# PART III

# Fragmentation and Other Nonharvest Human Impacts

# 13

# Mammalian Densities and Species Extinctions in Atlantic Forest Fragments

## THE NEED FOR POPULATION MANAGEMENT

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The Brazilian Atlantic Forest (Mata Atlântica) is one of the most threatened ecosystems on earth, currently at risk of large-scale destruction. The forests in this ecosystem have been fragmented and reduced to about 7% of their original extent (SOS Mata Atlântica and INPE 1993). The Mata Atlântica also harbors one of the greatest levels of biological diversity in the world, containing nearly 7% of the world's species, many of which are endemic to this region and threatened with extinction (Quintela 1990).

Currently, most of the remaining forest cover in the Mata Atlântica is found on the hillsides along the coast. Very little forest remains in the interior region because agricultural and industrial expansion has resulted in the loss of more than 98% of these forests. As a consequence of deforestation, most of the remaining interior forests are scattered in a mosaic of forest fragments. Today a combined area of only about 280,000 ha of these forests remains, and nearly all of the interior forests that still exist are found in the Pontal do Paranapanema region located in the western part of the state of São Paulo. This region alone comprises 84% of the remaining interior forest cover and is considered one of the poorest and most underdeveloped areas of the state (SOS Mata Atlântica and INPE 1993).

In landscapes dominated by humans, one of the major challenges for conservation biologists is remedying the long-term deleterious consequences of population fragmentation and extinctions. This is the scenario in the interior region, where patches of the original habitat are increasingly being encroached upon by new human settlements, and plant and animal populations are being extirpated by illegal timber extraction and poaching. In addition to selective logging and poaching, genetic, demographic, and environmental forces can harm small and isolated populations (Soulé and Wilcox 1980; Ralls and Ballou 1983; Soulé 1987; Malcolm and Ray 2000; Bessinger and McCullough 2002). For their long-term persistence, isolated populations will most probably require monitoring, effective law enforcement, protection, and management (Gibbs, Snell, and Causton 1999). For protection and management, information on population size and long-term viability is essential.

Few studies have analyzed density and population size of mammals in remnants of the Brazilian Atlantic Forest (Chiarello 2000). In this study we estimate population sizes for some medium- and large-bodied mammalian species living in different forest remnants of the Atlantic Forest in the state of São Paulo. With this information we discuss the viability and the need for management of these mammalian populations. We also analyze the sudden extinctions observed among white-lipped peccaries (*Tayassu pecari*) and tapirs (*Tapirus terrestris*) in some heavily hunted sites and discuss the possible long-term consequences of their absence on the interior forest remnants. We conclude by recommending some research priorities that should contribute to the future of wildlife conservation in the Brazilian Atlantic Forest.

## METHODS

### STUDY SITES

During the period of June 1995 through December 1996, five forest fragments were studied within the interior forests range. Three of the sites are in the western part of the state of São Paulo (Fazenda Tucano, Fazenda Mosquito, and Morro do Diabo State Park) (fig. 13.1), and two sites are in the central part of the state (Fazenda Rio Claro and Caetetus Ecological Station). The greatest distance between sites is 300 km. Sites were categorized as slightly, moderately, and heavily hunted based on several indicators of human activity (Cullen, Bodmer, and Valladares-Padua 2000; table 13.1). Climatic descriptions of the region can be found in Valladares-Padua (1987) and geomorphologic descriptions in Setzer (1949).

Most of the interior forests are considered a transitional ecosystem, bordered in the east by the Tropical Evergreen Broadleaf Forest, which originally covered most of the Atlantic coastline (Eiten 1974; Ab'Saber 1977; Alonso 1977). At the other extreme, most of the western and northern range of the interior forests are bordered by the dry *cerrado* vegetation of Mato Grosso do Sul state and northern São Paulo state. Cerrado is a "tall dense semideciduous xeromorphic savanna vegetation" (Redford 1983:126).

Morro do Diabo State Park is located right on the edge of the cerrado, and accordingly, the best classification of the park's forest would be an "upland semideciduous Atlantic Forest interspersed with some areas of Cerradão" (Baitello et al. 1988; cited by Valladares-Padua 1993). The region is characterized by a pronounced dry season: the park annually receives an average of 1,131 mm of rain, of which 30% falls between April and September (Valladares-Padua 1993). Most of the emergent trees lose their leaves during the dry months (Hueck 1972). The region is also known for its generally nutrient-poor sandy soils (Setzer 1949).

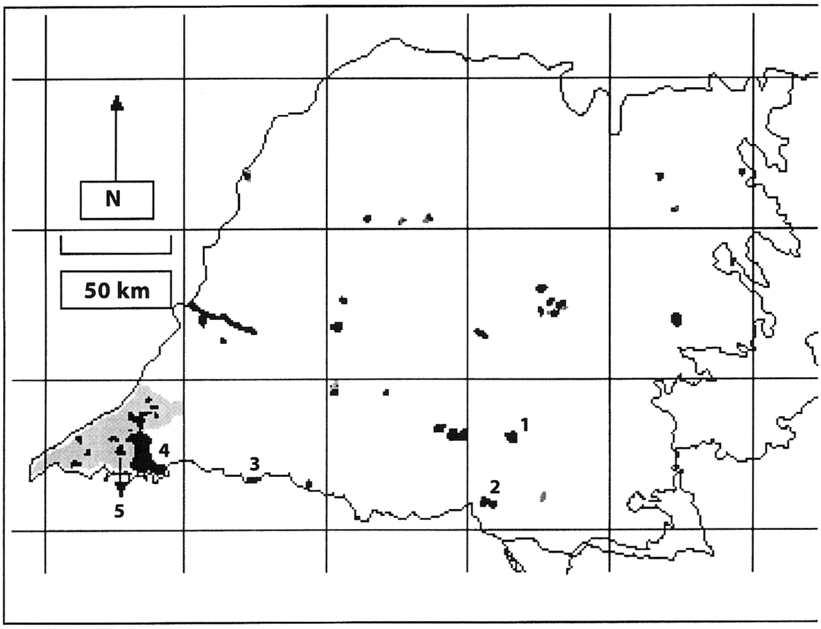

**FIGURE 13.1** Map of forest fragments in the Plateau region of São Paulo state, Brazil. The sites used in this study are Caetetus Ecological Station (1), Fazenda Rio Claro (2), Fazenda Mosquito (3), Morro do Diabo State Park (4), and Fazenda Tucano (5). Shaded area is the Pontal do Paranapanema Region.

## DENSITY ESTIMATES

Abundances of species were determined by censuses along line transects (Emmons 1984; Caro 1999; Cullen, Bodmer, and Valladares-Padua 2000). Four to eight transects were established in each forest fragment, away from hunting trails and in such a way as to incorporate the known diversity of landscape features (Cullen, Bodmer, and Valladares-Padua 2000). Transects ranged from 0.5 to 8 km in length. The cumulative distance censused at each fragment ranged from 161 to 618 km (mean = 381), with a total of 2,287 km censused. Transects were censused between 6 and 10 A.M. and again between 3 and 7 P.M. Sampling effort was greatest for diurnal species but also included crepuscular and some nocturnal animals.

Transects were walked slowly (approximately 1 km/hour following Emmons, 1984) by an experienced biologist or park ranger, with brief stops every 50 to 100 m (Cullen, Bodmer, and Valladares-Padua 2000). The time, species, location along the trail, group size, and perpendicular distance from the trail were recorded for each sighting. Observations were ended after a maximum of 15 minutes, and only accurate counts were used to estimate average group size. For social species the distance was recorded to the closest individual. Densities were estimated using the

**TABLE 13.1** Estimates of Group Size

| SITES | M. D. E.PARK | | C. E. STATION | | FAZ. MOSQUITO | | FAZ. TUC 95 | | FAZ. TUC. 96 | | FAZ. R. CLARO | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Hunting Intensity | Unhunted | | Slight | | Moderate | | Heavy | | Heavy | | Heavy | |
| | N/SD | Min.<br>Avg.<br>Max. | N/SD | Min.<br>Avg.<br>Max | N/SD | Min.<br>Avg.<br>Max | N/SD | Min.<br>Avg.<br>Max. | N/SD | Min.<br>Avg.<br>Max. | N/SD | Min.<br>Avg.<br>Max. |
| *Tayassu pecari* | (4) | 38.00 | (3) | 30.00 | (3) | 5.00 | (3) | 1.00 | EXT | EXT | EXT | EXT |
| | 4.89 | 42.00 | 7.50 | 37.50 | 8.00 | 12.00 | 3.50 | 4.30 | | | | |
| | | 48.00 | | 45.00 | | 20.00 | | 8.00 | | | | |
| *Tayassu tajacu* | (6) | 6.00 | (3) | 4.00 | (4) | 4.00 | (5) | 1.00 | (4) | 2.00 | (8) | 2.00 |
| | 14.48 | 16.50 | 5.90 | 13.50 | | | 5.40 | 6.40 | 2.10 | 4.00 | 1.70 | 6.37 |
| | | 43.00 | | 15.00 | | | | 14.00 | | 7.00 | | 7.00 |
| *Sciurus aestuans* | (1) | 1.00 | (26) | 1.00 | (34) | 1.00 | (2) | 1.00 | (1) | 1.00 | (5) | 1.00 |
| | | | 0.40 | 1.80 | 1.83 | 1.64 | 1.41 | 2.00 | | | 0.54 | 1.40 |
| | | | | 2.00 | | 11.00 | | 3.00 | | | | 2.00 |
| *Nasua nasua* | (1) | 6.00 | (12) | 1.00 | (5) | 1.00 | (3) | 1.00 | (4) | 1.00 | (5) | 1.00 |
| | | | 4.70 | 6.30* | 3.50 | 5.80* | 4.10 | 5.70* | 2.10 | 4.00* | 5.50 | 5.40* |
| | | | | 11.00 | | 14.00 | | 9.00 | | 6.00 | | 14.00 |
| *Cebus appela* | (24) | 1.00 | (25) | 1.00 | (44) | 1.00 | (7) | 1.00 | (9) | 1.00 | (15) | 1.00 |
| | 4.23 | 10.20 | 3.30 | 7.40* | 3.30 | 5.95* | 4.90 | 8.50* | 3.70 | 8.00* | 3.50 | 6.46* |
| | | 25.00 | | 14.00 | | 12.00 | | 17.00 | | 13.00 | | 15.00 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Allouata fusca* | (6) | 1.00 | 4.0 | (78) | 1.00 | (12) | 1.00 | (23) | 2.00 | (33) | 1.00 |
| | 1.47 | 3.25 | | 1.90 | 4.06* | 1.30 | 4.58* | 2.40 | 4.78* | 1.80 | 3.33* |
| | | 4.00 | | | 10.00 | | 6.00 | | 10.00 | | 7.00 |

*Note:* N equals number of group counts considered accurate; SD, standard deviation; Min., smallest group observed based on (N); Max., largest group observed based on (N); Avg., average group size; and EXT, locally extinct.

*No significant difference in pairwise comparisons ($P > 0.05$)

DISTANCE sampling method and computer software developed by Buckland et al. (1993) and Laake et al. (1993).

DISTANCE selects a model (or density estimator) that best fits the detection function produced by the data. AIC (Akaike's Information Criterion; Akaike 1973) was used to aid in selecting the best model, especially in cases of small sample sizes and cases in which most of the sightings were concentrated at or near zero distance from the trail (Buckland et al. 1993). AIC was usually used for ungulates that were rarely encountered at the hunted sites. In some cases small sample sizes led to distortions of the detection curves and resulted in unrealistic density estimates, usually from the hazard rate model (Buckland et al. 1993). In these cases the analysis was done using the uniform model or the half-normal model. The model with the greatest AIC was selected, and its calculated density considered. Density values from data sets with small samples (less than thirty sightings) were still used for comparative analysis.

Of all mammals observed during the censuses, only four species of ungulates (*Tapirus terrestris*, *Tayassu tajacu*, *Tayassu pecari*, and *Mazama sp*), three primates (*Allouatta fusca*, *Cebus apella*, and *Leontopithecus chrysopygus*), one edentate (*Dasypus novencintus*), one carnivore (*Nasua nasua*), and two rodents (*Dasyprocta azarae* and *Sciurus aestuans*) were considered in the analysis. *Mazama gouazoubira* and *M. americana* were pooled in the analysis due to difficulty in visual identification; track evidence, however, indicates that the gray brocket deer (*M. gouazoubira*) is the more abundant of the two species at our study sites.

## POPULATION ESTIMATES

In the case of social species, group density was estimated first, and then transformed to individual density by multiplying by the average group size. Data for each species were analyzed separately, giving a density value for each species at each study site. To estimate population sizes for each species, the individual density data were multiplied by the total forest habitat available at each study site.

## POPULATION VIABILITY

Estimating viability of these populations is not possible without population viability analyses based on extensive life-history, ecological, and threat data specific to each population (Beissinger and McCullough 2002). This estimate is not yet possible with the populations included in our study. However, an effective population size of fifty has been suggested as a size sufficient to mitigate the deleterious effects of inbreeding (Franklin 1980; Allendorf and Ryman, 2002). Effective population sizes are on average about 11% of census population sizes (Frankham 1995). Therefore, the number of 500 individuals was considered as a rough estimate of the minimum number of individuals required for avoidance of significant inbreeding effects over the short term in these population fragments.

When considering the interactions of multiple population fragments at the metapopulation level, longer-term (i.e., evolutionary) considerations are also needed. Franklin (1980), Lande (1995), and Frankham and Franklin (1998) suggest that populations with effective sizes of 500 to 5,000 are needed to balance the loss of genetic diversity caused by drift with the gain in genetic diversity due to new mutations. This requirement translates to actual population sizes on the order of at least 5,000 individuals (Frankham 1995). We therefore used 5,000 as a rough guide to the number of individuals required for metapopulation persistence.

While these guidelines are based on genetic considerations, it is likely that estimates of the number of animals needed to maintain population viability when taking into consideration all types of threats (genetic, demographic, environmental, and catastrophic) will be at least several thousand (Beissinger and McCullough 2002). This number does correspond to our use of 5,000 as a guideline for determining viability at the metapopulation level.

## RESULTS

### GROUP SIZES

White-lips (*Tayassu pecari*) exhibited larger average group sizes at Caetetus Ecological Station than at all other sites (37.50 versus 7.50) (table 13.1). Smaller groups were found at sites with some degree of poaching. Collared peccary (*T. tajacu*) herd sizes were more constant across sites, with Caetetus Ecological Station having on average larger herds (13.50 versus 5.96) than all other sites. All four herds of collared peccaries observed at Fazenda Mosquito had four individuals each. At the other hunted sites, collared peccaries were observed with greater frequency with group sizes having approximately half the numbers of individuals in herds observed at Caetetus Ecological Station. Coati (*Nasua nasua*) groups seemed to be constant across all sites ($x = 5.44$, $P = 0.926$), as were the capuchin monkey (*Cebus apella*) ($x = 7.20$, $P = 0.165$), howler monkeys (*Alouatta fusca*) ($x = 4.15$, $P = 0.086$), and black lion tamarins (*Leontopithecus chrysopygus*).

### DENSITY ESTIMATES ACROSS SITES

Mammalian densities and population estimates are presented in tables 13.2 and 13.3, respectively. On the basis of average density estimates, Morro do Diabo State Park met the requirements for maintaining local populations of at least 500 individuals for most of the species evaluated (shaded areas in table 13.3). The only other area holding a short-term viable population was Fazenda Mosquito for *Alouatta fusca*. Species without any short-term viable population in any of the surveyed areas include tapirs, *Mazama spp.*, *Dasypus*, and *Sciurus*. The black lion tamarin is a very endangered endemic species that occurs in low densities, and local populations at these 2,000-ha fragments are far below the minimum recommended. The

**TABLE 13.2** Density of Groups (individuals/km$^2$)

| SPECIES/SITES | MORRO DO DIABO ST. PARK (35,000 HA), PROTECTED | CAETETUS ECOLOGICAL STATION (2,178 HA), SLIGHTLY HUNTED | FAZ. MOSQUITO PRIVATE (2,100 HA), MODERATELY HUNTED | FAZ. TUCANO PRIVATE (2,000 HA) (1996), HEAVILY HUNTED | FAZ. RIO CLARO PRIVATE (1,700 HA), HEAVILY HUNTED |
|---|---|---|---|---|---|
| *Tapirus terrestris*[a] | 0.20–0.41–0.84<br>(8) | 0.24–0.47–0.91<br>(9) | 0.12–0.30–0.97<br>(6) | EXT | EXT |
| *Tayassu pecari*[a] / G | 3.49–6.94–13.79<br>(10) | 3.87–6.30–10.25<br>(12) | 1.08–3.60–15.22<br>(3) | EXT | EXT |
| *Tayassu tajacu*[a] / G | 3.19–5.67–10.06<br>(17) | 3.71–6.41–11.22<br>(12) | 0.15–0.81–3.22<br>(4) | 0.97–2.21–5.05<br>(5) | 3.62–5.63–8.79<br>(14) |
| *Mazama* spp.[a] | 0.31–1.13–4.12<br>(6) | 0.88–1.82–3.75<br>(13) | 0.50–1.75–1.13<br>(14) | P | P |
| *Dasyprocta azarae*[a] | 18.41–26.80–35.47<br>(82) | P | 0.11–0.39–1.23<br>(3) | 2.53–4.10–6.32<br>(32) | 0.22–0.91–4.81<br>(2) |
| *Dasypus novencintus*[a] | 0.12–0.80–5.10<br>(1) | 8.29–23.63–67.33<br>(19) | 4.11–16.97–37.92<br>(14) | 2.07–9.60–26.32<br>(6) | P |
| *Nasua nasua*[a] / G | 0.89–4.20–11.30<br>(3) | 2.84–4.47–8.01<br>(14) | 1.72–3.40–5.97<br>(15) | 0.33–3.11–7.46<br>(2) | 1.56–5.20–17.98<br>(3) |
| *Sciurus aestuans* / G | 0.18–0.37–0.78<br>(5) | 6.13–11.31–28.40<br>(28) | 17.31–20.20–23.23<br>(37) | 0.10–3.91–21.02<br>(1) | 0.97–2.71–5.92<br>(5) |
| *Cebus appela* / G | 7.44–9.96–13.17<br>(48) | 14.67–17.64–21.16<br>(122) | 6.27–8.31–11.02<br>(56) | 5.53–8.57–13.29<br>(31) | 6.59–10.18–15.71<br>(28) |

| | | | | | |
|---|---|---|---|---|---|
| *Allouata fusca* / G | 2.94–15.66–82.32 | 0.60[b] | 27.42–36.30–48.07 | 7.26–10.91–16.20 | 10.60–16.27–24.95 |
| | (6) | | (90) | (30) | (36) |
| *L. chrysopygus* / G | 2.66[c] | 0.52–1.71–2.75 | 0.25[d] | 1.00[c] | 3.23–3.66[e]–4.10 |
| | | (5) | | | |

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*Note:* Left and right values represent 95% confidence intervals. G equals species where the value of the number of group counts represent sightings of groups; EXT, locally extinct and; P, present in the area but not recorded during transects.

