	0.000	0.123	0.181	0.098
<i>Tayassu pecari</i>	White-lipped peccary	0.228	0.156	0.039	0.020	0.084
<i>Narua narua</i>	Coati	0.151	0.065	0.043	0.021	0.055
<i>Mazama spp.</i>	Brocket deer	0.106	0.081	0.018	0.016	0.043
<i>Tayassu tajacu</i>	Collared peccary	0.022	0.056	0.023	0.013	0.027
<i>Tupinambis teguixin</i>	Tegu lizard	0.000	0.012	0.019	0.006	0.011
<b>Sum</b>		<b>0.959</b>	<b>0.944</b>	<b>0.973</b>	<b>0.944</b>	<b>0.956</b>

\*Sample sizes are 1980, 2191 kg; 1981-1985, 3513 kg; 1994-1995, 4301 kg; 1995-1996, 4096 kg.

Second, the Aché food-sharing system depends heavily on redistribution of wild game (Kaplan et al. 1984; Kaplan and Hill 1985). Domestic animals do not carry the same sharing obligations as wild game, and Aché leaders recognize that food sharing is central to the Aché way of life. It is a practice that distinguishes them from their ethnic neighbors. Aché society is economically very communal, and a certain egalitarian ethic that is associated with equal shares of wild game permeates all social interaction. Aché often characterize their own people as "those who really share," and there is a strong sentiment to retain that character. There is a good deal of concern that the loss of food sharing would lead to economic stratification, something that most Aché wish to avoid.

Finally, the Aché recognize the need for hunting as a social and psychological outlet. Several leaders recently commented while justifying the maintenance of a tribal forest reserve that a major purpose of continued hunting in the future will be to "allow depressed and stressed individuals to escape the pressures and worries of the modern world" and relax in a life-style that is comfortable and enjoyable to them (figure 5-4), to seek an environment where they can feel equal to or better than the outsiders who constantly impose their superiority on the Aché. After several days in the forest, most Aché adults return with newly invigorated self-esteem, more relaxed and ready to face the difficulties of adjusting to a new world. Thus, Aché hunting sometimes serves the same purpose as weekend outings and vacations do for Americans. This might ultimately be critical to the long-term psychological health of the population.

### *Animal Densities*

Densities in hunted and unhunted zones of the eight important hunted mammal species in order of annual biomass harvest are shown in table 5-4. (The density of *T. teguixin* is not estimated because this species is detectable only during a few months of each year.) The density estimates of *T. pecari* are somewhat

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Figure 5-4. Evening meal with nine-banded armadillo (*Dasyus novemcinctus*). Photo courtesy of Kent H. Redford.

unreliable because this species was encountered only three times in our sample, thus we are unable to obtain a good estimate of estimated strip width for it. The significance of the association between encounter rates and distance from the Aché settlement has been analyzed, and the results have been presented elsewhere (Hill et al. 1997). These data showed that encounter rates with *D. novemcinctus*, *M. americana*, and *T. terrestris* increase significantly with distance from the Aché village after other variables are controlled. Encounter rates with *C. apella* might

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**Table 5-4. Density of Major Game Animals in the Mbaracayu Reserve and Comparison with Other Neotropical Sites**

Species	Total Encounters	Mean Group Size	Effective Strip Width (m)	Total Transect Distance (km)	Encounter Ratio Indirect/Direct <sup>a</sup>
<i>D. novemcinctus</i>	205	1	3.4	1496.100	19.7
<i>C. apella</i>	102	18	18.2	2054.850	1.4
<i>A. paca</i>	40	1	3.3	1874.850	27.8
<i>T. pecari</i>	3	80	200.0	2054.850	12.0
<i>N. nasua</i>	15	8	13.3	2054.850	4.2
<i>M. americana</i>	91	1	13.0	2030.850	24.2
<i>T. terrestris</i>	33	1	16.1	2030.850	43.8
<i>T. tajacu</i>	14	1.5	10.0	2054.850	71.5

