# Wildlife Survival Beyond Park Boundaries: the Impact of Slash-and-Burn Agriculture and Hunting on Mammals in Tambopata, Peru

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**Abstract:** *Finding a balance between strict protection and multiple use requires data on wildlife survival in human-managed ecosystems. We examined the habitat use and species composition of mammals >2 kg in size inhabiting an agroforest ecosystem neighboring a park in the Peruvian Amazon. First, we recorded wildlife presence in fields, fallows, and forests within one settlement over a 9-month period. Then we monitored wildlife presence over 21 months in 42 fields across a 65-km transect, including remote and highly disturbed sites. We tested for correlations between the size and number of mammal species visiting fields and human activities measured at different scales. Hunting intensity more powerfully predicted the average biomass and species diversity observed in fields than did vegetation disturbance. The number of commercial hunters in the surrounding community had a stronger impact than did the individual field owner's hunting intensity. Large-bodied species appeared only in remote farms neighboring uninhabited areas in the reserve, indicating that undisturbed forests act as sources for wildlife dispersing into agricultural regions. Farmers in these remote areas experience greater crop and livestock losses to wildlife, but by hunting large game they are able to offset losses with bushmeat gains. In more disturbed areas, crop losses exceeded bushmeat gains, although both occurred at negligible levels. Our case study suggests that large herbivores, large carnivores, and most primates are unlikely to persist in multiple-use zones in Amazonian forests unless hunting is effectively restricted. Even highly disturbed agroforests are not empty of wildlife, however, but are inhabited by a suite of adaptable, fast-reproducing species able to withstand human activity (e.g., brown agoutis [*Dasyprocta variegata*], armadillos [*Dasypus novemcinetus*], and red brocket deer [*Mazama gauazoubira*]). These "weedy" species may not be of immediate concern to conservation biologists, and they will not attract tourists. But they have both economic and ecological value and deserve to be taken into account in management decisions.*

Sobrevivencia de Fauna Silvestre por Fuera de los Límites del Parque: el Impacto de la Agricultura de Roza y Quema y de la Cacería sobre Mamíferos en Tambopata, Perú

**Resumen:** *El equilibrio entre la protección estricta y el uso múltiple requiere datos de sobrevivencia de fauna silvestre en ecosistemas manejados por humanos. Se examinó el uso de hábitat y la composición de especies de mamíferos >2 kg que habitan un ecosistema agroforestal adyacente a un parque en la Amazonía Peruana. Primero, se registró la presencia de fauna silvestre en campos cultivados, campos sin cultivar y bosques en una comunidad durante un período de 9 meses. Luego se realizó un seguimiento de la presencia de fauna silvestre durante 21 meses en 42 campos a lo largo de un transecto de 65 km, incluyendo sitios remotos y altamente perturbados. Se intentó identificar las correlaciones que pudieran existir entre el tamaño y el número de especies de mamíferos registrados en los campos y las actividades humanas medidas a diferentes escalas. La intensidad de cacería fue mejor indicador de la biomasa promedio y la diversidad de especies ob-*

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*servadas que la perturbación de la vegetación. El número de cazadores comerciales en la comunidad circundante tuvo mayor impacto que la intensidad de cacería por los dueños de campo. Las especies de tamaño grande solo aparecieron en los ranchos remotos aledaños a áreas deshabitadas en la reserva, lo que indica que los bosques no perturbados actúan como fuentes de vida silvestre que se dispersa a regiones agrícolas. Los campesinos en estas áreas remotas sufren mayores pérdidas de sus cultivos y su ganado debido a la fauna silvestre, pero pueden compensar estas pérdidas con ganancias derivadas de la venta de carne resultante de la caza de animales grandes. En áreas más perturbadas, las pérdidas de cultivos excedieron las ganancias derivadas de la venta de carne, aunque ambas ocurrieron a niveles insignificantes. Nuestro estudio de caso sugiere que los herbívoros y carnívoros grandes y la mayoría de los primates probablemente no persistan en zonas de uso múltiple de bosques amazónicos a menos que se restrinja la cacería. Sin embargo, aun los bosques más perturbados no carecen de fauna silvestre; están habitados por un conjunto de especies adaptables, de reproducción rápida capaces de resistir la actividad humana (por ejemplo, agutíes [*Dasyprocta variegata*] armadillos [*Dasypus novemcintus*], venados [*Mazama gauazoubira*]). Para los biólogos de la conservación estas especies comunes pueden no ser de atención inmediata y no atraerán turistas, pero tienen valor tanto económico como ecológico y merecen ser consideradas en las decisiones de manejo.*

## Introduction

A forest full of people is a forest empty of animals, claim prominent conservationists who advocate national parks as the optimal strategy for biodiversity conservation in the tropics (Redford 1992; Terborgh & van Schaik 1997). Their position is bolstered by studies revealing the depletion of large-bodied species in rainforests where humans hunt and farm (Carrillo et al. 2000; Lopes & Ferrari 2000; Peres 2000; Bodmer & Lozano 2001). The loss of large mammals in turn may lead to a cascade of ecological effects that compromise the diversity of forest ecosystems (Dirzo & Miranda 1991; Terborgh 1999; Roldán & Simonetti 2001). Other experts counter that people-free parks are impractical or unethical in the tropics, given local residents' direct economic dependence on the forest (Ghimire 1994; Schwartzman et al. 2000). In advocating extractive reserves and multiple-use areas, they point to the lengthy history of human influence on tropical forests (Denevan 1992). In practice, protected-area managers often promote both preservation and sustainable use by delineating multiple-use buffer zones around strictly protected core areas (Chicchón 2000; Peres & Zimmerman 2001). In attempting to balance protection with sustainable use, managers face difficult decisions. How many hectares must be strictly protected? Which wildlife species will survive in multiple-use zones?

Balancing strict protection and multiple uses requires data on wildlife survival in human-managed ecosystems, particularly in slash-and-burn agriculture systems, which are predominant in remote areas of the tropics. Several species of rainforest mammals are drawn to swidden fields to forage on crops and fruit trees or regenerating vegetation (Janzen 1976; Salafsky 1992; Fimbel 1994; Thiollay 1995). Similarly, rainforest carnivores occasionally prey on livestock and poultry (Quigley & Crawshaw 1992; Bisbal 1993). Wild animals entering swiddens and fallows will likely encounter rich food sources, but they will also fall prey to hunters. Anthropologists call this practice garden hunting (Linares 1976). In the idealized garden hunting scenario, people's crop losses are balanced with protein gains, and game species thrive in the habitat mosaic of swiddens and forest (Linares 1976; Peterson 1981; Posey 1985). Some anthropologists claim that garden hunting "enhances biodiversity" (Gadgil et al. 1993:151), whereas wildlife biologists are more likely to view swidden gardens as sinks because of their heavy hunting levels (Jorgenson 1993). Wildlife survival amid swidden farms ultimately depends on a variety of conditions, including hunting intensity, forest cover, cultural norms, and property rights (Cuaron 2000; Escamilla et al. 2000; Naughton-Treves & Salafsky 2003). Moreover, some rainforest species are better able to withstand human disturbance than others. Anthropologists refer to these species inhabiting human-managed ecosystems as anthropogenic fauna (Donkin 1985). Protected-area managers must consider the value of anthropogenic fauna for different interest groups. International conservationists, local hunters, and forest farmers all attach different values to wildlife, and these values translate to different environmental agendas. Recognizing these distinct agendas is important for effective wildlife conservation beyond park boundaries, such as in buffer zones or corridors inhabited by agriculturalists (Naughton-Treves & Salafsky 2003).