[a] Considered game animals in the study region.

[b] Density value is derived from the minimum number of three groups known to occur in the area.

[c] Density estimates is taken from Valladares-Padua (1993).

[d] Represent the density from the only five individuals translocated to the area in 1996.

[e] Density estimate from Valladares-Padua and Cullen Jr. (1992).

**TABLE 13.3** Population Estimates of Groups (individuals/site)

| SPECIES/SITES | MORRO DO DIABO ST. PARK (35,000 HA), PROTECTED | CAETETUS ECOL. STATION (2,178 HA), SLIGHTLY HUNTED | FAZ. MOSQUITO PRIVATE (2,000 HA), MODERATELY HUNTED | FAZ. TUCANO PRIVATE (2,100 HA) (1996), HEAVILY HUNTED | FAZ. RIO CLARO PRIVATE (1,700 HA), HEAVILY HUNTED | METAPOPULATION |
|---|---|---|---|---|---|---|
| *Tapirus terrestris*[a] | [70–143–294] | [5–10–18] | [2–6–19] | EXT | EXT | [77–159–286] |
| *Tayassu pecari*[a] / G | [1,221–2,429–4,826] | [78–127–206] | [22–72–304] | EXT | EXT | [1,321–2,628–5,336] |
| *Tayassu tajacu*[a] / G | [1,116–1,984–3,521] | [74–130–226] | [3–16–64] | [19–44–101] | [62–96–148] | [1,274–2,270–4,060] |
| *Mazama* spp.[a] | [109–396–1,442] | [17–36–75] | [10–35–23] | P | P | [136–467–1,240] |
| *Dasyprocta azarae*[a] | [6,443–9,380–12,414] | P | [2–8–25] | [51–82–126] | [4–15–82] | [6,500–9,485–12,647] |
| *Dasypus novencintus*[a] | [42–280–1785] | [167–476–1,358] | [82–339–758] | [41–192–526] | P | [332–1,287–4,427] |
| *Nasua nasua*[a] / G | [312–1,470–3,955] | [57–90–161] | [34–68–119] | [7–62–149] | [27–88–306] | [437–1,778–4,690] |
| *Sciurus aestuans* / G | [63–130–273] | [124–228–573] | [346–404–464] | [2–78–420] | [16–46–101] | [551–886–1,831] |
| *Cebus appela* / G | [2,604–3,486–4,610] | [296–356–426] | [125–166–220] | [111–171–266] | [112–173–267] | [3,248–4,352–5,789] |
| *Alouatta fusca* / G | [1,029–5,481–28,812] | [12][e] | [548–726–961] | [145–218–324] | [180–277–424] | [1,914–6,714–24,533] |
| *Leontopithecus chrysopygus* / G | [931][b] | [10–34–55] | [5][c] | [20] | [55–62–70][d] | [1,021–1,052–1,081] |

*Note*: Left and right values represent 95% confidence interval. G equals species where the value of number of group counts represent sightings of groups; EXT, locally extinct; and P, present in the area but not recorded during transects.

[a] Game animals.

[b] Density estimates taken from Valladares-Padua (1993).

[c] Five individuals translocated to the area in 1996.

[d] Density estimate from Valladares-Padua, and Cullen (1992).

[e] Number of three groups known to occur in the area.

confidence intervals of the population estimates are quite large. However, when compared, the estimates using the mean with estimates based on the more conservative lower 95% confidence intervals, only one additional species, *Nasua hancy*, can be considered nonviable in Morro do Diabo. Still, when we sum mean population sizes in different forest fragments and consider a metapopulation scenario (i.e., fragmented populations are considered subpopulation of a regional population), interior fragments still hold short-term viable populations of most mammalian species.

## DISCUSSION

### MAMMALIAN POPULATION VIABILITY IN THE ATLANTIC FOREST OF THE INTERIOR

Conservation biologists who manage small and isolated forest fragments must ask the question, "How many individuals should be maintained within a particular reserve to ensure that a local population will still be thriving 100 years from now?" Although there has been much discussion over the optimum numbers (Lande 1995; Lynch and Lande 1998), the 50-500 rule is still the most commonly accepted (Hunter 1996). This rule states that a local population of 50 effective individuals (i.e., about 500 actual individuals) is a reasonable minimum viable population size (MVP) required to avoid significant problems of inbreeding in the short term. However, long-term survival requires that the MPV should be at least 500 effective individuals (i.e., 5,000+ actual individuals) so that a population will not lose genetic variability and will be able to cope with and evolve in changing enviornments (Lande 1995; Frankham and Franklin 1998). Accordingly, we use 500 individuals (adults and juveniles) as the minimum number required for the short-term conservation of the species. We examine the potential effectiveness of the last remaining forest patches of interior for conserving faunal species.

The Morro do Diabo State Park (35,000 ha) seems to be large enough to support viable populations in the short term for at least 85% of the species examined. *Tapirus terrestris* and *Mazama* spp are probably below the viable number of 500 at the Morro do Diabo State Park. *Sciurus aestuans* and *Dasypus novencintus* also do not meet the MVP levels at Morro do Diabo State Park. However, the results for these two species should be considered with caution since the figures were derived from a small number of observations. Morro do Diabo State Park can also be considered as one of the two recommended reserves to maintain core wild populations of around 2,000 individuals of *Tayassu tajacu* and *T. pecari* proposed by the pigs and peccaries specialist group (Taber and Oliver 1993).

Each site can be considered a subpopulation of a metapopulation, occupying a patch of the metapopulation (Hanski and Gilpin 1991; Gilpin 1997). A metapopulation is a population of populations in which dispersion of animals promotes gene flow and recolonization of extinct patches (Hanski and Simberloff 1997). However, dispersion of animals within this metapopulation would not be frequent since these fragments are separated either by long distances (e.g., 300 km) or by unsuitable habitat.

Therefore, long-term conservation would require artificially moving animals from one forest patch to another. Management may include the shifting (reintroduction, translocation, and managed dispersal) of individuals among fragments. The populations of different patches should not be treated as separate populations in terms of genetic isolation in this metapopulation scenario. Some populations are sources (e.g., Morro do Diabo State Park) because they produce a substantial number of emigrants that could disperse to the other sites. Smaller fragments are sinks because they cannot maintain populations without a net immigration of individuals from the other patches. Thus, some of the small, hunted, or locally extinct populations could be recovered by the rescue effect (Brown and Kodric-Brown 1977; Harrinson 1991; Novaro, Redford, and Bodmer 2000).

Neither *Dasypus* nor *Sciurus* currently exist in any fragments in sufficient numbers to maintain short-term viability (N > 500). However, metapopulation management would effectively increase the numbers of individuals to sizes sufficient to meet these objectives. The total number of *Dasypus* and *Sciurus*, if managed under a metapopulation management strategy, would increase to an average estimate of 1,287 and 886 individuals, respectively.

Through regional metapopulation management, wild populations of most of the species examined can still be maintained as genetically healthy populations over the short term, despite the extreme fragmentation of the interior forests, the current forest encroachment, and the illegal poaching. Large cats like jaguars and pumas, and some of the smaller ones (e.g., *Leopardus* spp), are likely to be an exception, and their long-term survival will require the incorporation of other forested and protected areas that occur outside the interior range (Crawhaw et al. this volume).

## FOREST FRAGMENTS AND SUDDEN LOCAL EXTINCTIONS

In forest patches poaching could quickly exhaust species populations, especially for large-bodied species that occur at lower densities and are preferred by hunters (Robinson 1996). This argument is based on the following premises: a) game species are usually more exposed and locked inside fragments; b) fragmented populations are less resilient to poaching since fragmentation and isolation hinders recolonization; and c) poachers usually have greater access to fragments surrounded by roads and other means of transportation.

Fazenda Tucano can be used to examine some of the premises stated above by examining the changes in mammalian biomass from 1995 to 1996 (table 13.4). This period coincides with an increase in the numbers of potential poachers living around Fazenda Tucano and with the arrival of new landless families in the region. Total biomass of mammals dropped from 296 kg/km$^2$ in 1995 to 201 kg/km$^2$ in 1996, a 35% decrease that represented approximately 1,875 kg of animal biomass. Howev-

**TABLE 13.4** Change in Crude Biomass (kg/km$^2$) from 1995 to 1996 at Fazenda Tucano

| SPECIES | BODY WEIGHT (KG)[a] | FAZ. TUCANO PRIVATE (2,000 HA) (1995) |  | FAZ. TUCANO PRIVATE (2,000 HA) (1996) |  | CHANGE IN C.B, 1995–96 |
|---|---|---|---|---|---|---|
|  |  | D | C.B | D | C.B | +/– |
| *Tapirus terrestris*[b] | 148.95 | 0.34 | 50.64 | 0.00 | 0.00 | — |
| *Tayassu pecari*[b] | 31.67 | 1.22 | 38.67 | 0.00 | 0.00 | — |
| *Tayassu tajacu*[b] | 19.10 | 2.38 | 45.45 | 2.21 | 42.21 | — |
| *Mazama* spp.[b] | 21.72 | 1.07 | 23.24 | P | P | — |
| *Dasyprocta azarae*[b] | 2.84 | 0.43 | 1.22 | 4.10 | 11.64 | + |
| *D. novencintus*[b] | 3.54 | 10.25 | 36.28 | 9.60 | 33.98 | — |
| *Nasua nasua*[b] | 3.88 | 1.82 | 7.06 | 3.11 | 12.06 | + |
| *Sciurus aestuans* | 0.38 | 4.54 | 1.72 | 3.91 | 1.50 | — |
| *Cebus appela* | 3.44 | 6.80 | 23.39 | 8.57 | 29.48 | + |
| *Alouatta fusca* | 6.46 | 10.44 | 67.44 | 10.91 | 70.47 | + |
| *L. chrysopygus* | 0.60 | 1.00 | 0.60 | 1.00 | 0.60 | ø |
| TOTAL BIOMASS |  | % | 295.71 | % | 201.94 |  |
| Total biomass of primates |  | 30.91 | 91.43 | 49.79 | 100.55 | + |
| Total biomass of ungulates |  | 53.43 | 158.00 | 20.90 | 42.21 | – |
| Total biomass of nongame |  | 31.49 | 93.14 | 50.53 | 102.05 | + |
| Total biomass of game |  | 68.49 | 202.56 | 49.46 | 99.89 | – |

*Note:* Crude biomass was calculated for each species using the average body weight of adult individuals (BW) and multiplying by the estimated individual densities (D) (BW*D - kg/km$^2$). Mean body masses were taken from the literature (Robinson and Redford 1986a), with the exception of peccaries and the black lion tamarin for which data were available from the study sites. Percentage contribution (%) refers to a group's relative contribution in relation to the total biomass value of the mammalian species. D equals density (individuals/km$^2$); C.B., crude biomass (kg/km$^2$); P, present but not seen during census.

[a] Average of mean body weights taken from Robinson and Redford (1986a).

[b] Game animals.

er, primate biomass increased by 10%, while ungulate biomass had a fourfold decrease. The decrease in ungulate biomass was mainly due the local extinction of tapirs and white-lips. Deer also had lower biomass in 1996. Collared peccary biomass remained about the same.

The sudden extinction of tapir and white-lips suggests that in forest fragments large game species can be overhunted rapidly when poaching pressure becomes too excessive. The future of these isolated game populations will thus probably depend on the poaching pressure imposed on them. Poaching may override other effects of fragmentation (i.e., genetics and demographics) and be the ultimate factor responsible for causing the extinctions observed among the large mammalian fauna (Cullen, Bodmer, and Valladares-Padua 2000; Cullen, Bodmer, and Valladares-Pauda 2001).

## RECOMMENDATIONS AND RESEARCH PRIORITIES FOR THE INTERIOR ATLANTIC FORESTS

The results of this study provide some empirical suggestions for developing management and conservation strategies for the threatened interior forests. We recommend areas in which we think immediate actions are needed. Results suggest that the implementation of these recommendations should contribute to wildlife conservation in the Atlantic Forest.

**Environmental Education** Environmental education and community participation are essential for successful conservation. A successful program already established for the Morro do Diabo region showed that the local community became aware of the importance of the park as a conservation site and has been contributing to its protection (Padua 1991, 1997). We recommend that environmental education initiatives and efforts for the interior region for the next few years focus more intensively on large landowners and the rural people, with the goal of increasing the awareness of the importance of other isolated forests as well. These communities should be provided with the knowledge, attitudes, and skills to conserve nature. Past experience and new results suggest that with a continued and systematic team effort, including local community education and participation, ecological research and management, legislation, and law enforcement, we will be able to conserve wildlife. Conservation at the combined community, ecosystem, and landscape levels probably offers the most promising alternative to biodiversity conservation of the interior forests.

**Metapopulation Approaches** As our results suggest, despite being highly fragmented and isolated, interior fragments together still sustain a viable population of most of the original biota. Subpopulations should be managed as a metapopulation that may include the reintroductions or translocations of animals among these last remaining forest patches. This approach should especially be emphasized for endangered and endemic species, such as the black lion tamarin. Source and sink habitats need to be included in conservation plans; otherwise, the metapopulation could be threatened. New reserves need to be established, the existing ones protected, and community-based programs implemented. Particular emphasis has to be directed at reducing current poaching and degradation of forest remnants.

**Studies on Landscapes and Animal Dispersion** In highly fragmented landscape areas like the interior region, the existing reserves and forest remnants are definitely islands in a matrix of agricultural lands. This situation should always be kept in mind during the development of new studies and conservation measures. Interior forest patches are parts of a landscape mosaic, and the presence and survival of species may be a function not only of poaching, patch size, and isolation but also of the kind of neighboring habitat around these forest fragments. Some species that are habitat generalists may survive in very small patches because they can exploit surrounding resources. Future studies should focus on the adaptability of species to the new landscape. New studies should investigate ecological and behavioral attributes of species that might help to enhance their survival in the surrounding matrix. One of the most immediate pieces of information needed is the dispersal behavior of species in a habitat mosaic and thus their likelihood of recolonizing the surrounding fragments. Future conservation measures will have to involve effective monitoring and metapopulation approaches that will make the forest patches functional and linked.

**Agroforestry Buffer Zones** Agroforestry is a type of land management in which woody perennials are planted on the same land management units as agricultural crops or as animals in either a special arrangement or a temporal sequence and with ecological and economic interactions between the different components (Fernandes and Nair 1986). Local people that live and farm on the borders of the fragments are currently depleting forest fragments. Poaching, trees blown down by wind, vine colonization, desiccation by wind, fires, cattle grazing, the spread of aggressive grasses, and pesticides are some of the processes leading to a gradual and continuous erosion of these forest edges (Laurence 1991). These processes in the long term are likely to affect forest structure and cause the loss of many plant and animal species, mainly by the known consequences of the edge effects.

A case project has been implemented in which an agroforest surrounding a forest fragment is functioning as a benefit zone to supply services, vegetables, fruits, grains, and protein to the local farmers, thus relieving some of the pressure on the forest (Cullen, Bodmer, and Valladares-Pauda 2001). This benefit zone is providing an insulative/protective zone around fragments and reducing edge effects. Implicit in this conservation approach is the assumption that stimulating the planting and use of multiple-use trees in these edge areas places a value on the resources, and this ascribed value will help to pave the way to conservation of wildlife. Effective programs often begin by encouraging villagers to establish very simple demonstration experiments or vivid examples and to evaluate and share their results with others.

In places like the Pontal do Paranapanema Region, the economic value of forest fragments is low, and economic, political, and demographic pressures are bringing about overexploitation and unsustainable uses of these fragments. This study shows that, except for the Morro do Diabo State Park, the largest protected area of the interior Atlantic Forest, none of the other remaining forest fragments in the Pontal do Paranapanema sustain viable populations for most of the species evaluated. Hence, we must develop and implement innovative and active management schemes that will represent the marriage between these forests and the local people around them.

## ACKNOWLEDGMENTS

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# 14

# Abundance, Spatial Distribution, and Human Pressure on Orinoco Crocodiles (*Crocodylus intermedius*) in the Cojedes River System, Venezuela

ANDRÉS E. SEIJAS

Crocodilians in general, and the Orinoco crocodile (*Crocodylus intermedius*) in particular, have been traditionally hunted by both aboriginal and rural people in Venezuela because of their value as a food resource or because of the putative medicinal or magical properties of their teeth and fat (Petrullo 1939; Codazzi 1940; Tablante-Garrido 1961; Gumilla 1963). The first attempt to commercialize crocodile skins in Venezuela was initiated in 1894–1895 by a U.S. company that established its headquarters in El Yagual, in Apure state (Calzadilla 1948; Medem 1983). At that time crocodiles were hunted with firearms during the day, a highly inefficient method in which many dead and injured animals could not be recovered from the river. That early commercial enterprise failed. The expenses of preparing and transporting the hides proved to be so great that the work had to be abandoned (Mozans 1910; Calzadilla 1948). Despite this early commercial exploitation, during the first quarter of the twentieth century the Orinoco crocodile was probably as abundant as it was when Humboldt (1975) and other nineteenth-century naturalists were amazed by its numbers.