Species	Mbaracayu			Other Neotropical Sites		
	Density All Zones <sup>b</sup>	Density Unhunted Zones <sup>b</sup>	Density Hunted Zones <sup>b</sup>	Mean Density (No./km <sup>2</sup> ) <sup>c</sup>	Minimum Density (No./km <sup>2</sup> ) <sup>d</sup>	Maximum Density (No./km <sup>2</sup> ) <sup>d</sup>
<i>D. novemcinctus</i>	19.9 (15.7-25.2)	23.35	12.03	21.90	12.00	25.00
<i>C. apella</i>	24.5 (15.3-39.3)	34.56	11.16	12.40		
<i>A. paca</i>	3.2 (2.2-4.8)	5.87	3.88	27.50	27.50	50.00
<i>T. pecari</i>	0.3 (0.1-0.8)	1.70	1.00	4.90	1.40	8.13
<i>N. nasua</i>	2.2 (1.2-4.2)	2.30	3.12	15.10	4.00	22.00
<i>M. americana</i>	1.7 (1.3-2.3)	1.72	1.20	10.50	1.00	1.30
<i>T. terrestris</i>	0.5 (0.3-0.9)	0.60	0.54	1.60	0.40	1.60
<i>T. tajacu</i>	0.5 (0.2-1.2)	0.69	0.36	11.90	3.35	14.50

<sup>a</sup>The ratio of all encounters with fresh signs of a species divided by all direct encounters with the species.

<sup>b</sup>Density measures are given in animals per km<sup>2</sup>; 95% confidence intervals are shown in parentheses.

<sup>c</sup>Mean neotropical density from various sites (from Robinson and Redford 1989, table 2.)

<sup>d</sup>Range of best estimates of neotropical densities (from Townsend 1995, table 7-1).

also increase with distance from the Aché village, but the trend was not statistically significant. Other prey species show no significant trends in encounter rate with distance from the Aché village.

The comparison with Mbaracayu density data from other studies suggests that *M. americana*, *T. terrestris*, *D. novemcinctus*, and perhaps *T. pecari* all show densities within the range of other reliably measured neotropical sites. *A. paca*, *N. nasua*, and *T. tajacu* are rare in Mbaracayu relative to other sites, whereas *C. apella* is abundant. Although some of these conclusions might be affected by our group size estimates, the low density of *A. paca* must be a real feature of Mbaracayu. The sample size of encounters is high enough to eliminate sample error as a cause of the low estimate, and because most *A. paca* were censused in their burrow, many of the potential problems of censusing mobile and wary prey do not apply. Aché informants state that *A. paca* is usually found only within about 100 m of surface water in Mbaracayu. Our data lend support to that view (Hill et al. 1997). Thus, much of the Mbaracayu Reserve might be unsuitable habitat for *A. paca*, leading to low average densities. The low density of *T. tajacu* is not so easily explained. The estimate we obtained is about sevenfold lower than the minimum reliable estimate from the neotropics reported by Townsend (1995). We suspect that this is partially due to the fact that *T. tajacu* are exceptionally wary in Mbaracayu and not accurately censused by diurnal transects. This can be studied further by analyzing indirect

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encounters with the species. The number of fresh indirect encounters (tracks, feces, etc.) with *T. tajacu* was more than 70 times the number of direct encounters. Other ungulates of similar body size such as *M. americana* or *T. pecari* showed a much lower ratio of indirect to direct encounters (table 5-4), suggesting that although *T. tajacu* is present, the species is difficult to observe using our transect methods.