We examined wildlife habitat use and survival amid swidden agriculture in the heavily forested Tambopata Province in the Peruvian Amazon (Fig. 1). We tested the impact of human activities on wildlife within a multiple-use reserve neighboring a park and beyond the protected area. We focus on terrestrial mammals >2 kg in size because of their value to local hunters and their ecological significance in lowland forests (Dirzo & Miranda 1991; Roldán & Simonetti 2001). We also examined patterns of crop loss to wildlife among local agriculturalists.

Our research is designed to test the impact of human activities at different scales, from the farm to community and regional levels. Our multivariate analyses reveal the relative impact of hunting versus vegetation disturbance and allow us to identify the suite of mammal species surviving in swidden agricultural systems

## Methods

### Study Site and Sociopolitical Context of Research

Tambopata Province is in the Department of Madre de Dios, a remote and biodiverse region of Peru (Fig. 1) (Foster 1994). This lowland, forested region was isolated from international markets until the rubber boom of the late 1800s, which gave rise to *ribereño* society (Amazonian residents of mixed ancestry), and decimated indigenous populations (Chicchón et al. 1997). The rubber industry collapsed in the early 1900s, and the local population remained relatively stable until the mid 1960s, when a road was constructed into Madre de Dios. Andean peasants were drawn to the region by gold, available land, and economic incentives for ranching and farming (Chicchón et al. 1997; Alvarez & Naughton-Treves 2003). Tambopata's population grew five-fold in 25 years, reaching 76,610 in 1997, with roughly half the population residing in the capitol city of Puerto Maldonado (Fig. 1) (GESUREMAD 1998). Despite rapid population growth, the area continues to have the lowest population density in Peru (0.9 inhabitants/km$^2$) and the largest tracts of undisturbed forest (GESUREMAD 1998).

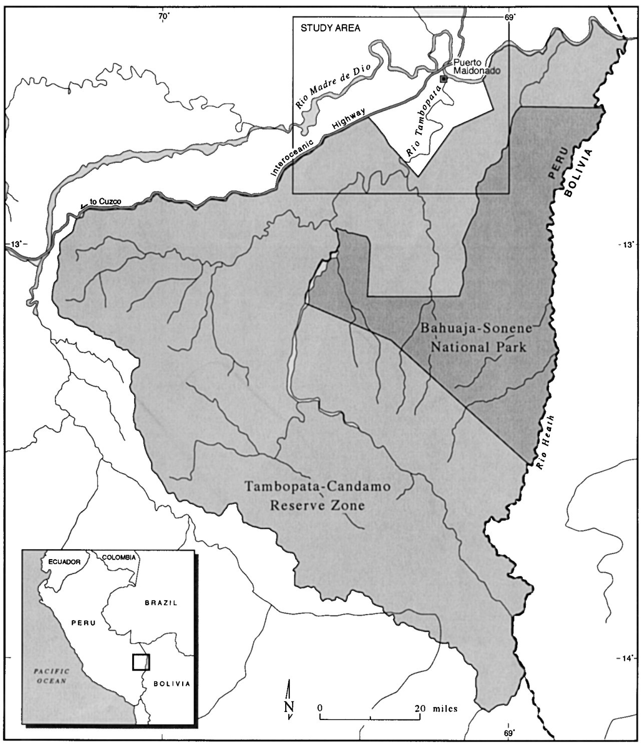


*Figure 1. Tambopata-Candamo Reserve Zone, Bahuaja-Sonene National Park and study region (displays official boundaries of protected area during study period 1997–2000).*

Conservationists value Tambopata for its species richness, habitat diversity, and intact populations of giant river otters, large-bodied monkeys (e.g., *Lagothrix lagothricha* and *Ateles paniscus*), jaguars, capybaras, and white-lipped peccaries (Foster 1994; Ascorra et al. 1999). (Scientific names are provided in Tables 1 & 2.) In 1990 the Peruvian government created a 1.5-million-ha transitory reserve zone called Tambopata-Candamo (TCRZ) (Fig. 1) (Chicchón 2000). Most of TCRZ covered uninhabited forests, but roughly 3200 people lived just inside the northern border of the Reserve. These residents engaged in swidden farming (90.5% of all residents), fishing (50.2%), hunting (42.6%), mining (25.7%), logging (23.1%), and harvesting of Brazil nuts (15.1%) (Chicchón 1996). Officially, the only forest extraction and land-use activities allowed within the reserve were those already operating when the reserve was created (Ascorra et al. 1999). Subsistence agriculture was permitted, but not beyond the boundaries of pre-existing land claims. However, given the impermanent status of the reserve and the limited capacity of Peru's National Institute of Natural Resources (INRENA) to manage such a vast area, rules governing resource use were poorly communicated and enforced (Varese 1995). For example, mining was prohibited but nonetheless occurred in the reserve (Ascorra et al. 1999).

Restrictions on hunting within the reserve were even more uncertain (Varese 1995). Peruvian hunting regulations are tied to forestry and other laws, and they often change (Varese 1995). Local residents, representatives of nongovernmental organizations, and public officials in Tambopata offer conflicting explanations about which animals can be killed where. In general, however, Peruvian law designates wildlife as national patrimony under the government's protection. During this study, all Amazonian animals in Peru were protected from hunting except for 15 species groups, including red brocket deer, peccaries (*Tayassu pecari* and *T. tajacu*), Brazilian tapirs, pacas, agoutis, capybaras, armadillos (*Dasypus* spp.), turtles, and some game birds (Varese 1995). Hunters were allowed to kill these animals for subsistence and local sale within small communities, including reserves. Hunting is also legal whenever wildlife threatens crops or livestock (Ascorra 1996). Local residents refer to this form of hunting as *cacería sanitaria* (sanitary hunting), particularly in reference to predator removal (Ascorra 1996). Commercial hunting is forbidden in settlements of ≥3000 inhabitants (Varese 1995). Despite this rule, game meat is sold illicitly in the city of Puerto Maldonado.

During the 1990s, a group of Peruvian nonprofit organizations led by Conservacion Internacional–Peru (I-Peru) worked to increase public support for conservation, particularly within the reserve zone (TCRZ) (Ascorra et al. 1999; Chicchón 2000). The impetus for our research project came from public discussions led by CI-Peru about the future of the reserve. During public meetings, residents of TCRZ described the difficulty of making a living where transportation was costly and infrequent, soils were poor, and wild animals raided crops (Ascorra 1996). Communities were generally receptive to our research effort, and they helped shape the goals and methods of this project. Some residents were employed as research assistants, and this aided local acceptance of the project.

### Fine-Scale Monitoring of Mammals in Fields, Fallows, and Forest

To assess the response of mammals to vegetation disturbance associated with swidden agriculture, we monitored the community of Infierno (Fig. 2) for 9 months. Infierno is 19 km from the city of Puerto Maldonado, or roughly 2.5 hours by river (Loja et al. 2000). Infierno lays adjacent to large tracts of uninhabited forest on 18,000 ha of land designated as an indigenous reserve. We worked with Ese'Eja and ribereño residents of Infierno, both of whom pursue a variety of forest-based economic activities, including fishing, hunting, and swidden agriculture (Loja et al. 2000).