A new phase of commercial exploitation started at the end of the 1920s (Medem 1983). New hunting methods (flashlights and harpooning) and an international demand for crocodilians hides combined to bring to the brink of extinction in less than three decades a species that originally could be counted in the millions. The peak of the exploitation occurred in 1930–1931, when between 3,000 and 4,000 skins were traded daily in San Fernando de Apure. From 1933 to 1935 Venezuela exported 900,000 crocodile hides. The large-scale exploitation ended in 1947–1948, due mostly to the scarcity of the resource by that time. Independent hunters persisted in this activity for several years, but the export of *C. intermedius* hides from 1950 to 1963 was minimal (Medem 1983).

Commercial exploitation extirpated the Orinoco crocodile from most of its historic distribution range (Godshalk 1978; Medem 1981, 1983; Thorbjarnarson 1992; Ross 1998). Today, the Orinoco crocodile is one of the most threatened crocodilian species in the world (Ross 1998). The species is listed as critically endangered in the Venezuelan Red Data Book (Rodriguez and Rojas 1995). Although *C. intermedius* has been legally protected both in Colombia and Venezuela for more than thirty years and although international trade has been prohibited by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) since the middle 1970s (King 1989), little recovery of wild populations has occurred.

Even though commercial exploitation of Orinoco crocodiles in Venezuela is today probably negligible, occasional killings of individuals still occur because they are considered vermin. Also, they are hunted for their meat or fat, and their eggs and hatchlings are collected as food or pets, respectively.

Currently, the most important, and probably the only viable, populations of the Orinoco crocodile (Arteaga et al. 1997), are found in two areas of divergent characteristics in Venezuela. First is the Capanaparo River in the state of Apure (Godshalk 1978; Thorbjarnarson and Hernández 1992), a prime-quality habitat, more than 100 m wide, that is impacted relatively little by human activities and that is in the center of the species' range, where it reached its historically highest densities. Second, in the states of Cojedes and Portuguesa is the Cojedes river system (CRS), a set of highly modified and contaminated narrow river sections (in general less than 20 m wide), near the periphery of the distribution of the Orinoco crocodile and very close to some of the most important agricultural, urban, and industrial centers in the country (Ayarzagüena 1987, 1990; Seijas and Chávez 2000).

Although the survival of the Orinoco crocodile in a river like the Capanaparo is easy to understand, the presence of a dense population of this species in the CRS is somehow paradoxical. One of the factors that may explain the survival of *C. intermedius* in the CRS (Ayarzagüena 1987) is the isolation in which that region remained during the years of intense commercial exploitation of the species (1929–1945). The CRS today is, however, not as isolated as it was in the recent past. Some areas of the river are closer to human population centers, and presumably under greater human pressure, than others. Human population in the CRS is mostly concentrated in the north, close to the piedmont of the Coastal Range. The southern part is sparsely populated by humans, with El Baúl (5,236 inhabitants) the most important town. Is this distinct pattern of human occupation of space a factor that could explain the current distribution of the Orinoco crocodile in the CRS? In this paper I explore that possibility. My hypothesis is that human proximity negatively impacts crocodile survival, and consequently, crocodiles should be found more frequently in river sections far from human settlements.

## STUDY AREA

For the purposes of this study, the Cojedes River System is defined as the middle and lower portions of the Turbio-Cojedes River basin. It covers a wide fringe of land along the Cojedes and Sarare Rivers. The study area in the CRS encompasses

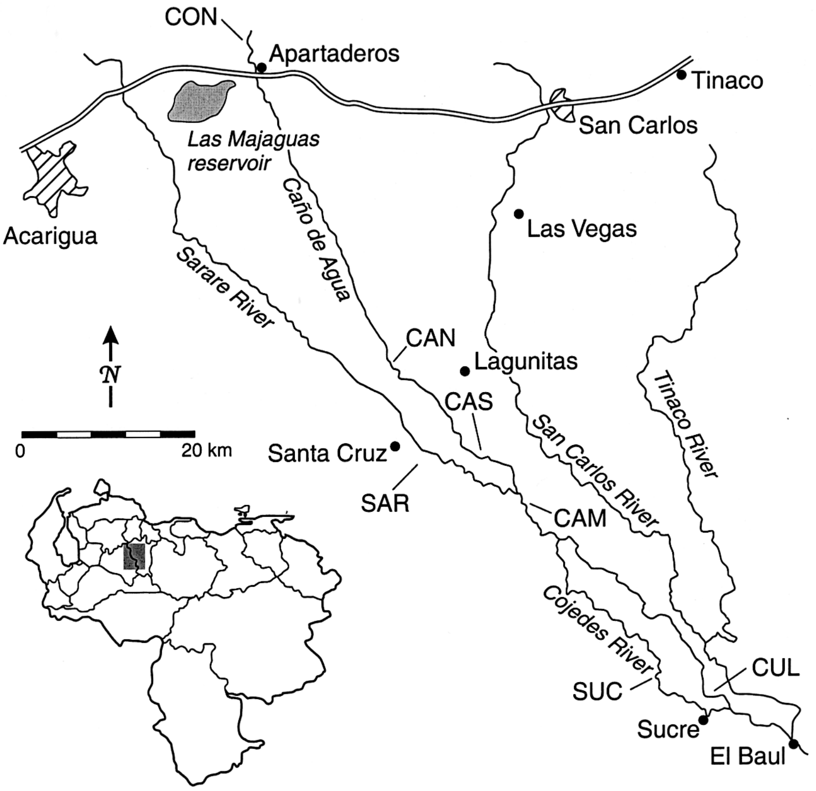


**FIGURE 14.1** Cojedes River System, Venezuela. Rivers flow toward the south. Major cities are located in the north, whereas the south is sparsely populated. The acronyms indicate the locations of the river sections surveyed: CON, Cojedes Norte; CAN, Caño de Agua Norte; CAS, Caño de Agua Sur; SAR, Sarare; CAM, Caño Amarillo-Merecure; SUC, Sucre section; and CUL, Caño La Culebra.

the cities of Acarigua and San Carlos to the north and extends southeast to the confluence of the main course of the Cojedes River with Caño Amarillo-La Culebra near the town of El Baúl (fig. 14.1).

In the northern part of the CRS, agricultural lands dominate the landscape and are interspersed with large- and medium-sized urban centers and cattle ranches. The southern part of the region (south of the Lagunitas-Santa Cruz road) is a matrix of forested savannas and cattle pastures intermixed with forest relicts, scattered agricultural lands, wetlands, and other less extensive land-cover categories. The CRS has zones of relatively high human population densities in the north, where the cities of San Carlos (≫ 80,000 people) and Acarigua (~ 200,000 people) are located and where the rivers have been modified by damming, canalizing, dredging, contamination, and deforestation. In the south the rivers retain more of their original conditions, and El Baúl (6,000 people) is the largest town.

## METHODS

Based on two landsat TM satellite images of the study area, taken on January 10 and February 27, 1990 (early dry season), and on data from more than 1,500 GPS locations, I updated the previously existing cartographic information of the region. The basic land cover features considered for mapping were agriculture, pasture lands and open savannas (taken together as a unit), urban areas, water bodies, forests, permanent rivers, and roads. Maps were converted into raster images for Geographic Information System (GIS) analyses (IDRISIS 1997). The initial raster image generated from the classification of the satellite images had a spatial resolution of 32 x 32 m. Because of the extension of the land surface being modeled (9,660 km$^2$) and in order to speed up the GIS analyses, the raster images used for the final analyses had a spatial resolution of 64 x 64 m.

With the GIS I generated a cost-distance (CD) layer for every major city as well as for small towns, villages, and other human settlements located close to the river. Each CD layer modeled the cost of movement from a particular human settlement to any location on the landscape, i.e., it represented the ease with which people could reach every spot in the study area, considering the friction offered by different land-cover types. The value assigned to a pixel in the CD layer was a function of its distance to the human settlement under consideration and of the friction exhibited by the land surface between them.

The friction surface used to calculate the cost-distance layer was generated according to the relative cost shown in table 14.1. Primary roads were assigned a friction of 1. This value, in fact, means that there was no cost for travel by car on that surface and that cost-distances measured along them were equivalent to Euclidean distances. Because it is possible to travel on average at 80 km/h on primary roads, the friction values assigned to other land-cover types were calculated relative to how much longer it takes to travel an equivalent distance on or through them (using the fastest transportation method that can be used on that surface). Friction values assigned to rivers were somewhat arbitrary but larger than the values assigned to most land-cover surfaces in order to reflect the fact that they are important obstacles to human movements (although river sections that are navigable facilitate human movements). The highest friction was assigned to lakes, which were considered barriers to human movement for the purposes of this study.

The CD layer obtained for each town or city was used to model the presumed human pressure exerted by that city on every reach of the Cojedes River system (indeed, on every location within the study area). The human pressure index (HPI) is a value that indicates the strength of the expected impact of a particular urban area on every point (pixel) in its surrounding landscape. The HPI of a particular spot (i.e., pixel in the raster layer) was calculated as a function of its proximity to human settlements and of the human population size of these particular human settlements. That river reaches close to cities and towns were assumed to be under greater human pressure than river reaches located farther from those urban areas.

**TABLE 14.1** Relative Cost of Movement (friction) Through Different Land Cover Types in the Study Area

| LAND COVER TYPE | MEAN SPEED (KM/HOUR) | RELATIVE FRICTION |
|---|---|---|
| Primary roads | 80 | 1.00 |
| Secondary roads | 60 | 1.33 |
| Improved roads | 40 | 2.00 |
| Dirty roads | 20 | 4.00 |
| Urban areas | 35 | 2.29 |
| Main rivers | — | 80 |
| Secondary rivers | — | 60 |
| Intermittent rivers | — | 40 |
| Agriculture fields | — | 20 |
| Savannas | 4 | 20 |
| Forests | 2 | 40 |
| Lakes | — | 100 |

*Note:* See text for calculation of friction values. The high friction value assigned to river may not apply to navigable river sections.

On the other hand, large cities were expected to exert a higher pressure than small ones. Mathematically,

$$HPI_i = P_i \cdot CD_i^{-2} \quad (1)$$

where $P_i$ is the population size of a particular human settlement and $CD_i$ is the cost-distance layer obtained for that particular human settlement. Equation 1 is in essence a particular case of a gravity model (Forman 1995), which states that the movement or interactions between two nodes increase with node size but decrease with the square of the distance between nodes. In my case one of the nodes (the pixel for which the *HPI* was been calculated) received, arbitrarily, a unit free value of 1. The *HPI* as expressed in Equation 1 has the units of density (inhabitants/km$^2$).

The urban centers considered in the model are listed in table 14.2. Many other small villages (among them, Retajao, El Estero, and La Palmita) and cattle ranching operation centers (including La Batea, Merecure, and Las Guardias) were used to generate cost-distance surfaces. Because of a lack of precise information on human population size in these human settlements, I assigned a figure of 500 inhabitants to small villages and hamlets and 100 to the cattle ranching operation centers.

Because any particular point on the study area may be simultaneously under the influence of several human settlements, the layer of Total Human Pressure (THP) of the entire study area was obtained adding the $HPI_i$ layers of all these settlements (fig. 14.2). In this way every pixel, including those representing the rivers, had an associated *TPH* value. Mathematically,

**TABLE 14.2** Towns and Other Human Settlements in the Cojedes River System, Venezuela, Used to Model the Human Pressure in the Study Area

| TOWNS | NUMBER OF INHABITANTS |
|---|---|
| Portuguesa state | |
| Acarigua-Araure | 171,850 |
| Agua Blanca | 9,393 |
| San Rafael de Onoto | 7,206 |
| Pimpinela | 4,563 |
| Santa Cruz | 4,090 |
| Cojedes state | |
| San Carlos-Tinaco | 68,325 |
| Las Vegas | 6,897 |
| El Baúl | 5,236 |
| Apartaderos | 4,260 |
| Cojeditos | 4,911 |
| Lagunitas | 3,353 |
| Sucre | 1,886 |
| El Amparo | 1,105 |

*Note:* The number of inhabitants is based on OCEI (1993).

$$THP = \Sigma HPI_i \qquad (2)$$

In the CRS several river sections, ranging from 5.2 to 16 km, have been repeatedly surveyed since 1991 (Seijas 1998; Seijas and Chávez 2000). In 1996 and 1997 the position of most crocodiles seen in those river sections during nocturnal spotlight surveys was recorded with a GPS. The GPS locations for those surveys with the highest number of crocodile sightings were used to generate a new map layer. The THP of the spot (pixel) in which each crocodile was seen was obtained by overlaying the crocodile locations layer on the THP layer.

For all surveyed river sections the frequency of pixels with a particular THP value was calculated and tabulated in ranges. That gave an indication of the availability of river habitat under different THP values and allowed the calculation of the number of crocodiles expected to be found in each of these THP ranges. Chi-square analyses ($G^2$, likelihood ratios; Sall and Lehman 1996) were used to compare frequency distribution of THP of crocodile sightings in relation to the frequency distribution of THP for the surveyed river sections.

To assess the importance of other human-related factors in determining the abundance of crocodiles in the CRS, I performed a nonparametric correlation analysis between crocodile density in each river section (table 14.3) with the rela-

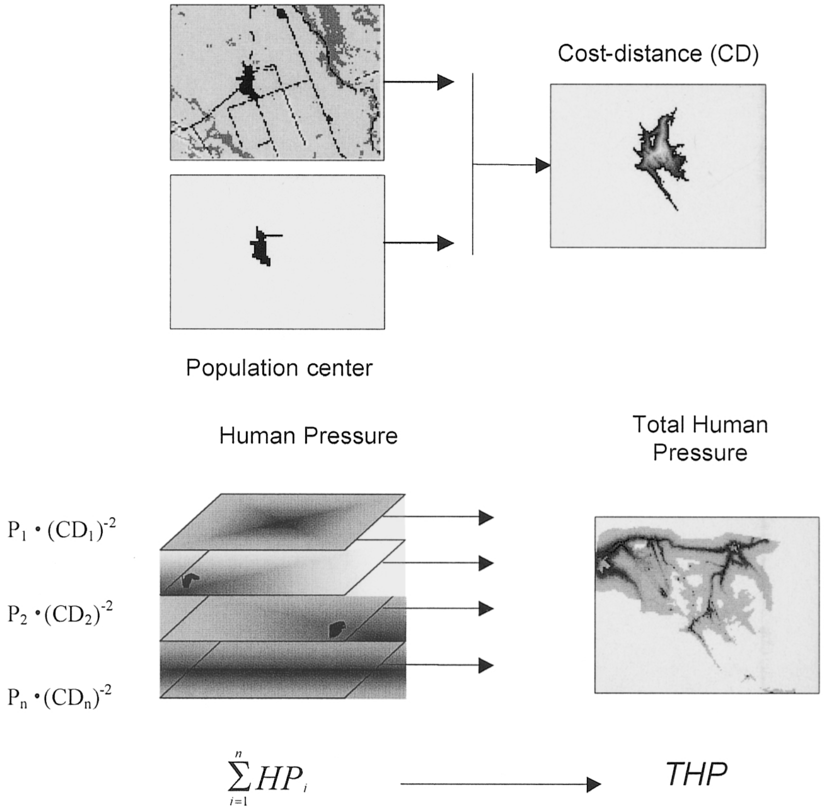


**FIGURE 14.2** Flow chart indicating the procedure followed to obtain the Total Human Pressure (THP) over every place in the study area. From a friction surface and each population center a cost-distance (CD) surface was generated using a geographic information system. The population size of each town, divided by the $CD^2$, allowed the calculation of the human pressure (HP) it exerted over every place in the study area. The Total Human Pressure was calculated adding the HP of all population centers.

tive importance of the following variables: isolation from human populations, navigability, and contamination. I ranked each river section according to the relative importance of these variables (table 14.4). Information on isolation from human population was obtained from data in table 14.3. Ranking according to contamination was based of information presented by Campo and Rodríguez (1997) and Seijas (1998).

Regarding navigability, the only river sections that are navigated on a regular basis are those close to Sucre (SUC) and, to a lesser extent, La Culebra (CUL). For people living in Sucre and El Baúl, the Cojedes River is an essential means of year-round communication with cattle ranches. There is also commercial and subsistence fishing and, presumably, illegal spectacled caiman (*Caiman crocodilus*)

**TABLE 14.3** Total Human Pressure (THP) and Mean Crocodile Population Index in Surveyed River Sections of the Cojedes River System, Venezuela

| RIVER SECTION | LENGTH (KM) | MEAN THP (INH./$KM^2$) | RANGE THP | MEAN CROCODILE DENSITY (IND./KM)* |
|---|---|---|---|---|
| Cojedes Norte (CON) | 7 | 15.6 | 7–56 | 2.0 |
| Caño de Agua Norte (CAN) | 16 | 7.2 | 1–100 | 4.4 |
| Sarare (SAR) | 8.4 | 11.7 | 1–78 | 3.1 |
| Caño de Agua Sur (CAS) | 5.2 | 2.0 | 1–6 | 7.3 |
| Caño Amarillo-Merecure (CAM) | 8.4 | 1.2 | 1–3 | 4.9 |
| Sucre (SUC) | 11.6 | 1.7 | 1–19 | 0.6 |
| La Culebra (CUL) | 12.8 | 1.0 | 1 | 1.4 |

*Note:* River sections are listed from north to south (from upstream to downstream).
*Taken from Seijas and Chávez (2000).

**TABLE 14.4** Ranks of Crocodile Densities, Isolation from Urban Areas, Contamination, and Navigability of the Different River Sections That Were Surveyed in the Cojedes River System, Venezuela

| RIVER SECTION | CROCODILE DENSITY | ISOLATION FROM HUMANS | CONTAMINATION | NAVIGABILITY |
|---|---|---|---|---|
| Cojedes Norte (CON) | 5 | 7 | 1 | 6.5 |
| Caño de Agua Norte (CAN) | 3 | 5 | 2 | 6.5 |
| Sarare (SAR) | 4 | 6 | 5 | 4 |
| Caño de agua Sur (CAS) | 1 | 4 | 3 | 5 |
| Merecure-Caño Amarillo (CAM) | 2 | 2 | 4 | 3 |
| Sucre (SUC) | 7 | 3 | 6 | 1 |
| La Culebra (CUL) | 6 | 1 | 7 | 2 |

*Note:* Contamination ranks were based on information presented in Campo and Rodriguez (1997) and Seijas (1998) Navigability is based on personal observations.

hunting around Sucre and in La Culebra. Upriver from Sucre the river section Merecure-Caño Amarillo (CAM), although navigable year round, seems to be navigated only sporadically since only one family with a small canoe was observed there. Caño de Agua Sur (CAS) is difficult to navigate because of obstructions created by fallen trees and urban debris and garbage that drift from upstream towns.