### Harvest Rate and Sustainability

Data on harvest rates, prey densities, and size of the Aché catchment basin and potential source areas for depleted prey species allow us to assess whether the catchment basin really is a sink, and whether the harvest rate is likely to be sustainable given the prey population in the source area. Data on harvest rates per consumer, or per km<sup>2</sup>, also allow us to compare the specifics of the Aché economy with other areas of the neotropics. In table 5-5, we present data on the 1994 to 1996 harvest rate of each of the eight important game species, per consumer and per km<sup>2</sup>. The mean annual number of animals harvested by the Arroyo Bandera-Aché is calculated from the total 1994 to 1996 hunting data. These data show that the Aché are typical in their dependence on *C. apella*, *A. paca*, *N. nasua*, and *T. terrestris*. Annual harvest rates per consumer are close to the mean of other neotropical studies for those prey species. The Aché harvest rate per consumer of *D. novemcinctus* is the highest ever reported thus far. Per consumer harvest rates of *Tayassu* species and *M. americana* are considerably lower than the neotropical averages, and in the case of *T. pecari*, the lowest rates in the literature review of neotropical hunters. Thus, the Aché are exceptionally dependent on armadillos, whereas peccaries are considerably less important than in most other neotropical sites. The lack of importance of white-lipped peccaries, however, is a recent phenomenon (table 5-3) and might be due to multi-annual fluctuations in peccary location and abundance. From the prevalence of traditional Aché names, we can determine that collared peccaries have never been important in the Aché economy in this century.

The annual harvest per km<sup>2</sup> in the Aché sink area is also presented in table 5-5. We assume that 95% of all animals are killed in the Aché sink (56.5 km<sup>2</sup>). The total biomass from these eight species harvested was 75 kg/km<sup>2</sup>. Because these species represent 95% of the total game biomass, we can estimate that the Aché harvest about 75 kg of vertebrates per km<sup>2</sup> in their primary hunting zone. Comparison with other sources again suggests that the Aché harvest a high number of *D. novemcinctus* per km<sup>2</sup>, and a low number of *Tayassu* species per km<sup>2</sup>. It is interesting that the Aché harvest of *A. paca* is higher than that in the other reported neotropical sites despite the fact that we measured *A. paca* at a density about eightfold lower than the neotropical average. Dietary dependence on *A. paca* (number killed per consumer year) is also higher than average among the Aché. Our observations from having hunted with a half dozen other neotropical native groups is that the Aché are exceptionally skilled at killing *A. paca* and use a technique (Hill and Hawkes 1983) to extract animals from their burrow that we have never observed elsewhere.

Table 5-6 shows the estimated number of prey for each species in the Aché

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**Table 5-5. Annual Harvest of Game by Aché Hunters in the Mbaracayu Reserve and Comparison to Other Sites**

Species	Annual Harvest	Annual Harvest per Consumer			Annual Number Killed per km <sup>2</sup>		Biomass Harvest per km <sup>2</sup>	
		Aché	Indigenous Mean <sup>a</sup>	Neotropical Range <sup>a</sup>	Aché <sup>b</sup>	Neotropical Range <sup>c</sup>	Aché <sup>b</sup>	Piro <sup>d</sup>
<i>D. novemcinctus</i>	507	6.18	0.79	0.030-4.12	8.52	4.49	32.65	
<i>C. apella</i>	183	2.23	2.51	0.003-8.63	3.07		7.03	
<i>A. paca</i>	125	1.52	0.92	0.009-4.39	2.10	1.12	14.16	
<i>T. pecari</i>	7	0.09	0.92	0.166-4.70	0.12	0.30-1.48	2.93	
<i>N. nasua</i>	49	0.60	0.59 <sup>e</sup>	0.005-2.75	0.82	2.70	2.85	
<i>M. americana</i>	5	0.06	0.18	0.016-1.49	0.08	0.13-0.29	2.17	6.10
<i>T. terrestris</i>	4	0.05	0.05	0.009-0.12	0.07	0.08-0.09	11.89	14.10
<i>T. tajacu</i>	5	0.06	0.65	0.013-3.77	0.08	0.27-2.19	1.37	20.20

<sup>a</sup>From Redford and Robinson (1987), table 4.6.

<sup>b</sup>In the Aché sink area only, assuming 95% of all kills are made in that area.

<sup>c</sup>From Townsend (1995), table 5-2, and Bodmer (1994), p. 126.

<sup>d</sup>From Alvard (1993), table 6-2.