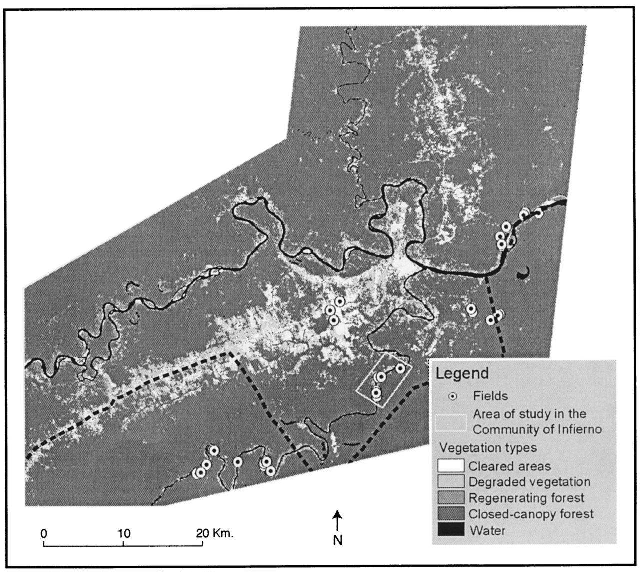


*Figure 2. Swidden field locations superimposed on Landsat thematic mapper 1997 image. Light shades indicate forest clearing along roads and rivers. Dashed line indicates boundary of Tambopata-Candamo Reserve Zone.*

We selected three habitat types to monitor: (1) swidden fields (average size: 0.59 ha, SD= 0.47), all polycropped in rice, maize and yucca; (2) fallows (regenerating fields, 2–10 years of age), and (3) closed-canopy forest (i.e., forest that had been selectively logged or tapped for rubber >40 years ago). Given the highly elusive nature of wildlife around human settlements, we chose an indirect sampling protocol. Nineteen lines of scent stations were set up: seven in fields, five in fallows, and seven in closed-canopy forest. Each line was separated by at least 500 m. Along each line, three pairs of stations were cleared (each station was 1 m in diameter), and each pair was separated by 25 m. Each month we cleared stations of vegetation, pulverized surface soil, and placed lures for 2 nights. We used a nonfood scent lure (MEGAMUSK), which attracts the widest range of mammalian species in the study region (Boddicker 1997).

Each month the same pair of observers recorded tracks in the beds. One of the observers (J.L.M.) was a biologist formally trained in track identification, and the other observer was an expert local hunter. During monthly visits, the density of understory vegetation around each track bed was sampled with a profile-board method modified by Ray (1996). This provided an estimate of understory cover, a potential influence on habitat use in heavily hunted areas. Also, at each station we ran a 5 × 100 m transect roughly parallel to the river edge and recorded the diameter at breast height (dbh) of all trees >10 cm.

### Regional-Level Monitoring of Mammals in Fields

To assess the broader impact of land use on wildlife survival, we monitored wildlife presence in farms along a 65-km transect covering a variety of social and ecological conditions. At one extreme were fields embedded in highly modified environments near Puerto Maldonado; at the other were newly cleared fields within the heavily forested reserve (Fig. 2).

The unit of our analysis was the swidden field, which averaged 0.57 ha in size (SD 0.49 ha, range 0.05–1.57 ha). To control for variation in crop type, we selected 42 fields planted in maize and yuca, two dominant local crops. We surveyed these 42 swidden fields over three planting seasons (19 months). Each month the same pair of observers canvassed each field entirely, searching for signs of wildlife (tracks, scat, digging, damaged crops). When we discovered evidence of wildlife, we recorded the species, location, and amount of crop damage, if any. We tested interobserver variation by having the observers canvas randomly selected fields independently. Comparing the two observers to each other and to local hunters tested the accuracy of species identification. These accuracy tests revealed that agouti and paca damage to yuca were difficult to distinguish, particularly in overgrown fields (20% error). We therefore combined these two species when estimating yuca damage.

The majority of farmers (74%) managing the 42 fields were second- or third-generation Amazonians who had moved to their present plot in Tambopata from elsewhere in Madre de Dios. The other 26% had arrived directly from the Andes during the 1980s. The average length of residence of the farmers on their landholding was 13 years. The average size of a landholding was 41.6 ha (range 19–140 ha), of which 24 ha was in forest (range 17–130 ha) and 4.3 ha in planted fields (range 0–23). Twenty-seven percent of the agriculturalists had pastures (average 17 ha, range 0–50).

Our goal was to explain variation in three measures of wildlife presence on farms: (1) number of wildlife species visiting each swidden field, (2) average body mass of wildlife species observed in fields, and (3) percentage of crops damaged by area (Naughton-Treves 1998). Against these three dependent variables, we assessed several independent local and regional predictor variables grouped in three categories: location, hunting intensity, and vegetation cover.

#### LOCATION

Given the mobility of wildlife, we predicted that the surrounding population sources and sinks (sensu Pulliam 1988) would shape local wildlife presence (Novaro et al. 2000). Thus, we examined the impact of a swidden field's proximity to the reserve (linear distance in meters) and to urban markets (travel time to Puerto Maldonado). These are both proxies of the intensity of human land use that have proven significant in studies of local game abundance (Mitchell & Raez Luna 1991; Ascorra 1996). We also tested whether fields planted in terra firme forest were visited by fewer mammals than those planted on high levees along rivers.

#### HUNTING INTENSITY

Individual hunting practices vary dramatically at Tambopata, from those of the *mitayeros* (professional hunters including both Ese'eja and ribereño residents), who often travel >10 km to hunt in uninhabited forests, to those of occasional hunters who shoot game in nearby forests or fields (Ascorra 1997; Loja et al. 1999). Roughly half the agriculturalists in Tambopata do not hunt at all (Chicchón 1996). We assessed hunting intensity at the farm level by interviewing people about their hunting activities and asking individuals to keep diaries of their hunting activities. We later classified individuals into one of three categories: nonhunter, occasional hunter, and professional hunter (*mitayero*) based on the number and size of game they reported hunting. To assess hunting intensity at the community level, we indexed each settlement after counting the number of mitayeros. Self-reporting was corroborated by key informants from each community who were familiar with their neighbors' hunting activities. We also drew data from a long-term study of mitayeros in the area (Ascorra 1996; Loja et al. 1999; Loja et al. 2000).

#### VEGETATION COVER

We sampled vegetation cover and age at the levels of field, farm, and surrounding community (up to 5 km). We chose these levels because land-use decisions are made at each. Only the field, however, was physically distinguishable from its surroundings and thereby distinct to wildlife. Around each field, we measured the basal area, canopy height, understory density (as per Ray 1996), and age of vegetation (via farmers' reports) along two 5 × 100 m transects randomly placed perpendicular to the field edge. We assessed land cover at the farm level through field interviews and mapping and recorded the number of hectares of tall forest (>15 years), fallow (3–15 years), pasture, and planted fields. Farmers at Tambopata are generally precise about land-use estimates on their property, given that many pay forest-clearing crews by area. In post hoc analysis, there was a strong correlation between farmers' estimates of farm area under forest and that measured in remote images ($r = 0.78, p < 0.0001$).