That section seems to be occasionally visited and sporadically navigated by hunters and campers. The Sarare (SAR) river section surveyed are in the same situation as CAM. Caño de Agua Norte (CAN) and Cojedes Norte (CON) are rarely, if ever, navigated by people other than myself and other crocodilian researchers.

## RESULTS

A tri-dimensional representation of the THP in the study area is shown in Figure 14.3. As would be expected, the highest THP, represented in the figure as high elevation plateaus, was located in and around the main cities (Acarigua and San Carlos). Consequently, the river reaches flowing through densely human populated areas were under relatively high human pressure (table 14.3). Cojedes Norte (CON) for example, which is very close to the towns of Apartaderos and San Rafael de Onoto, had THP ranging form 7 to 56 (mean 15.6, the highest of all surveyed river sections). At the other extreme, THP was relatively low near Sucre (SUC) and especially so in La Culebra (CUL), where all the pixels representing the river had THP of 1 (table 14.3).

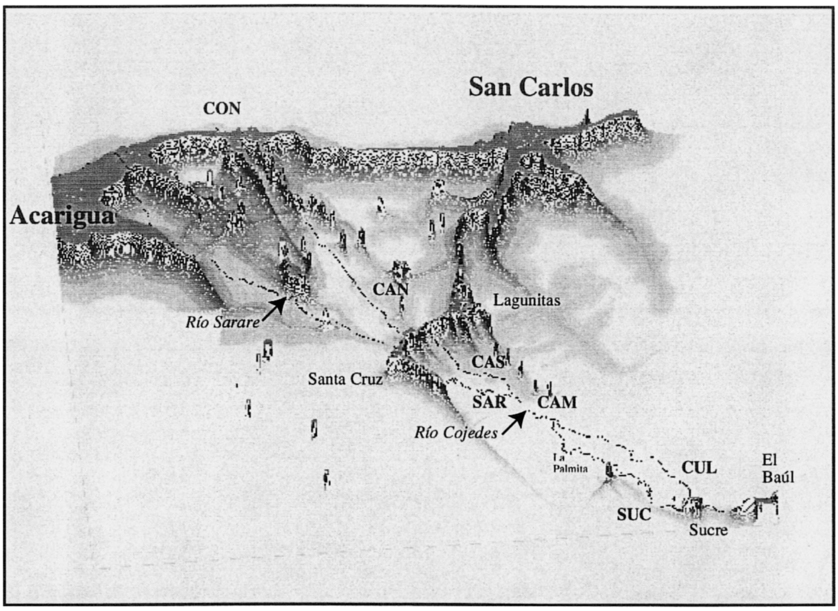
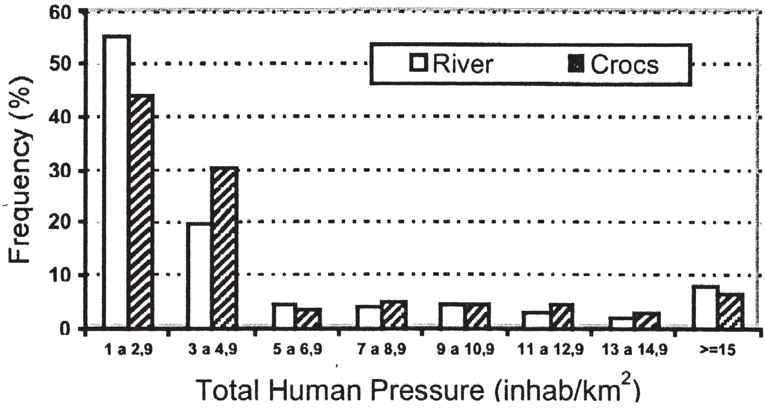


**FIGURE 14.3** Tridimensional representation, generated with the software IDRISIS, of Total Human Pressure (THP) on the Cojedes River System, Venezuela. Areas in clear gray or white are under low human pressure (THP < 2). Different tonalities of gray (elevation) represent the intensity of human pressure, with the highest THP (> 100) in dark gray found in towns and cities represented as plateaus. Acronyms indicate the locations of the river sections surveyed (see fig. 14.1).

According to my hypothesis, crocodile sightings should be more frequent in river spots (pixels) under relatively low THP. An analysis of the distribution of 226 nonhatchling crocodiles spotted in 1996 and 1997, according to the THP of the specific spot where they were observed (fig. 14.4, upper), indicated that, contrary to expectations, crocodiles were underrepresented in river spots (pixels) of very low human pressure (THP ranging from 1 to 2) ($G^2$ = 23.02, P = 0.002). That was a consequence of low densities of crocodiles in SUC and in CUL, the surveyed river



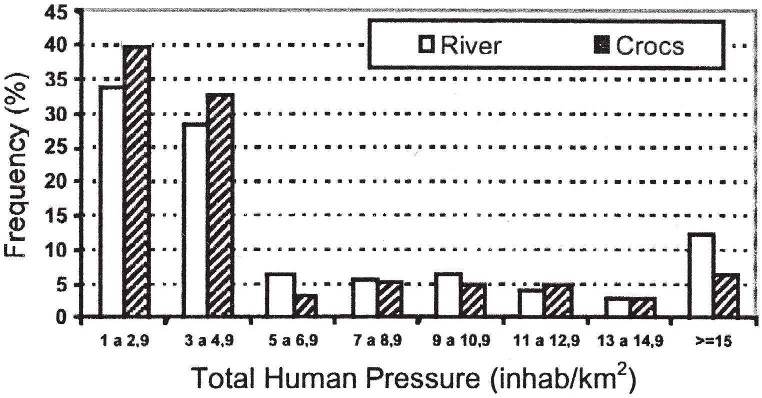


**FIGURE 14.4** Frequency of crocodile sightings compared to the frequency distribution of human pressure in different river sections of the Cojedes River System, Venezuela. Bars labeled river represent percentage of pixels (64 x 64 m) in each range of human pressure (HP) along river sections surveyed. Bars labeled crocs indicate the percentage of crocodiles seen in pixels within a particular range of HP. Upper graph includes all river sections; bottom graph excludes navigable sections.

sections under the lowest THP, whereas crocodile densities were highest in such river sections under moderate THP as CAS (mean THP = 2, range 1 to 6). In contrast to other river sections surveyed, CUL and SUC are navigated year round. When data from these river sections were dropped from the analysis, the frequency distribution of THP of locations of crocodile sightings and THP of river reaches differed in the direction predicted by the hypothesis ($G^2 = 15.42$, $P = 0.03$) (fig. 14.4b). Within the nonnavigable sections crocodile abundances were negatively related to human pressure (Spearman Rho = –0.9, $P = 0.04$, $n = 4$) (fig. 14.5).

Correlation analyses indicate that the variable with strongest relationship to crocodile densities was navigability, but that correlation (negative) was not statistically significant (Spearman Rho = –0.505, $P = 0.248$). The correlation between isolation and crocodile densities was also negative but not significant (Spearman Rho = –0.11, $P = 0.8$), in agreement, as would be expected, with the THP analysis presented above.

## DISCUSSION

Although the isolation of the Cojedes River may have played an important historical role in preserving a small population of Orinoco crocodiles (Ayarzagüena 1987),

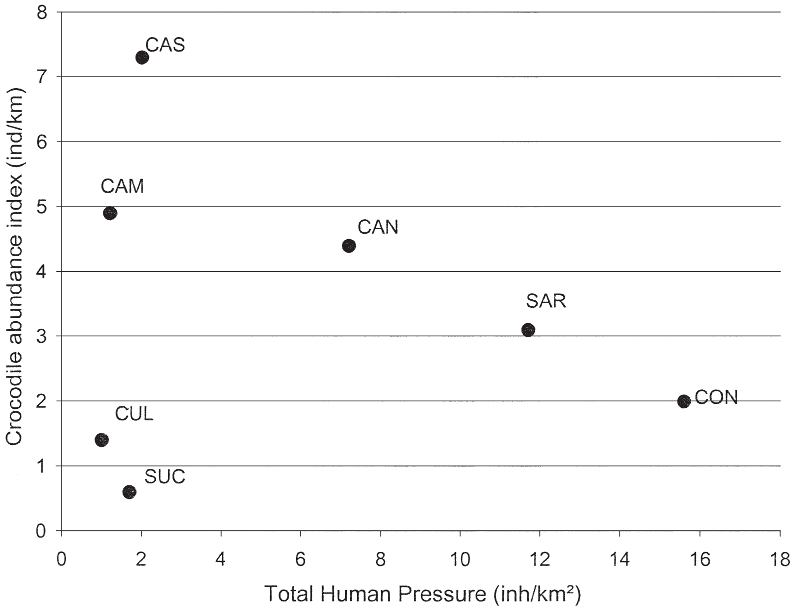


**FIGURE 14.5** Relationship between mean Total Human Pressure (THP) and mean crocodile population index in river sections of the Cojedes River System, Venezuela. La Culebra (CUL) and Sucre (SUC) are the only river sections that are navigable.

today the river sections most isolated from human settlements showed the lowest crocodile densities, whereas the areas with the highest crocodile densities were moderately isolated from urban centers. Low densities of crocodiles in parts of the study area, such as those river reaches close to Sucre or in caño La Culebra, suggest that navigability and difficulty of access are probably important factors explaining the current pattern of distribution of the species in the CRS.

A combination of isolation from humans and impossibility of navigation have been used to explain the persistence of other small population of Orinoco crocodile in the Tucupido River (Ramo and Busto 1986; Thorbjarnarson and Hernández 1992). According to Thorbjarnarson and Hernández (1992) crocodiles in the Capanaparo River are protected during the dry season when low-water levels make it unnavigable.

Proximity to towns and cities seems to explain the abundance and distribution of crocodiles in river sections of the CRS, but future studies should include more river sections under relative high human pressure, such as the upper section of CAN near Cojeditos and some of the Sarare River close to Pimpinela and south to Agua Blanca. In some areas with high THP that were not properly surveyed at night, some crocodiles were observed. Seven crocodiles, for example, were seen on January 14, 1993 in Toma Cojedes, an area with a high THP of 46 to 48. In Retajao, a hamlet along the left margin of CAN, a nesting female and a subadult crocodile were observed in 1996 and 1997. The latter individual was sighted just across the street from an elementary school, a spot with a very high THP of 50.

Anecdotal information indicated that downstream from Sucre, and particularly downstream from El Baúl, where the Cojedes river is routinely navigated by two or three dozen small boats and canoes, Orinoco crocodile populations remain as low as they were almost twenty years ago when first evaluated by Godshalk (1978). Young crocodiles are seen occasionally in the Cojedes River near El Baúl (M. González pers. comm.). They probably represent transient individuals or individuals that have been carried downstream by the river during the peak of the rainy season. Some of these crocodiles are taken by people in El Baúl as pets. Others are presumably killed by fishermen, accidentally or deliberately, or move farther downstream toward the Portuguesa River.

Most reproduction of the Orinoco crocodile in the CRS takes place in the middle sections of Caño de Agua and lower Sarare (Seijas 1998), where the species is protected by the relative isolation from towns and difficulty in navigation. These river sections are population sources, in which more than forty females nest every year (Seijas 1998). My data also indicate that reproduction is poor or absent near Sucre and in La Culebra sections, some 50 or 60 km downstream from the previously mentioned sections. No crocodile nest has ever been observed in that area. Under the current circumstances, because of low reproduction and presumably high risk of being killed by people, the later mentioned river reaches are population sinks for the Orinoco crocodile.

## ACKNOWLEDGMENTS

This study was made possible by a grant from the Wildlife Conservation Society. I thank John Thorbjarnarson from that institution for his continuous support. Satellite images were generously donated by the U.S. Geological Survey (EROS Data Center). Carlos Chavéz assisted me in the field work.

# 15

# Impacts of Damming on Primate Community Sructure in the Amazon

## A CASE STUDY OF THE SAMUEL DAM, RONDÔNIA, BRAZIL

ROSA LEMOS DE SÁ

The importance of tropical rain forests to global biodiversity is clearly appreciated when one realizes that they cover only 7% of the earth's land surface but that they contain more than half the species of the world's biota (Wilson 1988). Despite the importance of tropical forests and the fact that very little is known about their fauna and flora, development of tropical areas is occurring at a rapid pace and will bring about the extinction of species. To avoid mass extinction and to be able to guide developing agencies, a better understanding of the communities and their responses to environmental changes is needed. One increasingly important source of environmental change in the Amazon is the construction of large hydroelectric dams.

Until 1980 only two small hydroelectric dams were operating in the Brazilian Amazon: Curuá-Una, near Santarém, and Paredão in Amapá state. Each dam impacted an area of less than 100 km$^2$ (Junk and Nunes de Mello 1987). Since then, three large dams have been added to the region and are operating in the Amazon: Tucuruí, near Belém; Balbina, near Manaus; and Samuel, near Porto Velho. Collectively, these three dams have flooded an area of 5,350 km$^2$. If Eletronorte (Brazilian Agency for Hydroelectric Power Development in the Amazon region, the government agency responsible for hydroelectric dam constructions in northern Brazil) succeeds in completing all the dams projected for the Amazon in the 2010 plan, an area of roughly 100,000 km$^2$ will be flooded (Fearnside 1989).

The flooding of such large areas has a tremendous impact on humans and wildlife. The most significant effect is the loss of land with its consequent human and animal displacement and/or death that bring about extinction of species (Liao 1988). Eletronorte greatly improved its rescue operation policy between its first rescue at Tucuruí and the effort that took place at Samuel. The new policies of sending the bulk of animals to research institutions rather than releasing all of them and of creating protected areas are commendable changes on the part of Eletronorte. Greater changes, however, must be implemented in order to minimize impact and maximize conservation of the Amazonian region; these changes will require funding for both preliminary and follow-up ecological studies. This article documents the response of mammalian communities to environmental changes resulting from the construction of the Samuel Hydroelectric Dam in the Amazon.

## PROJECT DESIGN

The Samuel Dam is located on the Jamarí river in the state of Rondônia approximately 50 km east of the state's capital of Porto Velho (fig. 15.1). Construction on the dam began in 1982, actual filling of the reservoir in 1988, and completion in 1989. The total lake area is 502 km$^2$, of which 22 km$^2$ remained green in the form of islands (measured from landsat images 1:250,000 by Adolfo de La Pria Pereira, SEDAM-RO).

Two sites were monitored for this study, which I will refer to as the Reserve and Jusante. Prior to the filling of the reservoir, Eletronorte created a 21,000-ha ecological reserve (Estação Ecológica de Samuel) to compensate for the loss of 56,000 ha of forest flooded by the reservoir. This Reserve is located east of the reservoir's embankment, approximately 26 km from the dam, and its forests are continuous with those of the reservoir area. During the rescue operation, from November 1988 to March 1989, 2,374 mammals were released inside the Reserve (Eletronorte 1989).

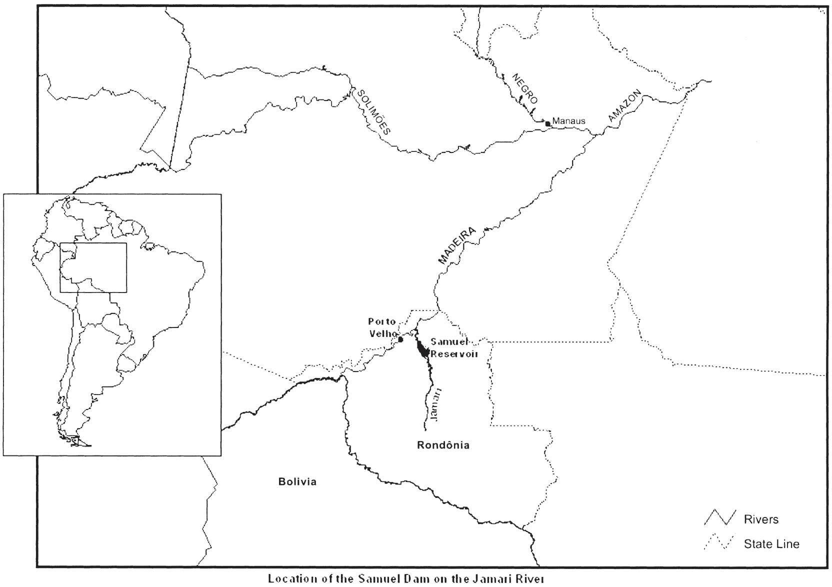


**FIGURE 15.1** Location of Samuel Dam.

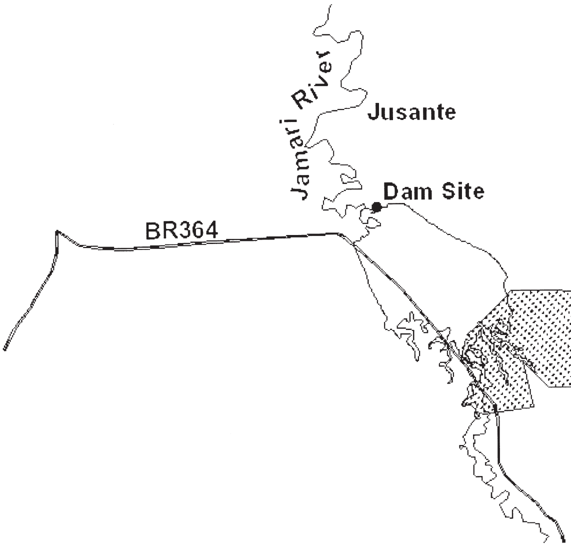


**FIGURE 15.2** Location of Reserve and Jusante study sites with reference to Samuel Dam. The size of the reserve was increased in 1994 to 74,300 thousand hectares, up from the original 21,000 ha established at the time the dam was built.