<sup>e</sup>*Nasua* taken from both native and colonist data.

hunting zone, the potential source area for the Aché hunting zone, and the whole Mbaracayu Reserve. We also calculated the annual harvest as a proportion of the estimated prey population in the Aché hunting zone, as a percentage of the prey population in the Aché hunting zone and the source area of the Reserve, and as a percentage of the total prey population estimated for the Mbaracayu Reserve. The size of prey populations in the Aché hunting zone (sink) and source areas, as well as the whole Mbaracayu Reserve, are calculated by multiplying those areas (defined above) by the animal densities in the hunted and unhunted zones (table 5-4). The data support the hypothesis that the Aché hunting zone is a sink for at least some species. *D. novemcinctus*, *C. apella*, *A. paca*, *N. nasua*, and *T. terrestris* are all harvested at a rate of more than 25% of the Aché hunting zone population per year, a rate that is unlikely to be sustainable. The annual harvest rate for other

**Table 5-6. Annual Harvest as a Percentage of Animals Estimated to Be in Hunted Areas, Source Areas, and the Mbaracayu Reserve**

Species	Total Animals			Proportion Harvested 1994-1996			Estimated Proportion Sustainable Harvest <sup>b</sup>
	Aché Sink	Aché Source	Mbaracayu Reserve	Aché Sink	Aché S-S <sup>a</sup>	Mbaracayu Reserve	
<i>D. novemcinctus</i>	680	9187	13,030	0.745	0.051	0.039	0.396
<i>C. apella</i>	631	13,598	18,711	0.290	0.013	0.010	0.024
<i>A. paca</i>	219	2310	3350	0.570	0.049	0.037	0.079
<i>T. pecari</i>	57	669	959	0.124	0.010	0.007	0.280
<i>N. nasua</i>	176	906	1453	0.278	0.045	0.034	
<i>M. americana</i>	68	677	987	0.074	0.007	0.005	0.107
<i>T. terrestris</i>	31	236	355	0.131	0.015	0.011	0.031
<i>T. tajacu</i>	21	272	387	0.244	0.017	0.013	0.340

<sup>a</sup>Aché source and sink areas combined.

<sup>b</sup>Calculated from Robinson and Redford (1991), tables 27.1 and 27.2, as described in text.

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species is 7% to 13% of the estimated population in the Aché hunting zone. However, when the annual harvest is divided by both the Aché sink population and the Aché source population for each prey species, no species shows a harvest rate above about 5%. Calculation of the Aché harvest rate for each species as a proportion of the total number of prey estimated in the whole Reserve provides the same general picture, namely that all species are harvested at very low annual percentages (< 4%) of the standing population.

Whether or not Aché harvest rates are sustainable is a complicated question, but we can begin to answer it by making a few simple assumptions. First, we assume that the source area really does provide immigrants to the sink areas in the Reserve. Because we can estimate the proportion of all prey in both the source and sink that is harvested annually, we need only determine whether a harvest of that proportion of the population will be sustainable over the long run. The best available estimates of harvest sustainability for neotropical mammals come from Robinson and Redford (1991b). Those investigators used estimated maximum reproduction rates with mean densities and life span information to determine a likely maximum sustainable harvest rate for a number of mammal species. Table 5-6 shows the percentage of the standing prey population that Robinson and Redford estimate can be harvested annually for each species without depleting the population through time. The sustainable harvest percentage is calculated by dividing the number of individuals that can be harvested per km<sup>2</sup> (Robinson and Redford 1991b, Table 27.2) by the mean density estimate of individuals per unit area (Robinson and Redford 1991b, Table 27.1) times 60% nonharvested density. The Aché data show that no species is harvested at a rate that exceeds the calculated maximum sustainable harvest percentage.

The sustainability of Aché harvest patterns through time also can be assessed with longitudinal harvest data. Figure 5-5 shows the mean return rate per hunter day from the three species, with the largest number of animals harvested over a 16-month period. No long-term decrease in harvest or return rate per hunter day is detectable; thus, it is not likely that game densities are decreasing markedly in the areas hunted by the Aché.