At the broadest scale, we measured vegetation cover based on a supervised classification of Landsat thematic mapper satellite data captured in 1997. We classified four broad vegetation types: (1) cleared areas (fields and pasture), (2) degraded vegetation (dominated by the invasive species of bamboo *Guadua* spp.), (3) regenerating forest <15 years old, and (4) closed-canopy forest. Classification accuracy was assessed based on field-ground-truthed data collected and georeferenced with a global positioning system. The classified satellite data were used to measure the abundance of land cover in a circular buffer around each field with radii set at 0.5, 1, 2, 3, 4, and 5 km. Conditions varied widely around study fields, ranging from sites dominated by old-growth forest to areas surrounded by pasture, bamboo thickets, and secondary forest (Fig. 2).

Land-cover proportions varied among buffers of different radii, but there were no abrupt changes with increasing buffer size. We thus decided to use the smallest and largest buffer radii (0.2 and 5 km) in further analyses. Independent variables derived from the land-cover maps were relative abundance of the four vegetation classes and total length of forest edge (both secondary and closed-canopy).

### Statistical Analysis

To assess the independent relationships between multiple predictors (vegetation, hunting, and location) and the wildlife data, we used a pair of sequential analyses of covariance (ANCOVA). An ANCOVA was most appropriate because we were assessing the simultaneous effect of continuous, nominal, and ordinal variables. Nevertheless, preliminary inspection of the data revealed analytical hurdles. Colinearity of vegetation variables was high, which we circumvented with a cluster analysis (Ward's) and the construction of two composite variables. The cluster analysis effectively discriminated between four categories of fields along a continuum of disturbance in adjacent vegetation (as per Medellin & Equihua 1998). We also created two composite variables to avoid colinearity in closed-canopy forest measured at the farm and 5-km levels and the negative correlation between closed-canopy forest and fallow of two types: (1) closed-canopy forest at 5 km + percentage of farm under closed-canopy forest and (2) closed-canopy forest at 5 km − fallow (Sokal & Rohlf 1981). Our two composite variables were not correlated with each other.

To meet the assumptions of ANCOVA, we examined residual plots to detect substantial departures from constant variance. Most such departures were mitigated by log-transformation of the response variables; however, no transformation could fix the departure caused by proximity to TCRZ. This variable was strongly bimodal, with a natural gap near the center of its distribution. Thus, we split proximity to TCRZ into two categories defined as "within TCRZ" ($n$ = 18 fields) and "outside TCRZ" (748–15,085 m from the reserve boundary, $n$ = 24 fields).

Proximity to TCRZ and proximity to Puerto Maldonado were highly correlated ($n$ = 42 fields, $r_s$ = −0.80, $p < 0.0001$), barring their simultaneous inclusion in any multivariate analysis. This dictated two ANCOVAs. The first used proximity to TCRZ (dichotomized as above) and omitted proximity to Puerto Maldonado. In the second, we analyzed fields within TCRZ separately from those outside TCRZ (effectively controlling for proximity to TCRZ) and included distance to Puerto Maldonado as a covariate. The large number of predictors remaining after these procedures led us to perform backward stepwise elimination of variables that failed to achieve $p < 0.10$. Results are presented for the last step.

## Results

### Wildlife Use of Fields, Fallows, and Forest

#### VEGETATION CONDITIONS

There were marked differences in vegetation structure between the three habitat types. The average summed basal area measured in planted fields was 688.0 cm$^2$/ha (SD = 77.3), 5510.4 cm$^2$/ha in fallows (SD = 454.1), and 9744.9 cm$^2$/ha in closed-canopy forest (SD = 2992). Understory density was greatest in fallows (Fig. 3). On average, fields had lower understory density than fallows or forests, but this varied dramatically over the planting season (Fig. 3).

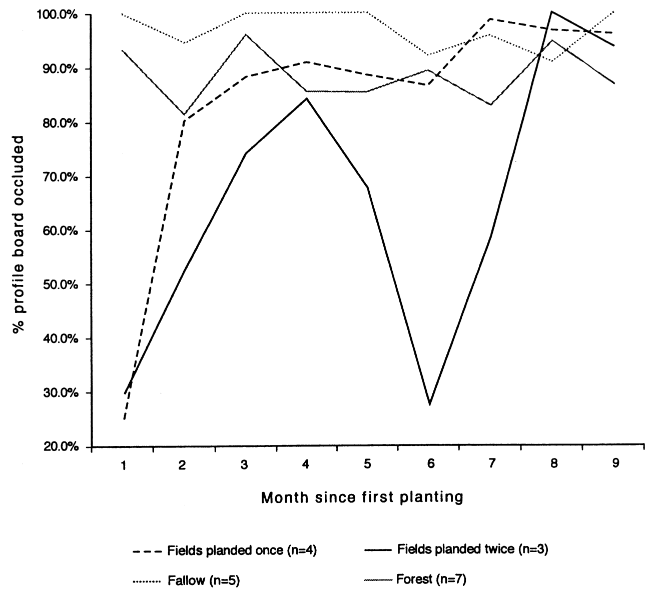


*Figure 3. Understory vegetation density in fields, fallows, and forest over a 9-month planting cycle in the community of Infierno.*

### Mammalian Habitat Use

Twelve species of mammals >2 kg in size occurred at scent stations in the three habitat types (Table 1). The most commonly recorded species were agoutis, followed by pacas, armadillos, and ocelots (Table 1). We observed eight species in fields and nine in forests and fallows. When data for all species were pooled and averaged across the study period, there was no difference in recorded activity between fields, fallows, and forest (Table 1).

A closer look at the data revealed significant variation in habitat use by different species and in monthly activity levels. In the fields, agoutis were recorded significantly less frequently than expected by chance (Table 1). Pooling the data for collared peccaries and brocket deer, we found greater than expected visits to forest. Ocelots tended to appear with greater than expected frequency in fallows.

The timing of wildlife visits to fields versus fallows or forests varied significantly. When all species were pooled, the distribution among months of visits to fields was different than that for forests or fallows (Kolmogorov-Smirnov test, field vs. forest: $\chi^2$ = 10.89, $p$ = 0.0086; field vs. fallow: $\chi^2$ = 8.00, $p$ = 0.0366; forest vs. fallow: not significant). Retesting the data with monthly averages (vs. averages for the entire period) revealed

**Table 1. Wildlife visits to scent stations in fields, fallows, and forest during 9 months sampling at Tambopata, Peru.**

| *Species recorded*[a] | *Field* (n = 7) *lines*[b] | *Fallow*[c] (n = 5 *lines)* | *Forest* (n = 7 *lines)* | *Habitat preference*[d] |
|---|---|---|---|---|
| Brown agouti | 9 | 12 | 31 | Forest, $\chi^2$ = 12.48, $p$ = 0.0019 |
| Long nosed paca | 11 | 15 | 13 | ns |
| Nine-banded armadillo | 3 | 6 | 7 | ns |
| Ocelot | 3 | 7 | 6 | Fallow, $\chi^2$ = 6.38, $p$ =0.0386 |
| Collared peccary | 1 | 5 | 5 | ns[e] |
| Red brocket deer | 0 | 5 | 2 | ns[e] |
| Brazilian rabbit | 2 | 1 | 0 | — |
| Jaguar | 2 | 0 | 1 | — |
| Tayra | 1 | 1 | 0 | — |
| Grey brocket deer | 0 | 0 | 2 | —[e] |
| Giant anteater | 0 | 0 | 1 | — |
| Giant armadillo | 0 | 0 | 1 | — |
| Total | 32 | 52 | 69 | ns |

[a]*Scientific names not provided in Table 2: grey brocket deer,* Mazama gouazoubira*; giant anteater,* Myrmecophaga tridactyla*; giant armadillo,* Priodontes maximus.
[b]*Each line had 3 pairs of scent stations, each pair separated by 25 m.*
[c]*Lower sample size for fallows corrected in analysis of habitat preference.*
[d]*Abbreviation: ns, not significant.*
[e]*When ungulates (collared peccary and gray and red brocket deer) were pooled, there were higher than expected observations in forest ($\chi^2$ = 8.00,* p *= 0.0093).*

significantly less recorded activity in fields than in either fallows or forests (Kruskal-Wallis, $H$ = 10.5, $p$ = 0.0053) (field average = 1 visit per line per month, range 0.43–2.29; fallow average 1.60, range 0.67–2.00; and forest average 1.29, range 0.86–2.29). Wildlife visits to fields peaked in the third month after maize was planted (Fig. 4) and correlated significantly with understory density (Spearman rank correlation, rho = 1.0, $p$ = 0.0049). Visits to scent stations in forests and fallows did not correlate significantly with understory density, and there was no significant correlation between monthly visits to scent stations and rainfall for any of the three habitat types.