The site was monitored during 1988 (before the flooding of the reservoir), 1989, 1990, and 1991. Monitoring in 1988 was carried out by Eletronorte personnel, not by the author. The second site, Jusante, was an undisturbed area located downstream from the dam on the right bank of the Jamarí river (fig. 15.2). It was monitored during the 1990 and 1991 field seasons. No animals were released into the site.

Before flooding, the area was undisturbed primary forest with little or no hunting pressure. The forests at both sites were continuous with the flooded area but presented some structural and floristic differences. Compared to Jusante, the Reserve had a higher and denser canopy, and greater basal area and tree density for trees than 30 cm. Adult *Bertholletia excelsia* (Brazil nut), and *Orbignya barbosiana* (babaçu) were very common at the Reserve but rare at Jusante. On the other hand, *Hevea brasiliensis* (seringueira) was very common at Jusante but never seen at the Reserve; the latter observation was expected because this particular species is known to occur along water courses and not in terra firme. Differences in elevation support the idea that the forest at Jusante (at lower elevation) is younger, probably because of disturbance effects related to its proximity to the river. The more open forest at Jusante allows for greater penetration of light, providing an opportunity for shrub and liana species to develop and creating a forest floor more densely covered by vegetation.

My hypothesis at the beginning of this study was that the mammalian community in the Reserve study site could have been affected by the release of rescued animals, by the migration of animals fleeing from the flooded reservoir, or by a combination of the two. The Jusante site, on the other hand, could only have been affected by the migration of animals from the reservoir area or not affected at all. More specifically, I hypothesized that the Reserve would experience animal overcrowding for an undetermined length of time, possibly surpassing the carrying capacity for the area. My hypothesis could be tested by estimating mammalian densities in the Reserve at different points in time and by examining differences in biomass values for the community.

If my assumptions were correct, the noted responses in density changes, regardless of site, would be immediate in the case of terrestrial mammals (because they would have to flee from the rising water) but possibly delayed for arboreal species (because they could stay on top of trees while the vegetation was still alive). The time frame in which density changes would occur was unknown. To increase the probability of detecting such changes (completely or partially), the sites were sampled repeatedly.

## METHODS

Five plots of 1 $km^2$ were established in the Reserve in 1989, and three plots at Jusante in 1990 (fig. 15.2), creating 4 km of transect lines along each plot's perimeter. Transect surveys were conducted by walking slowly (1 km/h) and by stopping periodically to watch and listen for animals. Transects were conducted between 6:30 and 7:00 A.M. (depending on the time of sunrise), 10:30 and 11:00 A.M., and 1:00 and 5:00 P.M. The number of transect samples in each area was divided equally between morning and afternoon surveys. Whenever possible, different transects were walked in the morning and afternoon of the same day. If that were not possible because of logistics, the two daily surveys of a plot always began in the same direction to give an interval of six hours between the morning and the afternoon survey (i.e., the same point in the trail would be traversed in the afternoon six hours after the morning survey). Transect surveys on different days began at opposite ends of the route to reduce potential biases resulting from direction of travel by the observer. Each transect had equal numbers of surveys originating in both directions. The time, transect identification, location on the trail, species, number of individuals sighted, angle of sighting, and distance from the observer to the animal when first seen was recorded for every nonvolant mammal encountered. Surveys were conducted by myself, an undergraduate student as an assistant, and two local field helpers. All medium- to large-sized mammals were recorded (Lemos de Sá 1995), but only primate data are analyzed in this paper.

Transects were surveyed for ten days each month from May to August 1989 and from May to October of 1990 and 1991. These months correspond to the dry season in the region. During 1989, because of logistical problems and to the lesser amount of time spent at the study site, data were gathered only at the Reserve and not at Jusante. Two of the five plots sampled in 1989 in the Reserve were abandoned in 1990 and 1991, again because of logistical difficulties. However, observations collected in these areas were included in the 1989 analysis to arrive at a density estimate for the entire site. Data from the various plots at a site were pooled within years to give an overall density estimate.

## DATA ANALYSIS

Data were analyzed using the computer program TransAn, version 1.00, which is a flexible computer program that uses a nonparametric, shape-restricted, density estimator (Payne 1992). The shape-restricted estimator, first introduced by Johnson and Routledge (1985) and later modified by Fyfe and Routledge (1991), involves modeling the probability of detecting an individual as a function of its perpendicular distance from the transect line. TransAn requires sightings from at least four independent transect lines to calculate confidence limits. Because I had only three transects per study site, the data were divided between morning and afternoon transects to increase the number of transects to six (for the 1989 data the total number of transects was ten because there were five different plots at the Reserve). Despite inherent biases, the transect censuses are currently the most cost-effective method to evaluate large mammal densities in rainforests (Emmons 1984).

## RESULTS

### PRIMATE SPECIES OBSERVED

Eight primate species were recorded in all years at both the Reserve and Jusante. They were *Aotus azare*, *Callicebus bruneus*, *Pithecia irrorata*, *Cebus apella*, *Saimiri ustus*, and *Ateles paniscus* in the Cebidae and *Callithrix emiliae* and *Saguinus fuscicollis* in the Callithrichidae.

### PRIMATE DENSITY ESTIMATES PRIOR TO DAMMING

Primate censuses were performed at the Reserve by Eletronorte researchers from September 1987 to February 1988 (table 15.1). Note that *Saimiri ustus* was not recorded at that time. Density estimates were based on 145 km of transect surveys. Techniques used were comparable to the ones used in this study (National Research Council 1981).

Primates represented 48.4% (n = 1,806) of all mammals captured and 47% (n = 1,352) of all animals released during the rescue/release operation (Eletronorte 1989; table 15.2). This was a relatively small number and probably had an insignificant effect on most density shifts during the years following flooding.

### PRIMATE DENSITY ESTIMATES AFTER DAMMING

Primate densities (ind/km$^2$) were estinated by calculating group density and multiplying by mean group size (table 15.3). Figures 15.3 and 15.4 summarize group den-

**TABLE 15.1** Primate Density Estimates at the Samuel Reserve Prior to the Flooding of the Reservoir

| SPECIES | D | MGS | IND/KM$^2$ |
|---|---|---|---|
| *Ateles paniscus* | 2.60 | 5.2 | 13.5 |
| *Cebus apella* | 4.02 | 5.4 | 21.7 |
| *Pithecia irrorata* | 1.38 | 3.8 | 5.2 |
| *Callicebus bruneus* | 0.26 | 2.6 | 0.7 |
| *Saimiri ustus* | — | — | — |
| *Saguinus fuscicollis* | 2.00 | 8.5 | 17.0 |
| *Callithrix emiliae* | 0.36 | 15.0 | 5.4 |

*Note:* D equals group density (km$^2$) and MGS mean group size (Eletronorte 1988). Saimiri were not recorded during the 1988 censuses.

**TABLE 15.2** Number of Primates Captured at the Samuel Dam Reservoir and Number of Primates Released at the Samuel Ecological Station

| SPECIES | NUMBERS CAPTURED | NUMBERS RELEASED |
|---|---|---|
| *Aotus* | 104 | 60 |
| *Ateles* | 35 | 35 |
| *Callithrix* | 71 | 42 |
| *Saguinus* | 171 | 76 |
| *Cebus* | 207 | 180 |
| *Callicebus* | 348 | 309 |
| *Pithecia* | 369 | 324 |
| *Saimiri* | 501 | 326 |
| ***Total*** | 1,806 | 1,352 |

*Source:* Eletronorte 1989.

sity changes at the Reserve and Jusante, respectively. Densities of *Ateles*, *Callithrix*, and *Saimiri* at the Reserve were high in 1990 and lower and approximately equal in 1989 and 1991. *Cebus* and *Saguinus* densities were also high in 1990 in the Reserve; however, their densities in 1991 remained high and similar to the 1990 densities instead of returning to values comparable to 1989. The densities of *Callicebus* and *Pithecia* in the Reserve were at their highest in 1989 and decreased steadily through 1990 and 1991(table 15.3, fig. 15.3). With the exception of *Pithecia*, whose density was similar in 1990 and 1991, all other primate densities decreased substantially from 1990 to 1991 at the Jusante site (table 15.3; fig. 15.4).

**TABLE 15.3** Primate Density Estimates at the Reserve and at Jusante Sites for 1989, 1990, and 1991

| SPECIES | SITE | YEAR | N | D | MGS | IND/KM$^2$ | 95% DCI |
|---|---|---|---|---|---|---|---|
| *Ateles paniscus* | Reserve | 89 | 27 | 3.15 | 4.2 | 13.2 | 1.53–07.43 |
| | Reserve | 90 | 72 | 6.06 | 3.9 | 23.6 | 3.95–09.91 |
| | Reserve | 91 | 66 | 3.69 | 3.0 | 11.1 | 2.14–07.06 |
| | Jusante | 90 | 04 | 0.60 | 9.8 | 5.9 | 0.17–02.63 |
| | Jusante | 91 | 01 | — | 1.0 | — | — |
| *Cebus apella* | Reserve | 89 | 54 | 5.42 | 3.7 | 20.1 | 3.21–09.22 |
| | Reserve | 90 | 71 | 6.63 | 4.3 | 28.5 | 4.15–10.31 |
| | Reserve | 91 | 72 | 6.45 | 4.2 | 27.1 | 4.01–10.32 |
| | Jusante | 90 | 32 | 2.92 | 6.0 | 17.5 | 1.59–06.15 |
| | Jusante | 91 | 27 | 2.12 | 3.8 | 8.1 | |
| *Pithecia irrorata* | Reserve | 89 | 33 | 3.43 | 3.0 | 10.3 | 1.76–06.59 |
| | Reserve | 90 | 17 | 2.07 | 2.5 | 5.2 | 0.75–05.06 |
| | Reserve | 91 | 12 | 1.17 | 3.0 | 3.5 | 0.35–02.49 |
| | Jusante | 90 | 21 | 2.60 | 2.9 | 7.5 | 1.16–05.57 |
| | Jusante | 91 | 16 | 2.38 | 3.2 | 7.6 | 1.08–06.39 |
| *Callicebus bruneus* | Reserve | 89 | 15 | 3.61 | 2.0 | 7.2 | 1.57–08.34 |
| | Reserve | 90 | 05 | 0.83 | 1.6 | 1.3 | 0.20–03.03 |
| | Reserve | 91 | 09 | 0.62 | 2.0 | 1.2 | 0.24–01.74 |
| | Jusante | 90 | 59 | 8.33 | 2.4 | 20.0 | 4.77–14.72 |
| | Jusante | 91 | 39 | 4.85 | 2.4 | 11.6 | 2.49–09.89 |
| *Saimiri ustus* | Reserve | 89 | 08 | 0.91 | 7.6 | 6.9 | 0.25–02.43 |
| | Reserve | 90 | 05 | 3.68 | 7.8 | 28.7 | 0.89–05.68 |
| | Reserve | 91 | 12 | 1.41 | 6.3 | 8.9 | 0.49–03.64 |
| | Jusante | 90 | 15 | 1.69 | 14.1 | 23.8 | 0.62–04.55 |
| | Jusante | 91 | 09 | 0.75 | 8.0 | 6.0 | 0.29–02.58 |
| *Saguinus fuscicollis* | Reserve | 89 | 14 | 1.85 | 3.3 | 6.1 | 0.71–03.88 |
| | Reserve | 90 | 24 | 4.08 | 3.5 | 14.3 | 1.92–09.18 |
| | Reserve | 91 | 20 | 3.70 | 3.8 | 14.1 | 1.51–06.53 |
| | Jusante | 90 | 34 | 5.83 | 3.5 | 20.4 | 2.88–11.23 |
| | Jusante | 91 | 28 | 3.67 | 3.7 | 13.6 | 1.74–07.79 |
| *Callithrix emiliae* | Reserve | 89 | 10 | 1.41 | 2.9 | 4.1 | 0.38–03.82 |
| | Reserve | 90 | 15 | 3.06 | 3.3 | 10.1 | 1.31–06.69 |
| | Reserve | 91 | 09 | 1.82 | 2.0 | 3.6 | 0.74–06.00 |
| | Jusante | 90 | 20 | 3.13 | 2.9 | 9.1 | 1.34–05.97 |
| | Jusante | 91 | 07 | 0.91 | 3.1 | 2.8 | 0.28–03.75 |
| ***Total*** | Reserve | 1989 | 161 | 17.59 | 3.6 | 63.3 | 13.86–22.81 |
| | Reserve | 1990 | 209 | 23.25 | 3.9 | 90.7 | 18.92–29.02 |
| | Reserve | 1991 | 200 | 18.03 | 3.6 | 64.9 | 13.71–23.68 |
| | Jusante | 1990 | 185 | 24.51 | 4.4 | 107.8 | 17.62–33.46 |
| | Jusante | 1991 | 127 | 13.83 | 3.5 | 48.4 | 8.86–23.14 |

*Note:* N equals number of sightings of groups; D, group density; and MGS, mean group size (based on total number of individuals sighted and total number of sightings per year).

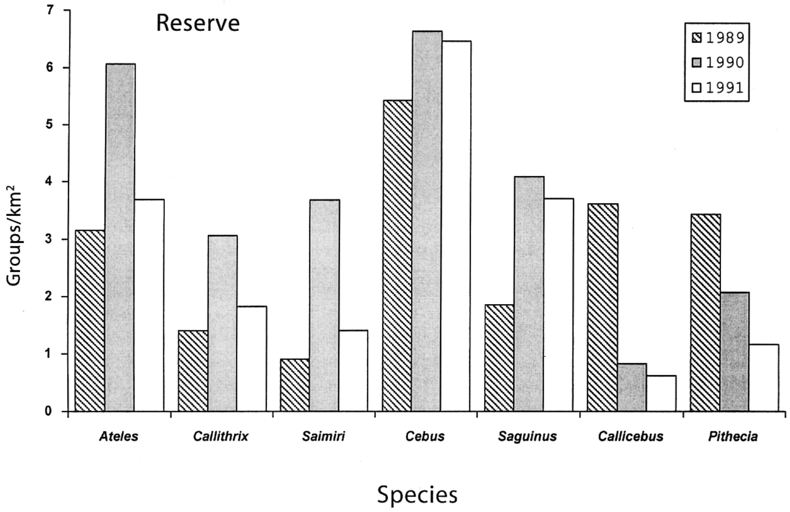


**FIGURE 15.3** Primate densities at the Samuel Ecological Station (groups/km$^2$).

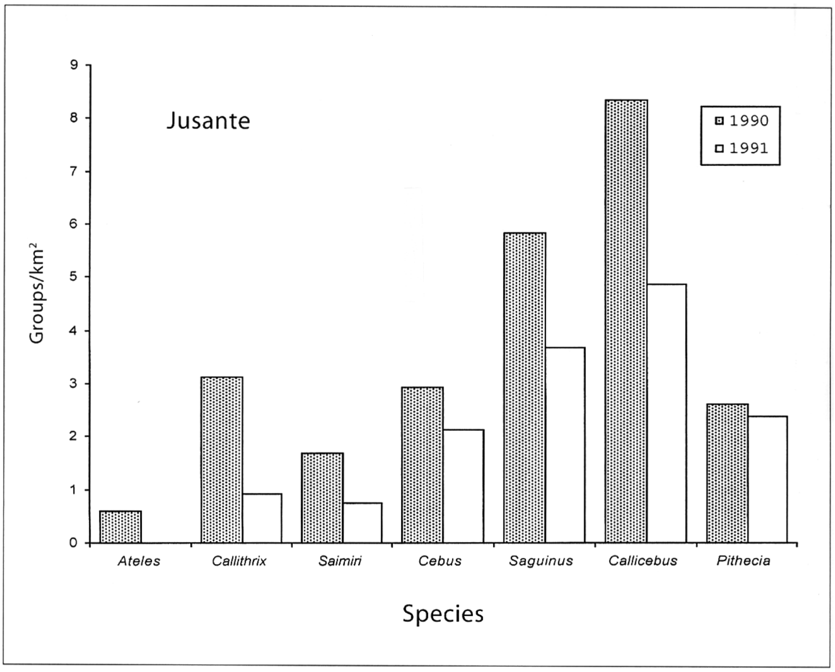


**FIGURE 15.4** Primate densities at the Jusante site (groups/km$^2$).

## TOTAL PRIMATE DENSITY ESTIMATES

Primates at the Reserve comprised 61% of all mammalian sightings in 1989, 69% in 1990, and 68% in 1991. When data for all primates are pooled and density estimates are calculated for the area as a whole, the result shows a 32% increase in group density from 1989 to 1990 and a 23% decrease from 1990 to 1991 (table 15.3).

Primates at Jusante comprised 71 and 58.5% of all mammal sightings for 1990 and 1991, respectively. Primate group density for the area as a whole decreased 44% from 1990 to 1991 (table 15.3). Even though a decrease in primate density occurred in both areas from 1990 to 1991, the decrease at Jusante was almost twice that of the Reserve. The changes in densities of ind/km$^2$ show the same pattern as the group density changes; however, Jusante shows a more abrupt reduction in total number of individuals than the Reserve (table 15.3).

## DENSITY CHANGES BETWEEN YEARS AT THE RESERVE

A cluster analysis comparing density results for all four years of data for the Reserve shows that the 1988 densities had only a 25.27 degree of similarity with the 1989 densities (all comparisons excluded *Saimiri* because this species was not recorded during 1988). The 1990 community still only shows a 27.94 degree of similarity with 1988. By 1991 the degree of similarity with the 1988 community increased to 61.92 (fig. 15.5).