## DISCUSSION

The data on Mbaracayu game densities and Aché annual harvest of major prey species suggest that the 450-km<sup>2</sup> sink and source areas for Aché prey are probably sufficient for a sustainable harvest at current rates. The only other study we know of that has calculated the minimum necessary combined sink and source for sustainability of observed neotropical hunting patterns is that of Townsend (1995). Townsend estimates that a Sirionó population of 192 consumers requires a minimum harvest area of between 221 and 1259 km<sup>2</sup> of forest land, depending on the species considered. However, one species (*Blastoceros dichotomus*) harvested by that community would require between 3245 and 5409 km<sup>2</sup> of savanna for a sustainable harvest. Without the savanna species, the Sirionó would still obtain more meat per consumer day than the Aché (and most other neotropical commu-

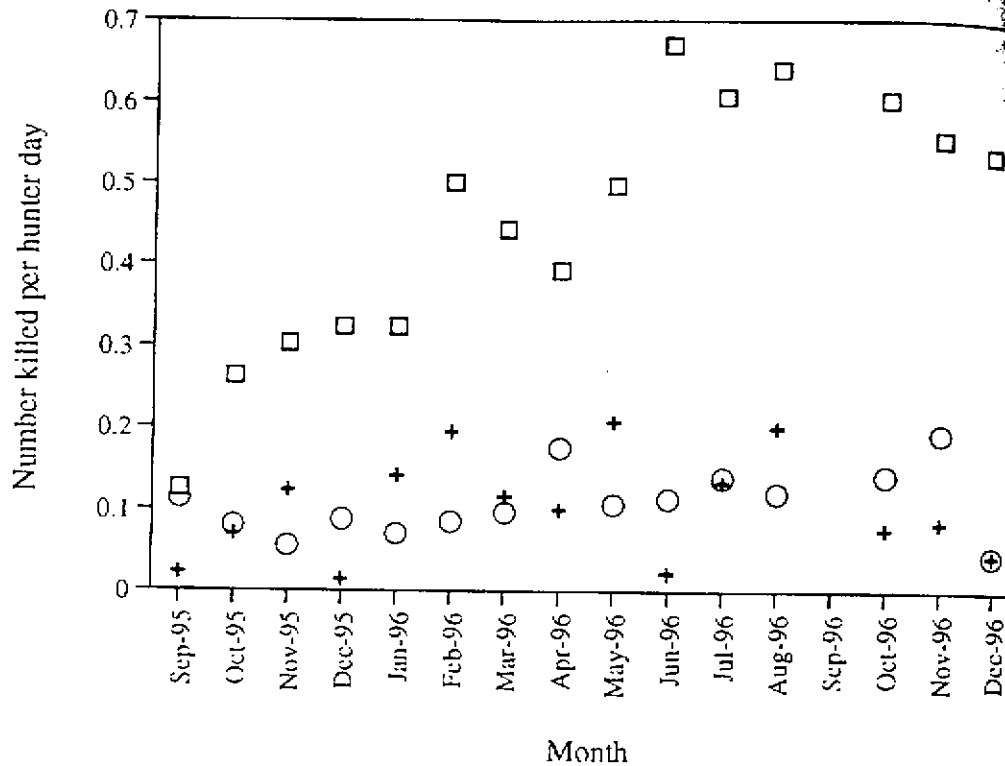
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**Figure 5-5.** Harvest rate for Aché hunters (animals killed per hunter day) of *D. novemcinctus* (squares), *C. apella* (crosses), and *A. paca* (circles) from September 1995 to December 1996. The data show no evidence of longitudinal depletion for these species during the study period.

nities). Thus, taking the mid-point of Townsend's estimate, we calculate that the Sirionó need about 3.8 km<sup>2</sup> of forest per consumer to achieve a sustainable harvest at the current meat consumption rate. This is similar to the 5.5 km<sup>2</sup> per consumer that the Aché currently use in Mbaracayu. Because both estimates are close, we might speculate that *terra firme* neotropical native populations can achieve sustainable harvest if the combined sink-source areas available to them total at least 5 km<sup>2</sup> per consumer. This would imply a maximum sustainable human population density in *terra firme* forests of about 0.2 person/km<sup>2</sup> given typical meat consumption rates. With more information on the range of biomass densities in the neotropics, and human meat consumption levels, it will be possible to test this hypothesis and specify a range of likely maximum sustainable human densities that will not deplete neotropical vertebrate fauna.