### Regional Analysis: Biomass, Species Number, and Crop Damage of Mammals Visiting Fields

We found indirect evidence of 15 species of mammals >2 kg in size in 42 fields during 18 months (Table 2). In one field, 6 species were observed, although the average count was 1.8 species (SD = 1.3) per field. Agoutis were the most commonly observed species, followed by armadillos, pacas, and brocket deer. Large mammals—capybara, tapirs, white-lipped peccaries—appeared in only four remote farms (average = 40 km from Puerto Maldonado, SD = 2.8) that neighbored uninhabited regions within TCRZ. Jaguar tracks were recorded in two swidden fields close to Puerto Maldonado (16 and 18 km). We did not observe any large-bodied primates on farms.

In multivariate tests, a field's proximity to TCRZ had a strong positive effect on the average body mass of wildlife visiting fields ($F_{1,40}$ = 10.5, $p$ = 0.0024), the number of wildlife species ($F_{1,40}$ = 9.0, $p$ = 0.0046), and crop damage by wildlife ($F_{1,40}$ = 17.2, $p$ = 0.0002). Only one other predictor variable emerged as important. The number of mitayeros in the surrounding community had a significant negative effect on crop damage by wildlife ($F_{1,40}$ = 9.8, $p$ = 0.0033).

The political boundaries of TCRZ are not physically demarcated and likely do not have real significance to wildlife. Rather, proximity to TCRZ reflects a host of correlated variables related to the intensity of human use (Table 3).

Given the overriding influence of proximity to TCRZ on wildlife, we ran subsequent, separate analyses on swiddens within and outside the reserve. For the 18 fields within the reserve, the number of hunters in the surrounding community had a significant main effect on the average size of wildlife species visiting fields ($F_{1,12}$ =11.5, $p$ = 0.0054), whereas individual hunting intensity af-

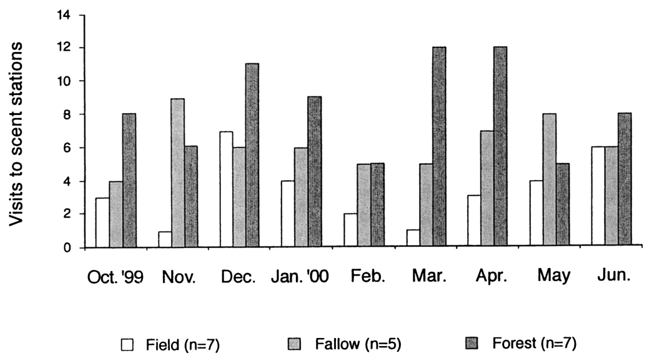


*Figure 4. Recorded monthly visits of mammals >2 kg in size to scent stations located in fields, fallows, and forest in the community of Infierno over a 9-month planting cycle.*

**Table 2. Wild mammals (>2 kg) observed in swidden fields in Tambopata, Peru, July 1998–January 2000.**

| Common name | Scientific name[a] | Body mass (kg)[b] | Estimated density in forest[c] (average no./km²) | Percent fields visited (n = 43) | Percent crops damaged per season in affected fields ($\bar{x}$ ± SD)[d] |
|---|---|---|---|---|---|
| Brown agouti | *Dasyprocta variegata* | 4 | 19.7 ± 21.0 | 75 | 3.5 ± 4.2 |
| Nine-banded long-nosed armadillo | *Dasypus novemcinctus* | 3.5 | 21.9 ± 21.1 | 51 | nd |
| Paca | *Agouti paca* | 8 | 27.9 ± 20 | 37 | 8.4 ± 23.4 |
| Red brocket deer | *Mazama americana* | 30 | 10.5 ± 13.1 | 36 | nd |
| Brazilian rabbit | *Sylvilagus brasiliensis* | 1 | 4.0 ± 2.9 | 13 | <1 |
| Collared peccary | *Tayassu tajacu* | 25 | 11.9 ± 14.9 | 12 | 7.6 ± 15.9 |
| Tayra[e] | *Eira barbara* | 5 | 1.0 ± 0.9 | 9 | 21.5 ± 16.2 |
| Ocelot | *Leopardus pardalis* | 9.3 | 0.8 ± 1.0 | 9 | nd |
| Capybara | *Hydrochaeris hydrochaeris* | 45 | 17.8 ± 7.4 | 5 | 15.8 ± 9.6 |
| Saddleback tamarin | *Saguinus fuscicollis* | <1 | 26.9 ± 32.6 | 5 | nd |
| South American coati | *Nasua nasua* | 4.5 | 15.1 ± 13.2 | 3 | nd |
| Brazilian tapir | *Tapirus terrestris* | 160.0 | 1.6 ± 2.6 | 3 | 58.5 ± 46 |
| Common squirrel monkey | *Saimiri sciureus* | 1 | 62.3 ± 62.8 | 2 | nd |
| White-lipped peccary | *Tayasu pecari* | 35 | 4.9 ± 4.4 | 2 | nd |
| Jaguar | *Panthera onca* | 35 | 0.1 ± 0.1 | 2 | nd |

[a] *As per Emmons et al. (p. 144) in Foster (1994).*
[b] *As per Emmons (1997).*
[c] *These regional data are presented for comparative purpose only and do not factor into any analyses (Robinson & Redford 1989).*
[d] *Abbreviation: nd, < 1% crop damage.*
[e] *Includes damage by unidentified opossum (*Didelphis *sp.).*

fected the amount of crops lost ($F_{2,10} = 7.7, p = 0.0094$). Proximity to Puerto Maldonado also influenced the size of animals observed ($F_{1,12} = 13.6, p = 0.0031$). Land-use intensity was influential at two scales. Farms with more land in crops were visited by smaller animals on average than those on more forested farms ($F_{1,12} = 10.6, p = 0.0069$). Similarly, fields surrounded by more disturbed vegetation within 5 km were visited by smaller animals than those surrounded by more closed-canopy forest ($F_{1,12} = 10.6, p = 0.0069$).

Fields located outside TCRZ showed considerable variation in the presence of wildlife according to their distance from Puerto Maldonado. Fields near Puerto Maldonado were visited by smaller animals ($F_{1,10} = 6.86, p = 0.017$) and fewer species ($F_{1,12} = 7.94, p = 0.0106$). The number of hunters in the surrounding community exerted a significant effect on the amount of crop damage (amount of damage: $F_{1,21} = 4.85, p = 0.039$). Finally, land-use intensity was also important. Swidden fields with more closed-canopy forest within 5 km were visited by more wildlife species ($F_{1,20} = 7.61, p = 0.012$) and larger wildlife species ($F_{1,20}=4.92, p=0.039$).