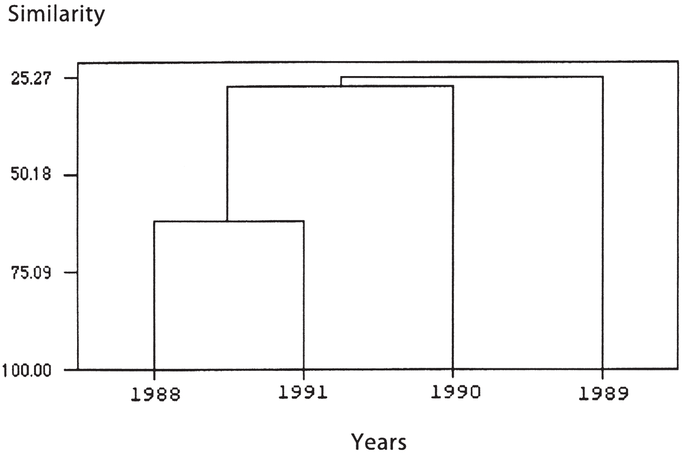


**FIGURE 15.5** Cluster analysis for all four years of density data at the Reserve. Similarity levels = 61.92, 27.94, and 25.27, respectively (Minitab 10, Hierarchical cluster analysis of observations).

## DISCUSSION AND CONCLUSION

The results suggest that the environmental changes created by the construction of the dam temporarily altered the mammal community in the areas adjacent to the reservoir. Degree of fluctuations in population levels for individual species varied, as did the persistence of the changes in population levels. Some of these differences can be explained by the interactions among the different species as well as by their autoecology.

### PRIMATE DENSITY ESTIMATES: RESERVE

Three different patterns can be seen with primate density changes at the Reserve (fig. 15.3). The first one, seen with *Ateles*, *Callithrix*, and *Saimiri*, is a large increase in density from 1989 to 1990 and then a sharp decrease in 1991, returning to density levels similar to those found in 1989. The second pattern, which involves *Cebus* and *Saguinus*, also involves an increase in density from 1989 to 1990; however, the 1991 densities remain high. The third pattern is very different, with the densities of *Callicebus* and *Pithecia* being at their highest in 1989 and declining in 1990, and 1991.

The increase in densities from 1989 to 1990 can be explained by the migration of animals from the reservoir into the Reserve. Sixty percent of the reservoir is, on average, only 3.5 m deep in water, which allowed several arboreal species to survive for at least eight months after the flooding began. I observed flowering and fruiting trees inside the reservoir in August 1989 (five months after the completion of the filling of the reservoir). Child (1968) observed the same phenomenon during the formation of Lake Kariba as a result of the impoundment of the Zambezi river in Zimbabwe. At Lake Kariba species had different survival times that varied from four to twelve months. Child also observed that "most species standing in water came into leaf and/or remained in leaf until they died" (Child 1968:37).

Because primates spend most of their time in the middle to upper forest strata, it is reasonable to assume that the majority of the primate population was still living inside the reservoir when the 1989 survey was carried out at the Reserve. This assumption is supported by the relatively low number (1,806) of primates captured during the rescue operation in a 56,000-ha area (0.03 ind/ha) (Eletronorte 1989). In contrast, at the Tucuruí Dam site (which has a much deeper reservoir), a total of 27,039 primates were captured in a 243,000-ha area (0.11 ind/ha) (Eletronorte 1985).

When I arrived at the Samuel Dam in May 1990 all vegetation inside the reservoir was dead. The only exception was in the higher elevation lands, which formed green islands inside the reservoir. Because the reservoir is bordered by dikes on both sides and by a paved highway on the left river bank, the Reserve constituted a natural escape route for displaced animals (figs. 15.1 and 15.2). Thus the increase in primate densities in the Reserve was likely a result of the natural migration of animals between August 1989 and May 1990, caused by the loss of habitat inside the reservoir.

This scenario does not explain the third pattern of density changes detected in *Callicebus* and *Pithecia*, whose population declined steadily after 1989. However, *Callicebus*, *Pithecia*, and *Saimiri* were the most frequently captured species, with over 300 individuals released (table 15.2). This suggests that the 1989 census in the Reserve documented the density increase in these species as a result of the release operation. This argument is even more convincing when density estimates from the preflooding study done in 1988 (Eletronorte 1988), are examined. Densities for all three species prior to flooding were much lower than the ones found in 1989.

The densities for *Ateles* and *Saguinus* in the Reserve were almost identical in 1988 and 1989. Because only a few individuals were released in the Reserve, there was no reason to expect otherwise. The higher 1989 estimates for *Saimiri*, *Callicebus*, *Pithecia*, and to some extent, *Cebusi* reflect the increase in density caused by the released animals. Because my study began only two months after the release was completed, it is reasonable to assume that the animals were still inside the Reserve, and that is why the 1989 densities were higher than those in 1988. As for *Callithrix*, the difference between the 1988 and 1989 densities may be a reflection of the species characteristics. *Callithrix* are among the most cryptic primates, in both pelage and habitat (Ferrari and Rylands 1994), making them difficult to detect during transect samples. Because the 1988 censuses were not performed by my team, their low density might be a consequence of differences in researcher's detection ability. Despite having similar body weight, the same detectability differences do not apply to *Saguinus*, which tend to use lower strata of the forest (Ferrari and Rylands 1994) and are therefore more visible during a census.

The decline in density estimates in 1991 for all species is most likely a consequence of the dispersal of animals to adjacent areas or to death. The Reserve is located adjacent to an area of continuous forest without human inhabitation or access roads (fig. 15.2), and dispersal into those areas would be the expected behavior for overcrowded animals. Because the rescue operation only removed a small fraction of the animals, the waters did not cover the tree tops and because there was no incidence of high primate mortality inside the reservoir, I can reasonably state that the animals moved into adjacent areas. Together with data on biomass (Lemos de Sá 1995), this dispersal out of the reserve implies that the Reserve was already at carrying capacity for these primate species. Not only does this information allow us to predict impacts of future reservoirs, it also gives us baseline data on carrying capacities for primates in an unhunted lowland Amazonina site, data which can be used in studies that model sustainable harvests of primates at other Amazonian sites (Bodmer and Robinson this volume).

## PRIMATE DENSITY ESTIMATES: JUSANTE

There was a sharp decline in density (between 37 and 71%) from 1990 to 1991 at Jusante for all primates, except *Pithecia* (fig. 15.4). The decline in density is not very apparent for *Cebus* and *Saimiri* if we only consider the number of groups per km$^2$, however, these two species showed drastic reduction in mean group sizes over the years (table 15.3). Richard-Hansen, Vié, and de Thoisy (2000) documented extensive fragmentation of troops for translocated *Alouatta seniculus* in French Guiana, attributing this reduction in group size to stress, interactions with resident animals, and lack of familiarity with the new environment, among other factors. A similar situation may have occurred with the naturally migrating primate groups in this study. Hence, if we consider the decline in the number of individuals per km$^2$, both species also show drastic decreases in densities from 1990 to 1991.

Even though there was no sampling at Jusante during 1988 or 1989, it is logical to assume a similar effect on primate communities in both areas as a consequence of the creation of the reservoir, that is, the 1990 densities were artificially high because of an influx of animals after creation of the reservoir. A buffer area for the protection of the dam turbines was created inside the reservoir by clear cutting the forest closest to the dam, which together with several construction projects and the concentration of human activities near the dam could have inhibited animal migration to Jusante. However, migration did occur, probably because of the sheer proximity of the area to the reservoir (animals stranded inside the reservoir near the dam could probably see green forest on the other side) (fig. 15.2).

Despite the lack of data for Jusante in 1989, density estimates for six of the seven primates sampled at Jusante most likely fit the first pattern of density change described for primates at the Reserve (density increase in 1990, followed by a sharp decrease in 1991). The seventh species, *Pithecia*, fits the second pattern of density change (density stays at similar levels from 1990 to 1991). Because no data exist for 1989, it is not possible to determine if the third pattern described at the Reserve (a continued decrease in density) was present at Jusante. However, because the explanation given for this pattern in density change was the active release of animals in the Reserve, such pattern would not be expected to appear at Jusante.

## SPECIES-SPECIFIC RESPONSES

Differences in crude densities and in the degree of density decline among species and sites are most likely the result of differences in species behavior and/or habitat requirements.

**Ateles** *Ateles* are frugivore-herbivores (Eisenberg 1981; Robinson and Redford 1986a, 1989), with 83 to 90% of their diet consisting of fruits and the remainder of other plant parts (van Roosmalen and Klein 1988). Because the distribution of fruits in a forest is widely scattered, *Ateles* density is probably restricted by the availability of this food type (Robinson and Ramirez 1982). Home-range size increases as group weight increases (Eisenberg 1979), and *Ateles* are the largest of all primates in the area requiring, in Surinam, 12.2 ha per individual (van Roosmalen 1980; Robinson and Janson 1987). The new arrivals at the Reserve were most likely displaced to areas outside the Reserve by the resident groups because of the unavailability of fruit crops large enough to maintain the higher population density.

Their almost complete absence from Jusante can be explained by the fact that they are restricted to or occur in higher densities only in primary forest, using upper levels of canopy and emergent trees (Mittermeier and van Roosmalen 1981; Robinson and Ramirez 1982; van Roosmalen and Klein 1988). Because the forest at Jusante has a lower, more open canopy with fewer emergent trees than the Reserve, it is not surprising to find that the Reserve represented a more suitable habitat for the species.

**Callithrix** *Callithrix* are insectivore-omnivores, with more than 50% of their diet consisting of invertebrates (Eisenberg 1981; Robinson and Redford 1986a, 1989). They are also adapted to feed on plant exudates at certain times of the year in order to compensate for seasonal scarcities in the availability of fruits (Ferrari and Lopes Ferrari 1989; Ferrari 1993; Rylands and Faria 1993). They attain highest densities in second growth forest and edge habitat.

*Callithrix* species tend to have larger group sizes and smaller home ranges than *Saguinus* species and generally occur at higher densities (Ferrari and Lopes Ferrari 1989; Rylands and Faria 1993). Average group size and densities of *Callithrix* in both of my study sites were lower than those of *Saguinus* (table 15.3), in contrast to previous studies. This difference may be partly a consequence of their cryptical nature, as described earlier.

**Saimiri** *Saimiri* are classified as frugivore-omnivores, with more than 50% of their diet composed of fruits and the remainder mostly of invertebrates and vertebrates (Eisenberg 1981; Robinson and Redford 1986a, 1989). They are habitat specialists, typical of flooded and riverine forests (Eisenberg 1979; Freese et al. 1982; Rylands and Keuroghlian 1988). The species is known for its preference for more open, secondary habitats, and they are most often encountered in liana forests (Mittermeier and van Roosmalen 1981; Johns and Skoruppa 1987). Neither of the study sites, the Reserve or Jusante, included flooded forests. Although the Jusante site is closer to the Jamarí river and has a more open forest structure, transect censuses started at a distance of 500 m away from the river's edge. Therefore high densities of *Saimiri* were not expected at either site. The high densities in the Reserve in 1990, as well as the very high number of individuals per km$^2$ at Jusante (due to a larger mean group size; table 15.3), probably occurred when animals living along the Jamarí river inside the reservoir moved to these areas in search of new suitable habitat. Because neither area is suitable habitat, the animals most likely dispersed along the Jamarí river, causing the density decrease seen in 1991.

**Cebus** *Cebus* are also classified as frugivore-omnivores, with more than 50% of their diet composed of fruits and the remainder mostly of invertebrates and vertebrates (Eisenberg 1981; Robinson and Redford 1986a, 1989). The species has a broad habitat tolerance (Eisenberg 1979). *Cebus* are opportunistic and usually well able to persist in disturbed forest (Johns and Skoruppa 1987), an ability that makes them the most adaptable primate species in the Neotropics (Mittermeier and van Roosmalen 1981). It is not surprising then that they were able to maintain high population density in the Reserve.

The reduction of 54% in the number of individuals estimated per km$^2$ at Jusante from 1990 to 1991 (table 15.3) seems inconsistent with their ecology. However, because Palmae species were more abundant in the Reserve than at Jusante and because *Cebus apella* rely heavily on palms in a number of different ways (insect foraging, fruits, seeds, flowers, and many other plant parts) (Mittermeier and van Roosmalen 1981; Terborgh 1983)), it is possible that the carrying capacity for the species is higher at the Reserve than at Jusante.

**Saguinus** *Saguinus* is classified as insectivore-omnivore, with more than 50% of their diet consisting of invertebrates (Eisenberg 1981; Robinson and Redford 1986a, 1989). According to Rylands and Keuroghlian (1988), optimal habitat for this species includes secondary forest and forest edge mixed with tall primary forest. Several studies have shown that the species occurs in greater densities in secondary forest near natural clearings than in mature forest (Eisenberg and Thorington 1973; Mittermeier and van Roosmalen 1981; Robinson and Ramirez 1982; Johns and Skoruppa 1987). Emmons (1984) concluded that *Saguinus* density appeared to have increased in some areas where large monkeys had been exterminated. *Saguinus* also overlap with *Cebus* in most habitat and diet categories (Mittermeier and van Roosmalen 1981). The lower densities of *Ateles* and *Cebus* at Jusante and the increased edged habitat at the Reserve created by the reservoir were most likely favorable factors influencing the maintenance of high *Saguinus* densities at both sites in 1990 and 1991.

**Callicebus** *Callicebus* is also classified as frugivore-omnivore, with more than 50% of its diet composed of fruits and the remainder mostly of invertebrates and vertebrates (Eisenberg 1981; Robinson and Redford 1986a, 1989). The species occurs in greatest densities in areas characterized by forest openings with early successional vegetation, spending more time in the lower canopy levels and understory vegetation (Kinsey 1981; Terborgh 1983; Robinson and Redford 1986a; Robinson, Wright, and Kinzey 1987). The more open vegetation at the Jusante site most likely created a more suitable habitat for *Callicebus* than in the Reserve, a possible explanation for their much higher densities at Jusante (figs. 15.3 and 15.4).

Interference competition with *Cebus* might also affect *Callicebus* densities. Both species are catholic in their diet, however, *Cebus* generally have larger group size and are more aggressive during interspecific encounters, possibly displacing *Callicebus* groups from feeding trees. According to Emmons (1984), troops of larger monkeys, such as *Cebus*, physically prevent access to fruit sources by small ones, such as *Saguinus* and *Callicebus*. The lower densities of *Cebus* at Jusante might benefit *Callicebus*, affecting their population positively.

**Pithecia** *Pithecia* are also frugivore-omnivores, with more than 50% of their diet composed of fruits and the remainder mostly of invertebrates and vertebrates (Eisenberg 1981; Robinson and Redford 1986a, 1989). They are usually found in the understory and lower to middle parts of the canopy (Mittermeier and van Roosmalen 1981), and they occur in gallery and both primary and secondary forest (Robinson and Ramirez 1982). *Pithecia* are always rare (Mittermier and van Roosmalen 1981; Robinson, Wright, and Kinzey 1987; Rylands and Keuroghlian 1988), despite the fact that they have no distinct habitat preference. However, their rarity may indicate that they are specialists within the forest they occupy or at least dependent on certain floristic communities (Rylands and Keuroghlian 1988). According to Johns and Skoruppa (1987), *Pithecia* are able to feed on fruits from some of the early colonizing trees, an ability that might explain their higher densities at Jusante.

## DENSITY CHANGES BETWEEN YEARS AT THE RESERVE

The low degree of similarity between the 1988 and 1989 densities (fig. 15.5) was most likely due to the increased densities of *Pithecia* and *Callicebus* as a result of both the release of captured animals and the movement of free-ranging individuals into the area. The 1990 community still shows a low degree of similarity with that of 1988, possibly due to the increase in densities as a consequence of the heavy migration of animals to the Reserve. By 1991 the degree of similarity with the 1988 community increased to 61.92. The community seems to be in the process of returning to its original community structure (fig. 15.5).

## TOTAL DENSITY

Estimates of total primate density show a general trend of density increase from 1989 to 1990 and then a decrease in 1991 (table 15.3). These changes are consistent with the assumption that the animals inside the forests of the reservoir moved to both study sites between August 1989 and May 1990 and then dispersed to adjacent forest between November 1990 and May 1991. Even though 1989 data for Jusante do not exist, I suspect that the total 1989 primate density for Jusante was, like the Reserve, similar to its 1991 estimate.

The sharper density decrease at Jusante is most likely related to lower capacity of the forest to support high primate densities. This is perhaps most obvious for *Cebus*, whose density remained at high levels in the Reserve but decreased drastically at Jusante (table 15.3). Because mean group size for *Cebus* and *Saimiri* at Jusante was much higher in 1990 than in 1991, the number of individuals per km$^2$ shows a more abrupt decline in density than the group density.

## CONCLUSIONS AND IMPLICATIONS FOR FUTURE DAMS

The cost-benefit ratio of rescue operations need to be reevaluated before future rescue operations are initiated. The rationale behind rescue operations has always been to save animals from unquestionable death. However, animal mortality at hydroelectric dam sites is related more to loss of habitat than to drowning. Several large mammals have relatively good swimming capabilities (Child 1968), birds may fly away, and amphibians and some reptiles may survive by swimming to dry land. On the other hand, habitat loss, measured by square kilometers flooded, is irreversible. Kariba reservoir flooded an area of 5,462 km$^2$ (ironically enough, its rescue operation captured the least total number of animals), Brokopondo 1,683 km$^2$, Tucuruí 2,430 km$^2$, Balbina 2,600 km$^2$, and Samuel, the smallest of all, 560 km$^2$.

Furthermore, animals captured during rescue operations are usually released on the nearest piece of dry land, without any concern for the animal community inhabiting the area of release. My results on primate density changes at the Samuel release site demonstrated not only that they can move from the flooded area on their own but also that the site's carrying capacity will determine if they will stay on the release area or not. Of the 3,729 mammals rescued from the Samuel reservoir, only 2,374 were released (1,352 of these were primates). The movement of animals after the flooding confirmed that primates can move on their own (provided that the filling of the reservoir does not cover the tree tops).