Two important conservation questions arise from these analyses. First, can the results be extended to other economically less important vertebrate species? And second, do measurements of game density differences in hunted and unhunted

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areas provide information about sustainability of harvest rates? We believe that the answer to the first question can be partially surmised through an understanding of human hunting patterns. In general, most prey species are more difficult to locate than they are to kill. Search time for game represents the majority of all hunting time, whereas pursuit time is considerably less important (Hawkes et al. 1982; Hill and Hawkes 1983; Hill et al. 1985; Hill et al. 1987). This means that each species that is hunted is taken in approximate relation to its abundance. Species that are not profitable are not hunted at all (Hawkes et al. 1982; Hill and Hawkes 1983; Hill et al. 1985; Hill et al. 1987). Some species are more vulnerable than others, but the relationship between density and annual harvest can be clearly shown with current Aché data. Figure 5-6 shows a regression of log number of animals killed per year by log density for each of the major prey species in the Reserve. Density is associated with 80% of the variation in the annual harvest amount. In this sample, *A. paca* was exceptionally vulnerable to human predation, whereas *M. americana* was greatly underharvested relative to its estimated density. This agrees with Aché informant statements that hunters actively seek out *A. paca* habitat through the day to the exclusion of other areas, and that deer are extremely wary and thus difficult to kill with bow and arrow. If the relationship between prey density and annual harvest holds for other mammalian game species, it suggests that most species found at proportionally lower densities will simply be harvested at proportionally lower rates.

The data thus suggest that if major game species are not overharvested, perhaps other animals will also be harvested sustainably. We are concerned, however, by the implications of harvest variance due to encounter luck for rare species. If few individual animals exist in a circumscribed area, then even though a species may on average be harvested at a sustainable rate, a single year of high harvest could be enough to start the population on a decline to extirpation. For example, from transect data we estimate that there are about 30 jaguars in the Mbaracayu Reserve. Only three have been killed by the entire Aché population in the past 19 years. However, if these were all killed in 1 year and if they were reproductive aged females, this loss might eliminate the Mbaracayu population. Such a perspective suggests that a rigid harvest cap should be placed on all species estimated to contain fewer than 100 individuals in a circumscribed area. We have discussed this with Aché leaders, and they are not opposed to limits being placed on rarely encountered game animals, as long as a few can be killed occasionally for naming purposes.

Finally, we can examine the relationship between density in hunted versus unhunted areas and the sustainability of the harvest. Concerned individuals might reach unwarranted conclusions about the unsustainability of human hunting because game depletion can be shown in hunted areas. Studies that simply compare densities in hunted and unhunted areas are not instructive, however, because all central place predators are expected to deplete prey items nearby their home base. Aché reservation lands within an hour's walk of the village center have been censused by our research team three times. Those lands are extremely depleted of game, with only four mammals (three *D. novemcinctus* and one *M.*