Fields planted on high levees versus terra firme forest showed no significant difference in the size or number of species of wildlife present, and amount of forest edge had no effect.

### Crop and Livestock Losses versus Bushmeat Gains

Agoutis were the most frequent source of crop damage; however, they caused less damage per individual field than larger species (e.g., capybara) (Table 2). The average market value of crop loss to all wildlife species during a single planting season (approximately 5 months) was $13 (SD = 23, range 0–99, $n = 42$ fields). Wildlife raiding on maize was positively correlated with monthly rainfall and peaked roughly 3 months after fields were planted (Spearman Rank correlation, rho = 0.5, $p = 0.0299$). Yuca raiding was more constant and showed no correlation with rainfall.

The majority of respondents (75%) reported losing poultry or pigs to wild predators. Ocelots and hawks were most frequently blamed, followed by jaguars (32%, 28%, and 5% of complaints, respectively). Also men-

**Table 3. Land-use intensity surrounding fields within and outside Tambopata-Candamo Reserve Zone (TCRZ), Peru.**

| | Fields within TCRZ (n = 18) (SD) | Fields outside TCRZ (n = 24) (SD) | Statistical significance, Mann-Whitney U test |
|---|---|---|---|
| Length of residence (years) | 9 (6.1) | 16 (9.8) | $Z = 2.63, p = 0.0086$ |
| Forest cover within 5 km (ha) | 6571 (257) | 5781 (1417) | $Z = 3.34, p = 0.0008$ |
| No. of mitayeros per settlement | 7.8 (2.7) | 8.5 (13.0) | $Z = 2.67, p = 0.0076$ |

tioned were tayras, jaguarundi (*Felis yagouaroundi*), and pumas (*F. concolor*). Reported losses to small carnivores averaged U.S. $54/year/complainant (SD = $59), but residents claiming attacks by jaguars or pumas reported losing $148/year (SD = $157, $n = 9$ complainants). These claims were not verified and may have been exaggerated. Farmers residing within TCRZ reported losing more domestic animals to a greater variety of predators than did those outside TCRZ. Mitayeros reported fewer predators on their land than did occasional hunters or nonhunters (ANCOVA, $F_{2,30} = 5.59, p = 0.009$).

Forty-nine percent of farmers reported hunting in their fields and fallows. Only one farmer reported planting crops (yuca) deliberately to attract game. Diaries from garden hunters revealed that each planting season they captured an average of 9 kg of game meat in their fields, worth $13.57 in Puerto Maldonado (SD 33.1, $n = 24$ diaries). The average size of (dressed) prey captured in fields and fallows was 12.6 kg, and the median was 3.25 kg (SD = 60, $n = 27$ animals). The average was composed of five species: agoutis (52% of total number of animals killed, 14% of total mass of game meat captured), pacas (30% by number, 4% by mass), armadillos (7%, 2%), collared peccaries (7%, 15%), and tapirs (4%, 65%). On average, garden hunters lost $2.50 more in crop damage to wildlife than they gained in game meat per season ($7 more/year). Only 3 out of 24 individuals earned more in meat than they lost in crops from wildlife in their fields.

Of the 24 garden hunters, 14 considered themselves mitayeros and also hunted in surrounding forests up to 10 km from their farms. There they hunted more and larger animals from a greater range of species. The 14 mitayeros' diaries revealed they hunted 30.1 kg of meat per month from the forest (>150 kg per planting season, worth $196), roughly 15 times more than what was captured in fields (Loja et al. 1999; J. Loja, unpublished data). The mitayeros also hunted a greater variety of game (24 species), including rare species of primates, giant anteaters, and game birds. The average size of the prey they killed in forests was 28.6 kg, three times the size of prey captured in fields (SD = 25.8, $n = 365$ animals).

## Discussion

### Microhabitat Use by Mammals in an Agroforest Mosaic

The scent-station data revealed that several wildlife species forage and hunt in swidden fields, fallows, and forests near human settlements. Our data do not allow for comparisons of wildlife abundance (Sargeant et al. 1998), but it is possible to draw inferences about preferential habitat use by some species. For example, agoutis used forest habitat more than fields or fallows. This came as a surprise given farmers' accounts of agoutis ubiquitous in fields. The difference is partly explained by the strong seasonality of field use by agoutis. Over a 9-month period, agoutis were more commonly observed in forests, but as maize ripened agouti activity in fields rose markedly. Maize has high sugar content and is a food preferred by crop-raiding wildlife elsewhere in the tropics (Sukumar 1989; Naughton-Treves et al. 1998). Rainforest mammals may respond to a ripe field of maize as they do to a mast-fruiting event. However, explanations of wildlife activity in fields based on food availability are confounded by parallel changes in understory cover. As maize matures, vegetation density in fields rises (in Tambopata, farmers seldom weed fields after the seedling phase). Understory density may be an important determinant of wildlife habitat use where hunting is intense. Our interviews with local residents confirm this conjecture. Hunters were reluctant to pursue game in overgrown fields or hot brushy fallows where visibility was poor. Visitation to trackbeds by other species was too rare to permit conclusions about their habitat preference.

The frequent use of fallows by mammals at Infierno accords with other studies that identify regenerating swiddens as prime habitat for several species. Medellin and Equihua (1998) found higher rodent abundance and diversity in regenerating fallows in Lacondon forests. Wilkie and Finn (1990) found higher densities of duikers and abundant game in secondary forests amid shifting agriculture in the Ituri, and Fimbel (1994) noted that some primates prefer abandoned farms to high forest in Sierra Leone (Fimbel 1994). Posey (1985) called regenerating fallows in Brazil "game farms." These conclusions offer support for those who favor multiple-use areas as a viable wildlife conservation strategy. Our results show, however, that heavy hunting levels can offset habitat "enhancement" from swidden agriculture, even in sparsely inhabited areas. Moreover, as land-use intensity increases and fields and regenerating forest replace high forest as the dominant land cover, only highly adaptable species will persist.

### Mammal Survival in Mosaics of Different Land Use and Hunting Intensity

Results from regional monitoring reveal that at least 17 mammal species >2 kg in size used agroforest habitats. Again, our indirect observations of wildlife in swidden fields cannot be used to compare the relative abundance of species, especially considering that some species displayed microhabitat preferences. But the data are useful for understanding patterns of presence and absence of species on land under different intensities of use. Agoutis, armadillos, pacas, and red brocket deer frequented fields even in highly disturbed areas, whereas larger mammals—tapirs, white-lipped peccary, and capybara—were observed only on remote farms. Throughout our study we observed no large-bodied monkeys on any farm, not even howler monkeys, a species able to utilize disturbed habitat (Lopes & Ferrari 2000). The only primates regularly sighted around human settlement were tamarins, an adaptable species too small to draw hunters' attention (Lopes & Ferrari 2000). Our results are corroborated by concurrent studies of wildlife abundance in the forests surrounding our study communities at Tambopata. Loja (1999, 2000) and Ascorra (1996, 1997) ranked the same remote sites highest in large game as we did, based on their observations of wildlife in forests and records of average prey size from local hunters.