Rescue operations have become a public relations strategy used by power companies to appease public opinion. The only way to make power companies change their policies is to inform the public and to give power companies better options for rescue/conservation programs. Some suggestions for future rescue programs are listed below:

1. Rescue operations should be confined to (a) species known to be endangered and/or vulnerable should be rescued when stranded; (b) species that are unable to escape their flooded environment; sometimes females with infants are trapped on small islands unable to swim with their young; (c) species that could be used for research; and (d) species that could be used for reestablishing depleted populations elsewhere; some areas in the Amazon have been heavily hunted, and large species are sometimes rare.
2. Animals should only be released on sites that have been studied previously and that have abnormally low densities, such as heavily hunted sites.
3. The practice, established at Balbina, of donating rescued animals to research in-

stitutions should be continued. If rescued animals are used to supply research institutions, there will be a decrease in the number of wild animals removed from other sites for research purposes.

4. Protected areas should be created to compensate for the habitat loss due to the construction of reservoirs.
5. Companies should invest in professional staff to design, conduct, and supervise conservation program at dam sites.

# 16

# Niche Partitioning Among Gray Brocket Deer, Pampas Deer, and Cattle in the Pantanal of Brazil

LAURENZ PINDER

The global introduction of domestic livestock into tropical savannas and temperate prairie ecosystems has raised debates about the conservation and management implications of these introductions on wildlife, in particular on native ungulates. In addition to the obvious impact caused by the introduction of extraneous pests and diseases on native ungulate populations, there is evidence that dietary overlap with livestock may derive positive or negative implications to the coexisting herbivores. For instance, seasonal grazing by livestock may improve the nutritive quality of autumn and winter browse for wild ungulates (Alpe, Kingery, and Mosley 1999). On the other hand, vegetation modification and overgrazing of shared scarce food items potentially causes a decrease of food availability for native species (Murray and Illius 2000; Puig et al. 2001).

Despite the fact that more and more savannas and prairies are encroached and replaced by agriculture and introduced pastures, extensive areas of South America still harbor a rich diversity and abundance of wildlife in coexistence with centuries-old extensive ranching on native pastures. In seasonally flooded plains, such as the Venezuelan Llanos and the Brazilian Pantanal, this long-lasting coexistence has been possible because of the low densities of livestock and the ecosystem's inaptitude for other agricultural economic activities. In these vast areas intensification of cattle operations and flood pulse/hydrologic alterations are the most threatening potential hazards to native ungulates.

Few studies have verified potential resource competition caused by livestock introduction into South American grasslands (Jackson and Giuletti 1988; Larghero 2001; Puig et al. 2001). The existing studies indicate that trophic resource competition would intensify with the decrease of food diversity and patchiness because of pasture management or because of dry years. Such studies are highly significant, and better ranching management practices need to be developed to allow wildlife and livestock to coexist as ranching operations within native grasslands intensifiy. A baseline for the development of better management practices is an understanding on how species segregate ecologically, i.e., how species share available resources.

Segregation along one or more niche dimensions facilitates partitioning of resources, and, thereby, ecological separation of species (MacArthur 1972). Among sympatric ungulates, coexistence is presumably correlated with digestive anatomy and mouth dimensions (Hofmann 1973; Owen-Smith 1989; Gordon 1989; Illius and Gordon 1991; Gross, Alkon, and Demment 1996). Many studies of ungulates have indicated that coexistence is facilitated principally by dietary differences (plant growth stage and parts eaten) and to a lesser extent by the plant species per se or by spatial and temporal differences in habitat use (Dunbar 1978; Jarman and Sinclair 1979; Hansen, Mugambi, and Baun 1985; Murray and Brown 1993). Yet, simulation modeling, incorporating bioenergetic requirements, suggests that partitioning is achieved primarily through habitat segregation and plant parts favored (Owen-Smith 1989). Thus, morphological differences in mouth dimensions and energy requirements lead distinct species of ungulates to achieve optimal foraging performance in those habitats where selected vegetation structures are abundant (Owen-Smith 1989; Gordon 1989; Perez and Gordon 1999; Perez, Gordon, and Nores 2001).

In this paper I examine mechanisms for segregation among gray brocket deer (*Mazama gouazoubira*), pampas deer (*Ozotoceros bezoarticus*), and cattle at Caiman, a 500-km$^2$ ranch in southeastern Pantanal, Brazil. I tested the hypotheses that these ruminant species should be segregated by at least one niche dimension and that each species should select those habitats in which their preferred foods were most abundant. The results of this study are particularly important to the conservation of these cervids in the Pantanal, as studies in Argentina suggested that cattle compete with pampas deer (Jackson and Giuletti 1988). Most of the remaining habitat for pampas deer today is restricted to cattle ranches (Pinto 1994; Por 1995).

## METHODS

The study area (19°57′ S, 56°25′ W) is located in a wetland savanna. Mean annual rainfall is 1,773 mm, with monthly means ranging from < 30 mm in August to > 320 mm in January. Flooding occurs in March at the end of the rainy season.

Five fresh fecal samples for each ruminant were collected monthly from November 1991 through October 1992. Samples were obtained opportunistically in the study area during behavioral sampling of different individuals of the deer and cattle populations. Pellets were collected and preserved in ethanol just after being dropped. Additionally, brocket deer pellets were collected from latrines early in the morning, at the edge of forest patches commonly used for rumination or resting. As individuals were observed throughout the ranch area, it is assumed that the fecal samples were representative of the deer population in the study area. Samples were pooled by season: rainy (November to January), flood (March to May) and dry (July to September). Fragments of plant species were identified microhistologically (Sparks and Malechek 1968).

The proportion of different plant species in the diet was estimated using frequency counts of 100 microscopic fields per sample (Sparks and Malechek 1968; Johnson 1982). Trophic diversity based on plant species present in the diet was expressed by the Shannon-Wiener Index and niche breadth by Levins' Index, as standardized by Hurlbert (Krebs 1989). Similarity of diet between paired ungulate species was calculated with the Percentage Similarity Index (Renkonen 1938) and niche overlap among ruminant species with Horn's Index of Overlap (Horn 1966; Ricklefs and Lau 1980).

Availability of plant species was estimated by surveying the vegetation, using a modification of the point-sampling method (Levy and Madden 1933; Croker and Tiver 1948; Mantovani and Martins 1990). Representative tracts of ten plant formations were selected for sampling in the study area: marsh ponds, moist basins, short grass, medium grass, medium/tall grass, short grass/tall grass, tall grass, scrub, forest edge, and improved pasture (native pasture seeded with introduced grasses). Plant formations are described by Pinder (1997) and Pinder and Rosso (1998). One hundred sampling points were collected using five 25-m$^2$ quadrats in each plant formation, totaling 1,000 sampling points per season, rainy, flood, and dry. The preference for consumption of a plant species by deer and cattle was calculated by subtracting the proportion of the species in the diet from the proportion of the species available in the environment (Strauss 1979).

Two monthly surveys were conducted in the early morning and late afternoon along a 30-km trail connecting the SE and NW ends of the ranch to estimate the density and habitat use of cervids and cattle (Routledge and Fyfe 1992). The maximum sighting distances were 150 m for pampas deer and 140 m for gray brocket deer. Density of cattle was calculated based on the average cattle population in the ranch in 1991/1992. It is assumed that deer or cattle neither avoided nor were attracted by the trail. Additionally, one adult male of each cervid species was radio-collared to provide an unbiased sample of habitat use during daylight hours. Data on habitat use for all individuals were analyzed only for animals observed foraging or traveling. Radio-collared individuals were sampled at 30-minute intervals to avoid autocorrelation of data (Swihart and Slade 1985).

The availability of the different habitats was estimated by randomly selecting five coordinates within the ranch as start points for five 500-m-long transects. The direction of each transect was also randomly selected. Plant formations were registered at 50-m intervals along the transects, totaling 500 points distributed randomly within the floodplain (Marcum and Loftsgaarden 1980). Use versus availability of habitats was tested with the Chi-square goodness-of-fit-test and the related multiple comparisons of the Bonferroni z-test (Neu, Byers, and Peek 1974; Byers, Steinhorst, and Krausman 1984).

Friedman's test was used to verify consistency in use of food categories, i.e., grasses, forbs, browse, and fruits, among the ungulates, and the STP test to verify which food categories were consumed in greater proportions by each species (Sokal and Rohlf 1969). The Kruskal-Wallis test was employed in multiseasonal comparisons of food categories within species (Sokal and Rohlf 1969). Differences between consumption of food categories among paired seasons were determined by the Mann-Withney U-test (Sokal and Rohlf 1969).

## RESULTS

### DENSITY AND BIOMASS OF CATTLE AND CERVIDS

Cattle had the highest ecological density among the three species of ruminants (36/km$^2$) and almost the totality of the biomass (8,640 kg/ km$^2$). Cattle density increased on higher elevations during the peak of flooding when part of the foraging area was covered by 10 cm of water. Pampas deer and gray brocket deer occurred in low densities (0.68 and 1.08/km$^2$, respectively). The estimated cervid population for the ranch was 205 (95% CI = 121–359) pampas deer and 412 (95% CI = 229–653) gray brocket deer. The sympatric marsh deer (*Blastocerus dichotomus*) was rare (0.05 individuals/km$^2$), and used swampland avoided by the other species. The red brocket deer (*Mazama americana*) did not occur in the study area.

### DIETARY SIMILARITIES

Fecal analysis demonstrated that cattle, pampas deer, and gray brocket deer consumed the same food categories but in different proportions (Friedman, P us 0.01). The cumulative number of species consumed by each ruminant throughout the year indicated that samples were adequate to perform the comparative analysis between and among species (fig. 16.1). Cattle concentrated their foraging on grasses, whereas pampas deer and brocket deer selected forbs and browse respectively (STP, P s 0.01) (fig. 16.2).

Similarities in consumption of food categories between cattle and the cervids were not significant but were high between pampas and brocket deer. Cattle selected grasses and sedges year round, whereas pampas deer preferred forbs and browse and gray brocket deer browse and forbs. The largest overlap in diet between cattle and pampas deer occurred during the rainy season when about 20% of the pampas deer diet was newly grown grasses. The burst of pasture growth makes competition among pampas deer and cattle unlikely. In fact, cattle may be beneficial to pampas deer, as grazing by cattle increases the abundance of sprouting grass, which is more nutritious and palatable for pampas deer. Additionally, cattle reduce the height of the pasture and probably make forbs within the pasture more accessible for pampas deer. The consumption of different plant species within the same food categories resulted in an overall low diet similarity between pampas and gray brocket deer (table 16.1a). Similarities in diet were higher between the two deer species during the flood season when pampas deer increased their

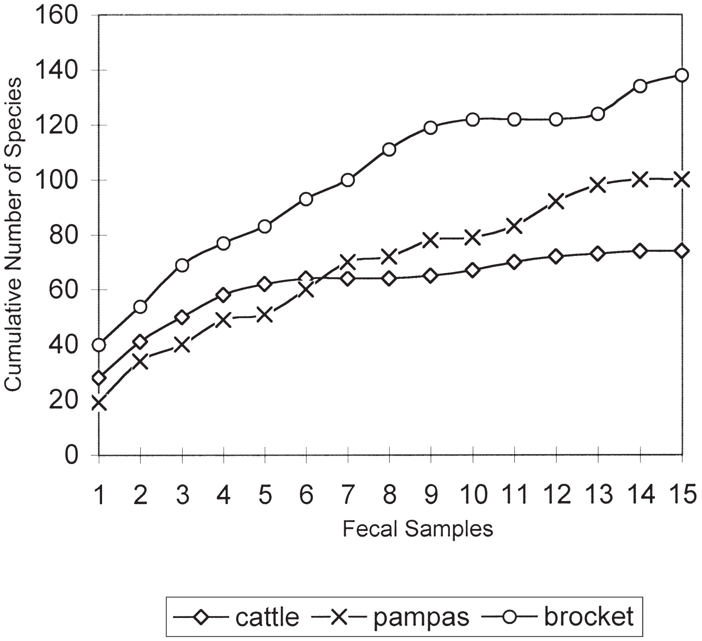


**FIGURE 16.1** Relationship between cumulative number of plant species in fecal samples, as determined by microhistological analysis, and number of cattle, pampas deer, and gray brocket deer fecal samples, Pantanal Study Area (Caiman Ranch), 1991–1992.

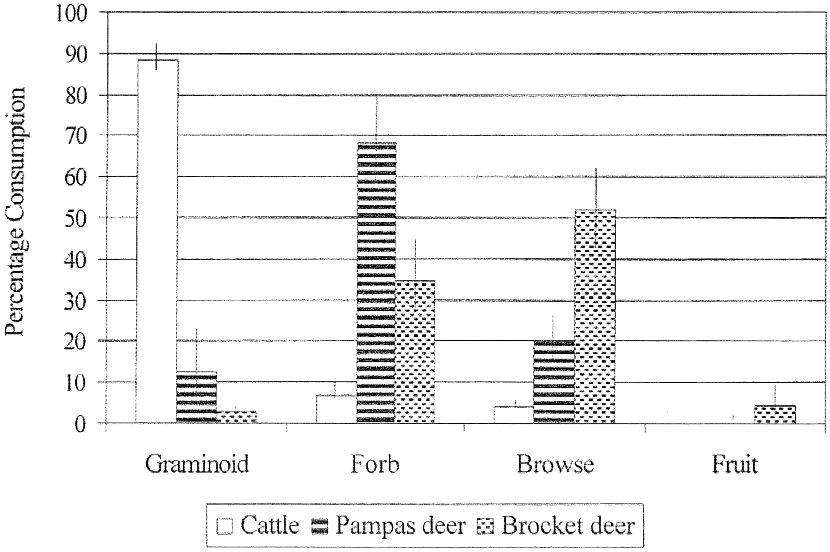


**FIGURE 16.2** Mean percentage consumption of food categories by cattle, pampas deer, and gray brocket deer, Pantanal Study Area, 1991–1992. Vertical bars indicate 95% confidence intervals.

**TABLE 16.1** Percentage Similarity Indices for Plant Species and Food Categories Consumed Seasonally by Cattle, Pampas Deer, and Gray Brocket Deer, Pantanal Study Area, 1991–92

**(A)** SIMILARITY OF CONSUMPTION OF FOOD SPECIES

| | CATTLE | | | PAMPAS DEER | | |
|---|---|---|---|---|---|---|
| | **Rainy** | **Flood** | **Dry** | **Rainy** | **Flood** | **Dry** |
| Cattle | — | — | — | — | — | — |
| Pampas deer | 33.44 | 10.85 | 9.49 | — | — | — |
| Brocket deer | 7.42 | 8.17 | 6.23 | 17.17 | 24.67 | 26.04 |

**(B)** SIMILARITY OF CONSUMPTION OF FOOD CATEGORIES

| | CATTLE | | | PAMPAS DEER | | |
|---|---|---|---|---|---|---|
| | **Rainy** | **Flood** | **Dry** | **Rainy** | **Flood** | **Dry** |
| Cattle | — | — | — | — | — | — |
| Pampas deer | 39.22 | 16.67 | 13.79 | — | — | — |
| Brocket deer | 14.30 | 11.06 | 13.55 | 55.62 | 81.49 | 65.48 |

consumption of browse, and gray brocket deer increased their consumption of forbs (table 16.1b).

However, only two plant species were consumed by both pampas and gray brocket deer in quantities exceeding 6% within the same season: *Melochia villosa* (Sterculiaceae forb) in the flood season (12.9% and 8.3%, respectively) and *Sida santamarensis* (Malvaceae forb) in the dry season (6.5% and 8.5%, respectively) (table 16.2). No plant species that contributed more than 6% in the diet of one cervid also contributed more than 6% in the diet of the other during the rainy season.

Gray brocket deer consumed species mostly associated with forest edge or scrub during the rainy and flood seasons: *S. santamarensis* (forb), *Melochia pyramidata* (shrub), *M. villosa* (forb), *Chomelia obtusa* (shrub), and *Vernonia scabra* (shrub). *Euphorbia thymifolia* (shrub) was the only species abundantly consumed by gray brocket deer that was associated with open vegetation (short grass). During the dry season, however, gray brocket deer consumed a greater proportion of forbs associated with tall grass and scrub: *Richardia grandiflora*, *Wedelia brachycarpa*, and *C. castaneifolia* (table 16.2). The majority of the forage consumed by pampas deer, especially during the dry season, was associated with moist soils, e.g., *Melochia simplex*, *Caperonia castaneifolia*, and *Hydrolea spinosa*.