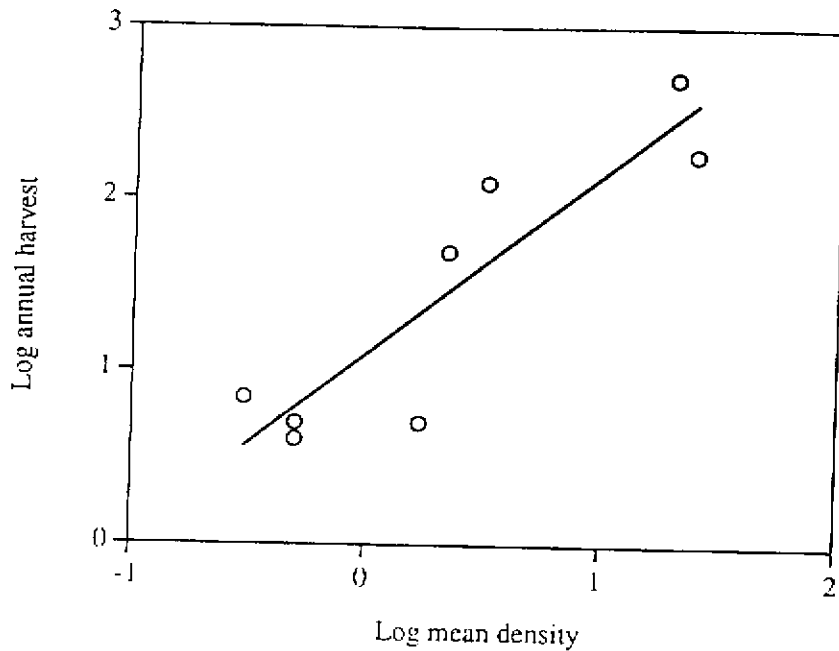


Figure 5-6. The relationship between the density of the eight major prey species in Mbaracayu and the number harvested annually by Aché hunters ( $r = 0.90$ ).

*americana*) encountered in 51,000 m of transect. However, of the eight major game species, only *C. apella*, *T. terrestris*, and *T. pecary* showed no signs at all on reservation land. Fresh tracks, feces, or feeding signs were encountered for *D. novemcinctus*, *A. paca*, *N. nasua*, *M. americana*, and *T. tajacu*. The Aché hunt on reservation land every day of the year, and all of the eight major prey items are consistently harvested at levels many times above sustainability. Yet even after more than 15 years of hunting, five of the eight species are present within a short distance of an Aché village. Clearly, there is a source prey population that continually resupplies this area. Thus, any calculations of hunting sustainability must include that source.

Do large differences in prey density between hunted and unhunted areas indicate that the prey harvest is unsustainable? Previous analyses on a smaller subset of our transect data showed that *D. novemcinctus*, *M. americana*, *T. terrestris*, and possibly *C. apella* are characterized by increasing encounter rates with distance from the Aché, even when habitat type and other variables are controlled (Hill et al. 1997). The current analyses show a large density difference between hunted and unhunted zones for *D. novemcinctus*, *A. paca*, and *C. apella*. Comparison of actual harvest to the estimated sustainable harvest, however, suggests that none of these species is in danger of being overharvested. This is true despite the fact that densities of the two most important game species are twice as high in unhunted areas as they are in the hunted zone near the Aché village. These observations suggest that density in hunted and unhunted areas might tell us more about dispersion rates and distances of each species than they do about sustainability of the harvest.

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Despite the ability to measure animal density differences between hunted and un hunted areas and estimate whether harvest rates are sustainable, we suggest that all conservation units should undergo longitudinal censusing to ensure that typical harvest rates are indeed sustainable. Because annual fluctuations in animal density are expected and not yet well understood (Glanz 1982), comparison of only two density estimates through time cannot be considered a reliable indicator of harvest sustainability. But continual monitoring will allow the discovery of a consistent population decline, which can then be counteracted by limitations on harvest rate.

Finally, data such as those presented here should induce conservation biologists to reflect on the status of humans as predators in conservation units. In the neotropics, native people are a natural predator in many conservation areas. Their hunting activity will not necessarily extirpate large or rare species if the ratio of consumers to prey is low. The simple 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 common sense evidence of this. As far as can be discerned, there were no uninhabited areas of the neotropics at European contact (Denevan 1992), and there have been no large uninhabited areas in the time since European arrival (Steward 1944-49).

Conservationists also should be aware that the current set of neotropical species has never existed as a "natural community" without human activity. The earliest human populations spread through the neotropics prior to the terminal Pleistocene extinctions (Meggers 1982; Roosevelt 1994), which led to modern neotropical faunal communities. 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 5,000 years (Balée 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 and Emmons 1990; Terborgh 1990).

## ACKNOWLEDGMENTS

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