The pattern we observed at Tambopata corresponds with observations from other tropical frontiers. As human disturbance increases, the mean biomass and diversity of mammals decline, and small, adaptable species become predominant (Wilkie & Finn 1990; Escamilla et al. 2000; Lopes & Ferrari 2000). Identifying the direct cause of these changes is difficult given that human disturbance activities are correlated (Cuaron 2000; Lopes & Ferrari 2000). For example, where there is swidden agriculture, there will likely be hunters. For this reason, it was not surprising that proximity to the reserve emerged as the strongest predictor of mammalian size and diversity, swamping all other predictor variables. Proximity to the reserve reflects a host of correlated variables related to the intensity of human use, and the large tracts of undisturbed forest in the reserve appear to act as a source for populations of large game (Novaro et al. 2000).

Despite the overlap in hunting and forest clearing for agriculture, our results suggest that hunting has a more immediate impact on mammals >2 kg in size than does vegetation disturbance, at least in a heavily forested area like Tambopata. Hunting emerged as a significant variable in the pooled analysis of 42 fields, as well as in separate analyses for fields located within versus outside the reserve boundary. Rather than measures of individual hunter effort, the number of mitayeros in the surrounding community emerged as the most powerful measure of hunting. Although only one in four households surveyed included a mitayero, these individuals are depleting large and slow-reproducing species up to 10 km away from settlements (Loja et al. 1999). Forest clearing also had a deleterious effect on large mammals. Fields surrounded by heavily disturbed vegetation were visited by smaller and fewer species, both within and outside the reserve. The widespread practice of "sanitizing" the forest by removing large carnivores suggests that jaguars and pumas are unlikely to survive near human settlements despite these species' ability to exploit disturbed habitats (Quigley & Crawshaw 1992). The removal of large carnivores may also contribute to an increased abundance of small game in and around swiddens.

## Wildlife beyond Park Boundaries

Our results reveal that even in sparsely inhabited (<1 person/km$^2$), remote areas, humans are altering the composition and abundance of wildlife communities. Our data bolster other studies' conclusions that large herbivores, large carnivores, and most primates are unlikely to persist in permanently settled, multiple-use zones around national parks unless hunting is restricted (Bodmer et al. 1997). The loss of these species may have long-term consequences for local forest function and composition (Redford 1992). Tambopata's agroecosystems are not empty of wildlife, however; they are inhabited by "anthropogenic" fauna, including agoutis, pacas, armadillos, collared peccaries, ocelots, and tamarins. These are adaptable, cosmopolitan species capable of exploiting secondary vegetation and crop lands, a key attribute for wildlife survival beyond park boundaries. These weedy species may not be of immediate concern to conservation biologists, and they will not attract tourists. But small game hold potential ecological and economic value and deserve management attention. Agoutis are the key seed disperser and predator for Brazil nuts, and their use of regenerating swiddens may be linked to the high regeneration rates of Brazil nut trees in these sites (Ortiz 1995). Small mammals may also serve as a fall-back protein source for the poor, particularly in areas where large species have been depleted (Redford et al. 1995; Suarez et al. 1995). Currently in Tambopata, however, most mitayeros dismiss small game such as agoutis as "not worth a bullet." And garden hunters with access only to small game were seldom able to offset crop losses with bushmeat gains. Only individuals neighboring uninhabited, lightly hunted forests continued to enjoy hunting big game and thus managed to compensate for crop and livestock losses.

During this project, many local residents expressed their awareness that large mammals were depleted around settlements, especially large-bodied primates. Paradoxically, the hunters who were most heavily exploiting local populations of game were the individuals most motivated to participate in community-based wildlife conservation projects promoted by nongovernmental organizations (Loja et al. 2000). Indigenous communities have also been receptive to sustainable-hunting initiatives (Loja et al. 2000). Conversely, the majority of residents hunts only occasionally or not at all and has little interest in wildlife conservation. Most residents are more concerned with improving market access for their crops and expanding pastures.

In 2000, a consortium of nongovernmental organizations and state agencies led a public process of rezoning land in Tambopata to accommodate both conservation and economic development goals. As a result of this process, Bahuaja-Sonene National Park was expanded to include 1 million ha of uninhabited forest. Uninhabited areas of TCRZ attained permanent status as a national reserve officially open to future sustainable use. However, the occupied areas of TCRZ (including the remote settlements where we recorded large game) were excised to accommodate the desire of resident communities to "remove themselves" from the reserve, build roads, and intensify their land use. This development shows that wildlife conservation did not factor high on the environmental agenda of many former residents of the reserve. Taken as a whole, the Tambopata case shows that many Amazonian species can be maintained in sparsely settled agroforest ecosystems *if* hunting is restricted. But the recent decision of several communities to remove themselves from the multiple-use reserve so as to be able to intensify their use of the land reveals greater long-term challenges in conserving biodiversity in human-managed ecosystems.

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### Literature Cited

Alvarez, N., and L. Naughton-Treves. 2003. Linking national agrarian policy to deforestation in the Peruvian Amazon: a case study of Tambopata, 1986–1997. Ambio **32:**269–274.

Ascorra, C. 1996. Evaluacion de fauna en sistemas agroforestales para el manejo sostendio. Conservación Internacional, Programa Peru, Lima.

Ascorra, C. 1997. Evaluacion de fauna: Puerto Maldonado. Conservación Internacional, Programa Peru, Lima.

Ascorra, C., et al. 1999. Zona reservada de Tambopata-Candamo. Conservación Internacional, Lima.

Bisbal, F. 1993. Impacto human sobre los carnívoros de Venezuela. Studies on Neotropical Fauna and Environment **28:**145–156.

Boddicker, M. 1997. Medium and large mammals: biodiversity assessment in the lower Urubamba region. Pages 351–376 in F. Dallmeier and A. Alonso, editors. Biodiversity assessment and long-term monitoring lower Urubamba region. Smithsonian Institution, Washington, D.C.

Bodmer, R., and E. P. Lozano. 2001. Rural development and sustainable wildlife use in Peru. Conservation Biology **15:**1163–1170.

Bodmer, R., et al. 1997. Hunting and the likelihood of extinction of Amazonian mammals. Conservation Biology **11:**460–466.

Carrillo, E., G. Wong, and A. Cuaron. 2000. Monitoring mammal populations in Costa Rican protected areas under different hunting restrictions. Conservation Biology **14:**1580–1591.

Chicchón, A. 1996. Subsistence system improvement and conservation in buffer areas of the Bahuaja Sonene National Park, Madre de Dios and Puno, Peru. Conservación Internacional, Programa Peru, Lima.

Chicchón, A. 2000. Conservation theory meets practice. Conservation Biology **14:**138–139.

Chicchón, A., M. Glave, and M. Varese. 1997. La lenta colonización del Inambari y el Tambopata: uso del espacio en la selva sur del Peru. Pages 551–587 in E. G. Olarte, B. Revese, and M. Tapia, editors. El problema agrario en debate. SEPIA VI, Lima, Peru.

Cuaron, A. D. 2000. A global perspective on habitat disturbance and tropical rainforest mammals. Conservation Biology **14:**1574–1579.

Denevan, W. M. 1992. The pristine myth: the landscape of the Americas in 1492. Annals of the Association of American Geographers **82:**369–385.

Dirzo, R., and A. Miranda. 1991. Altered patterns of herbivory and diversity in the forest understory: a case study of the possible consequences of contemporary defaunation. Pages 273–287 in P. W. Price, T. M. Lewinsohn, G. W. Fenandez, and W. W. Benson, editors. Plant animal interactions: evolutionary ecology in tropical and temperate regions. Wiley, New York.

Donkin, R. A. 1985. The peccary: with observation on the introduction of pigs to the New World. American Philosophical Society, Philadelphia, Pennsylvania.

Emmons, L. 1997. Neotropical rainforest mammals: a field guide. University of Chicago Press, Chicago.

Escamilla, A., M. Sanvicente, M. Sosa, and C. Galindo-Leal. 2000. Habitat mosaic, wildlife availability and hunting in the tropical forest of Calakmul, Mexico. Conservation Biology **14:**1592–1601.

Fimbel, C. 1994. The relative use of abandoned farm clearing and old forest habitats by primates and a forest antelope at Tiwai, Sierra Leone, West Africa. Biological Conservation **70:**277–286.

Foster, R. 1994. The Tambopata-Candamo Reserved Zone of southeastern Peru. RAP working papers, Conservation International, Washington, D.C.

Gadgil, M., F. Berkes, and C. Folke. 1993. Indigenous knowledge for biodiversity conservation. Ambio **22:**151–156.

GESUREMAD. 1998. Diagnóstico del departamento de Madre de Dios. Gerencia Sub-regional de Madre de Dios, Puerto Maldonado, Peru.

Ghimire, K. 1994. Parks and people: livelihood issues in national parks management in Thailand and Madagascar. Development and Change **25:**195–229.

Janzen, D. H. 1976. Tropical blackwater rivers, animals, and mast fruiting of the Dipterocarpaceae. Biotropica **6:**69–103.

Jorgenson, J. 1993. Gardens, wildlife densities, and subsistence hunting by Maya Indians in Quintana Roo, Mexico. Ph.D. thesis. University of Florida, Gainesville.

Linares, O. F. 1976. Garden hunting in the American tropics. Human Ecology **4:**331–349.

Loja, J., A. Pinedo, F. Torres, and B. Mozombite. 1999. Manejo sostenible de fauna silvestre en la comunidad nativa Infierno. Conservación Internacional, Program Peru, Lima.

Loja, J., A. Gironda, and L. Guerra. 2000. Biología y uso de la fauna silvestre en Tambopata: un caso de estudio. Conservación Internacional, Program Peru, Lima, Peru.

Lopes, M. A., and S. F. Ferrari. 2000. Effects of human colonization on the abundance and diversity of mammals in eastern Brazilian Amazonia. Conservation Biology **14:**1658–1665.

Medellin, R., and M. Equihua. 1998. Mammal species richness and habitat use in rainforest and abandoned agricultural fields in Chiapas, Mexico. Journal of Applied Ecology **35:**13–23.

Mitchell, C., and E. Raez Luna. 1991. The impact of human hunting on primate and game bird populations in the Manu Biosphere Reserve in Southeastern Peru. Wildlife Conservation Society, Bronx, New York.

Naughton-Treves, L. 1998. Predicting patterns of crop damage by wildlife around Kibale National Park, Uganda. Conservation Biology **12:**156–168.

Naughton-Treves, L., and N. Salafsky. 2003. Wildlife conservation in agroforestry buffer zones: opportunities and conflict. In press in G. Schroth, editor. Agroforestry and biodiversity conservation in tropical landscapes. Columbia University Press, New York.

Naughton-Treves, L., A. Treves, C. Chapman, and R. Wrangham. 1998. Temporal patterns of crop raiding by primates: linking food availability in croplands and adjacent forest. Journal of Applied Ecology **36:**595–606.

Novaro, A., K. Redford, and R. Bodmer. 2000. Effects of hunting in source-sink systems in the Neotropics. Conservation Biology. **14:** 713–721.

Ortiz, E. G. 1995. Survival in a nutshell. Americas **47:**6–17.

Peres, C. A. 2000. Evaluating the impact and sustainability of subsistence hunting at multiple Amazonian forest sites. Pages 31–56 in J. R. Robinson and E. L Bennett, editors. Hunting for sustainability in tropical forests. Columbia University Press, New York.

Peres, C. A., and B. Zimmerman. 2001. Perils in parks or parks in peril? Reconciling conservation in Amazonian reserves with and without use. Conservation Biology **15:**793–797.

Peterson, J. T. 1981. Game, farming, and interethnic relations in northeastern Luzon, Phillipines. Human Ecology **9:**1–22.

Posey, D. 1985. Indigenous management of tropical forest ecosystems: the case of the Kayapo Indians of the Brazilian Amazon. Agroforestry Systems **3:**139–158.

Pulliam, H. R. 1988. Sources, sinks and population regulation. The American Naturalist **132:**652–661.

Quigley, H., and A. Crawshaw. 1992. A conservation plan for the jaguar (*Panthera onca*) in the Pantanal region of Brazil. Biological Conservation **61:**149–157.

Ray, J. 1996. Resource use patterns among mongooses and other carnivores in a central African rainforest. Ph.D. thesis, University of Florida, Gainesville.

Redford, K. H. 1992. The empty forest. BioScience **42:**412–422.

Redford, K. H., R. Godshalk, and K. Ascher. 1995. What about the wild animals? Wild animal species in community forestry in the tropics. Food and Agriculture Organization, Rome.

Robinson, J., and K. Redford. 1989. Body size, diet, and population variation in neotropical forest mammal species: predictors of local extinction? Pages 567–594 in K. Redford and J. Eisenberg, eds. Advances in Neotropical Mammalogy. Sandhill Crane Press, Gainesville, Florida.

Roldán, A. I., and J. A. Simonetti. 2001. Plant-mammal interactions in tropical Bolivian forests with different hunting pressures. Conservation Biology **15:**617–623.

Salafsky, N. 1992. Mammalian use of a buffer zone agroforestry system bordering Gunung Palung National Park, West Kalimantan. M.S. thesis. Duke University, Chapel Hill, North Carolina.

Sargeant, G. A., D. A. Johnson, and W. E. Berg. 1998. Interpreting carnivore scent station surveys. Journal of Wildlife Management **62:** 1235–1245.

Schwartzman, S., A. Moreira, and D. Nepstad. 2000. Rethinking tropical forest conservation: perils in parks. Conservation Biology **14:** 1351–1357.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman, New York.

Suarez, E., J. Stallings, and L. Suarez. 1995. Small-mammal hunting by two ethnic groups in north-western Ecuador. Oryx **29:**35–42.

Sukumar, R. 1989. The Asian elephant. Cambridge University Press, Cambridge, United Kingdom.

Terborgh, J. 1999. Requiem for nature. Island Press/Shearwater Books, Washington, D.C.

Terborgh, J., and C. van Schaik. 1997. Minimizing species loss: the imperative of protection. Pages 15–35 in R. Kramer, C. van Schaik, and J. Johnson, editors. Last stand: protected areas and the defense of tropical biodiversity. Oxford University Press, New York.

Thiollay, J.-M. 1995. The role of traditional agroforests in the conservation of rain forest bird diversity in Sumatra. Conservation Biology **9:**335–353.

Varese, M. 1995. El mercado de productos de fauna silvestre en la ciudad de Puerto Maldonado, Madre de Dios. Conservación Internacional, Programa Peru, Lima.

Wilkie, D. S., and J. T. Finn. 1990. Slash-burn cultivation and mammal abundance in the Ituri Forest, Zaire. Biotropica **22:**90–99.