**TABLE 16.2** Seasonal Consumption of Plant Species (> 6% of the diet) by Cattle, Pampas Deer, and Gray Brocket Deer, Pantanal Study Area, 1991–92

| | | CONSUMPTION BY CATTLE (%) | | | |
|---|---|---|---|---|---|
| FAMILY | SPECIES | Rainy | Flood | Dry | Mean |
| Poaceae | *Axonopus purpusiii* | 10.10 | 8.06 | 20.60 | 12.92 |
| | *Hymenachne amplexicaulis* | 6.96 | 5.43 | 2.86 | 5.08 |
| | *Mesosetum chaseae* | 15.20 | 33.40 | 4.84 | 17.81 |
| | *Paspalum pontanalis* | 5.16 | 5.73 | 6.24 | 5.71 |

| | | CONSUMPTION BY PAMPAS DEER (%) | | | |
|---|---|---|---|---|---|
| FAMILY | SPECIES | Rainy | Flood | Dry | Mean |
| Poaceae | *Mesosetum chaseae* | 16.16 | 0.77 | 0.32 | 5.75 |
| Euphorbiaceae | *Caperonia castaneifolia* | 2.68 | 0.00 | 6.05 | 2.91 |
| Hydrophyllaceae | *Hydrolea spinosa* | 1.81 | 0.62 | 9.96 | 4.13 |
| Malvaceae | *Sida santamarensis* | 0.52 | 0.07 | 6.47 | 2.35 |
| Onagraceae | *Ludwigia longifolia* | 8.56 | 24.70 | 0.00 | 11.08 |
| Pontederiaceae | *Eichhornia azurae* | 0.00 | 16.97 | 0.00 | 5.66 |
| Sterculiaceae | *Melochia simplex* | 17.39 | 0.72 | 43.78 | 20.63 |
| | *Melochia villosa* | 9.61 | 12.90 | 3.39 | 8.63 |

| | | CONSUMPTION BY BROCKET DEER (%) | | | |
|---|---|---|---|---|---|
| FAMILY | SPECIES | Rainy | Flood | Dry | Mean |
| Compositae | *Vernonia scabra* | 6.81 | 16.16 | 1.02 | 8.00 |
| | *Wedelia brachycarpa* | 0.08 | 2.05 | 13.58 | 5.24 |
| Euphorbiaceae | *Caperonia castaneifolia* | 1.00 | 0.09 | 8.37 | 3.15 |
| | *Euphorbia thymifolia* | 0.04 | 7.21 | 0.00 | 2.57 |
| Malvaceae | *Sida santamarensis* | 12.21 | 11.52 | 8.48 | 10.74 |
| Rubiaceae | *Chomelia obtusa* | 3.57 | 10.49 | 0.42 | 4.83 |
| | *Richardia grandiflora* | 3.16 | 0.82 | 17.46 | 7.15 |
| Sterculiaceae | *Bytneria dentata* | 14.17 | 2.35 | 0.67 | 5.73 |
| | *Melochia pyramidata* | 19.29 | 1.57 | 5.00 | 8.62 |
| | *Melochia villosa* | 2.87 | 8.33 | 5.09 | 5.43 |

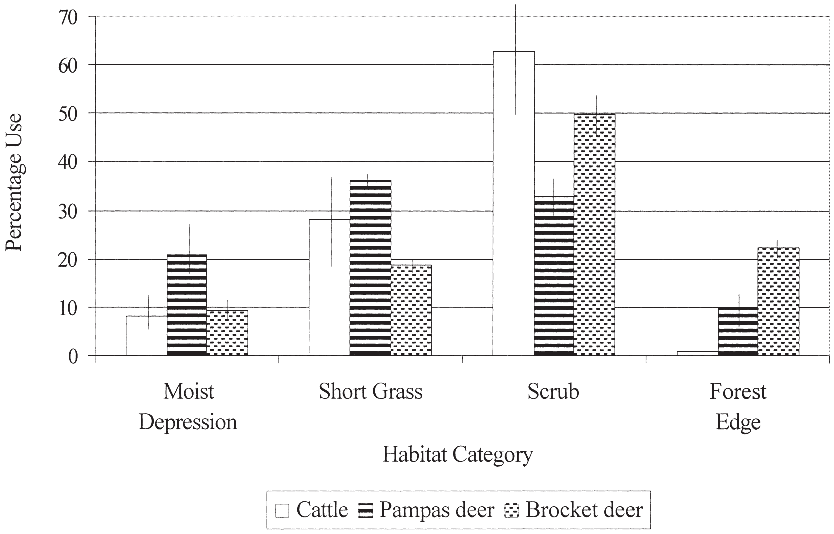


**FIGURE 16.3** Mean percentage use of habitats by cattle, pampas deer, and gray brocket deer, Pantanal Study Area, 1991–1992. Vertical bars indicate standard deviations.

## HABITAT USE

Pampas deer used open vegetation (moist depression and short grass) most frequently, whereas gray brocket deer selected habitats that were less affected by the flood and that had a higher density of shrubs (scrub and forest edge, fig. 16.3). Cattle had somewhat intermediary preferences, selecting grasslands and scrub and avoiding moist depression and forest edge.

Because climatic changes were extreme in the Pantanal (flooding versus drought), ungulates exhibited distinct habitat selection among seasons (table 16.3). Cattle selected short grass during the rainy season but used scrub almost exclusively during the flood season when water covered the short grass. During the dry season our observation of short grass habitat showed that graminoids were rapidly depleted there, and cattle once again selected scrub, where they found higher biomass of forage—medium and tall grasses growing in these plant formations along with shrubs and vines are eaten by cattle. Pampas deer were habitat-limited only during the flood season when inundation almost totally covered the vegetation in moist depressions. Gray brocket deer increased the use of open habitats only in the dry season when new growth in their most utilized habitats, scrub and forest edge, was reduced. During the dry season many trees shed their leaves as protection against excessive evapotranspiration. The only sources of green and nutritious leaves are the moist soils in depressions existing amidst the grasslands that become flooded during a few weeks of the year.

As a result of the shifts in habitat selection, the similarity in habitat use among

**TABLE 16.3** Seasonal Habitat Selection by Cattle, Pampas Deer, and Gray Brocket Deer, Pantanal Study Area, 1991–92

| | | HABITAT SELECTION[a] | | | |
|---|---|---|---|---|---|
| SEASON | SPECIES | MD[b] | SG[c] | SC[d] | FE[e] |
| Rainy | Cattle | Avoided | Selected | NS | Avoided |
| Rainy | Pampas deer | NS | Selected | Avoided | Avoided |
| Rainy | Brocket deer | Avoided | Avoided | Selected | NS |
| Flood | Cattle | Avoided | Avoided | Selected | Avoided |
| Flood | Pampas deer | Avoided | NS | NS | NS |
| Flood | Brocket deer | Avoided | Avoided | Selected | NS |
| Dry | Cattle | Avoided | Avoided | Selected | Avoided |
| Dry | Pampas deer | NS | Selected | NS | Avoided |
| Dry | Brocket deer | Avoided | NS | NS | Selected |

[a] Bonferroni z-test, $P < 0.05$. Avoided is habitat used less than expected based on its availability; selected, habitat used more than expected based on its availability; NS, no selection, habitat used in proportion to its availability.
[b] Moist depression.
[c] Short grass.
[d] Scrub.
[e] Forest edge.

**TABLE 16.4** Percentage Similarity Indices for Habitats Used Seasonally by Cattle, pampas deer, and gray brocket deer, Pantanal Study Area, 1991–1992

| | SIMILARITY OF USE OF HABITATS | | | | | |
|---|---|---|---|---|---|---|
| | CATTLE | | | PAMPAS DEER | | |
| | Rainy | Flood | Dry | Rainy | Flood | Dry |
| Cattle | — | — | — | — | — | — |
| Pampas deer | 75.91 | 53.92 | 68.03 | — | — | — |
| Brocket deer | 65.40 | 69.92 | 77.11 | 61.70 | 78.00 | 72.30 |

the three ungulates differed from season to season. The greatest habitat overlap between cattle and pampas deer occurred during the rainy season, whereas the greatest overlap between cattle and gray brocket deer occurred during the dry season. In contrast, the greatest overlap between pampas and gray brocket deer took place during the flood season (table 16.4).

## NICHE OVERLAP AND PARTITIONING

Overlap indices for the three ungulates indicated that they were segregated more on the basis of plant species consumed than either food categories consumed or habitats used. Dietary overlap among the three ungulates collectively, considering both plant species and food categories, was inversely related to the overlap in habitat use (table 16.5). Overlap in diet was greatest and overlap in habitat use was least during the rainy season when new growth was abundant.

## CATTLE AND DEER RESPONSES TO ENVIRONMENTAL CHANGES

Cattle and cervids exhibited the greatest diet diversities and niche breadths during the rainy season, which coincided with the season of surplus forage. Climate in the Pantanal affected cattle only during the flood season when their diet was less diverse. The inclusion of some browse species in the diet during the dry season allowed cattle to maintain a diet diversity comparable to the rainy season (table 16.6).

Gray brocket deer maintained diet diversity and niche breadth throughout the

**TABLE 16.5** Niche Overlap Indices for Cattle, Pampas Deer, and Gray Brocket Deer by Season, Pantanal Study Area, 1991–92

| | NICHE OVERLAP INDEX | | |
|---|---|---|---|
| **SEASON** | **Plant Species** | **Food Categories** | **Habitat** |
| Rainy | 0.83 | 1.50 | 2.14 |
| Flood | 0.73 | 1.32 | 2.16 |
| Dry | 0.66 | 1.34 | 2.20 |

**TABLE 16.6** Seasonal Diversity and Niche Breadth for Cattle, Pampas Deer, and Gray Brocket Deer by Season, Pantanal Study Area, 1991–92

| | CATTLE | | PAMPAS DEER | | BROCKET DEER | |
|---|---|---|---|---|---|---|
| | **H’**[a] | **Ba**[b] | **H’** | **Ba** | **H’** | **Ba** |
| Rainy | 3.15 | 0.20 | 3.08 | 0.11 | 3.24 | 0.11 |
| Flood | 2.79 | 0.09 | 2.82 | 0.07 | 3.20 | 0.10 |
| Dry | 3.31 | 0.18 | 2.39 | 0.04 | 3.20 | 0.09 |

[a] Shannon-Wiener Diversity Index

[b] Levins’ Standardized Niche Breadth

**TABLE 16.7** Percentages of Food for Cattle, Pampas Deer, and Gray Brocket Deer by Season, Pantanal Study Area, 1991–92

| | CATTLE | | | PAMPAS DEER | | | BROWN BROCKET DEER | | |
|---|---|---|---|---|---|---|---|---|---|
| | Rainy (%) | Flood (%) | Dry (%) | Rainy (%) | Flood (%) | Dry (%) | Rainy (%) | Flood (%) | Dry (%) |
| G[a] | 87.04 | 90.52 | 87.62 | 26.25[f] | 7.18 | 3.79 | 1.32 | 3.04 | 3.55 |
| F[b] | 10.00 | 7.00 | 4.41 | 41.02[f] | 47.02 | 81.13 | 22.71[f] | 34.12 | 47.13 |
| B[c] | 2.96 | 2.48 | 5.60 | 31.84[f] | 45.62 | 14.98 | 60.32 | 55.71 | 40.41 |
| Ft[d] | 0.00 | 0.00 | 0.00 | 0.05 | 0.00 | 0.10 | 8.42 | 2.76 | 1.71 |
| U[e] | 0.00 | 0.00 | 2.50 | 0.84 | 0.08 | 0.00 | 7.23 | 4.37 | 7.20 |

[a] Graminoids
[b] Forbs
[c] Browse
[d] Fruits
[e] Unidentified
[f] Percentage consumption is significantly different among seasons (Kruskal-Wallis test, $P < 0.05$).

year by increasing the contribution of grassland forbs in their diet during the flood and dry seasons. As browse matured and became less digestible, and presumably richer in secondary compounds, gray brocket deer foraged away from the forest edge more frequently.

Pampas deer were highly affected by seasonal changes in food availability as evidenced by a narrowing of their diet diversity and niche breadth from the rainy season to the dry season. To illustrate, pampas deer foraged on graminoids, forbs, and browse during the rainy season, principally on hydrophytic forbs and browse during the flood season, and mainly on forbs during the dry season (table 16.7). Foraging observations during the dry season indicated that pampas deer traveled from one moist depression to the next to forage on forbs. Therefore the dry season was the period when pampas deer diet was most specialized.

## DISCUSSION

### NICHE PARTITIONING

Ungulates in the Pantanal partitioned resources along all three niche dimensions (plant species, plant categories, and habitat type). These ruminants consumed different plant species, many of which occurred mainly on their preferred habitats, i.e., where those species were more abundant (Pinder 1997). Despite the fact that diet overlap decreased as habitat overlap increased among the three ungulates, there was no evidence that current competition was responsible for such segregation. Competition theory would predict that, when resources are limiting, the cervids should diverge in feeding characteristics because of competitive effects (Smith et al. 1978).

In contrast, the dyad pampas deer/gray brocket deer simultaneously increased habitat and diet similarities from rainy to dry season in a way comparable to that observed for some ungulates in the African savanna (Jarman 1971; Dunbar 1978). In those studies, ungulate species with low diet overlap during the rainy season increased overlap in the dry season, but species with generally high diet overlap in the rainy season decreased habitat overlap in the dry season when food availability was presumably reduced. Dunbar (1978) suggested that the simultaneous increase in diet and habitat similarities between those ungulates with low diet overlap in the rainy season indicated that there was no interspecific competition. Their niche overlap was probably too low to require any further reduction during the dry season, which appears to be the case with pampas deer and gray brocket deer in the Pantanal. Thus, the feeding habits of these ungulates supported the existence of a positive relationship between habitat and diet, i.e., as deer species increased use of the same habitat, diet overlap increased also (Gordon 1989; Owen-Smith 1989; Pinder 1997).

Distinct nutritional requirements of each ruminant and their respective gut capabilities for processing plant material were more likely responsible for the segregation observed. The gut capacity of herbivores determines, in part, their capability for digestion of fiber (Demment and Van Soest 1985; Hofmann 1988). Large herbivores, such as cattle, are able to survive on high-fiber diets because their larger digestive systems allows a lower passage rate necessary for the digestion of cell wall (Parra 1978; Van Soest 1982; Illius and Gordon 1991). Large herbivores would not be expected to feed on a low-fiber diets because low-fiber foods are rare, and thus the amount of energy expended in searching and consuming these foods is prohibitive in comparison to the total daily energy requirements of large herbivores (Parra 1978; Demment and Van Soest 1985; Murray and Brown 1993).

In contrast, a small ruminant, such the gray brocket deer, requires less total energy but more energy per unit of biomass. A faster energetic return from digestion of plant material can be reached by the fermentation and digestion of cell contents instead of cell walls (Van Soest 1982). Consequently, small ruminants need a low-fiber diet, which can be digested directly by vertebrate enzymes or fermented rapidly by microbes. In contrast to graminoids, low-fiber tissue is found in leaves of trees and shrubs, which constituted the main diet of gray brocket deer in the Pantanal. Pampas deer, which weigh twice as much as gray brocket deer, presumably have a larger gut capacity but require less energy relative to their body size compared to gray brocket deer. This larger gut capacity allows for a slower passage rate and better utilization of lower quality food than gray brocket deer.

Owen-Smith's hypothesis (1989), however, does not completely explain habitat segregation among pampas and gray brocket deer. If bioenergetic requirements were the only factor influencing habitat selection in the Pantanal, pampas deer and gray brocket deer presumably could exhibit a larger overlap in their diet. Other factors, such as predation, past and/or present, may have influenced the evolution of habitat choice by each cervid. Predation is a powerful force limiting the distribution of many animal populations to particular habitats. Dingos (*Canis dingo*), for example, can greatly depress kangaroo populations (Caughley et al. 1980). Many other vertebrate predators also can restrict prey species to particular habitats (Kettlewell 1955; Wilbur, Morin, and Harris 1983; Robinson 1985; Main, Weckerly, and Bleich 1996).

Thus different strategies of inherited behavior of predator avoidance adopted by pampas and gray brocket deer may have resulted in the observed habitat segregation. Pampas deer avoid predation by running through the open grassland, whereas gray brocket deer seek refuge within thickets. This differential pattern of habitat use by gray brocket deer and pampas deer at least partially explains the minimal overlap in their proportionate consumption of shared plant species.

Historically, interspecific competition as an explanation for niche partitioning may have been overemphasized (Cody and Diamond 1975). There is little evidence of current competition among vertebrate herbivore species because most of the observed partitioning may reflect past competition (Schroder and Rosenzweig 1975). The few cases in which interspecific competition among herbivores has been demonstrated, it involved either the recent introduction of an exotic species into an indigenous herbivore community or the introduction of a herbivore into a habitat different from that in which it exists normally (Fox 1989; Wray 1994; Putman 1996). If niche partitioning among herbivores is manifest, it is more likely maintained by optimal foraging (Owen-Smith 1989) rather than by interspecific competition.

In the case of the introduction of cattle into the Pantanal, there is no evidence that cattle are directly competing with native deer for food. However, bad management and overstocking of cattle in native habitats cause habitat alterations that indirectly may affect food and shelter availability for deer and other herbivores. For example, the habit of cattle sheltering within forest patches is causing an evident opening of the habitat and a decrease of tree and shrub species in the forests. As cattle trample and feed on the saplings and seedlings, little regeneration is occurring in these forests. Similarly, overgrazing on the grasslands may cause an increase of weed species, which in turn may decrease the availability of forbs and other species useful for deer. Finally, high abundance of cattle may increase the chances of interspecific disease infection.

## CLASSIFICATION OF THE CERVID-FEEDING STRATEGIES

Ruminants have been classified as concentrate selectors, grazers, roughage eaters, and intermediate types as determined by their diet and grastrointestinal anatomy (Hofmann 1988). Concentrate selectors, most commonly referred to as browsers, include cervids whose body size ranges from large, e.g., moose (*Alces alces*), to small, e.g., pudu (*Pudu puda*). Grazers are principally bovid species that also range in size from large, e.g., gaur (*Bos gaurus*), to small, e.g., sheep. Intermediate feeding types include representatives of cervids and bovids, which may shift diets between browse and grass depending on seasonal conditions (Hofmann 1988). Bodmer (1990) expanded this classification by including frugivory as a feeding strategy distinct from browsing. Frugivorous ruminants occur in tropical forests of South America, Africa, and Asia where fruits are abundant but where high quality browse for terrestrial herbivores is rare. Thus, ruminants can be classified along a continuum that ranges from frugivores to browsers to grazers.

If we accept this classification, the gray brocket deer would be classified in the frugivore-browser segment of the continuum, whereas the pampas deer would occupy the browser-grazer segment. Both cervids are predominantly browsers and concentrate selectors as inferred from their diet in the Pantanal. However, their digestive anatomy and possibly the absence of many competitors allow them to consume a greater proportion of other food types. This versatility is reflected in the diversity of habitats occupied currently by gray brocket deer and pampas deer. The former range from tropical forests to the savanna and the latter from the savanna to the temperate grasslands of South America (Avila-Pires 1959; Redford and Eisenberg 1992; Pinder 1997). This versatility also may have been responsible for their survival through the several climatic changes that eliminated a number of herbivorous species during the Pleistocene era (Stehli and Webb 1985).

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# 17

# Ecology and Conservation of the Jaguar (*Panthera onca*) in Iguaçu National Park, Brazil

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Jaguars (*Panthera onca*) now occupy less than 50% of their historic range (33% in Central America and 62% in South America; Swank and Teer 1989). With the exception of occasional dispersing animals, they have been extirpated from the southern United States, northern Mexico, coastal northern and western South America, and southern Argentina, among other regions (Sanderson et al. 2002). Athough their greatest stronghold is in the continuous forest of the Brazilian Amazon, jaguar populations also persist in highly fragmented and threatened regions, such as the Atlantic forest, Central American dry and moist forest and pine savannas, northern South American dry forests, and South American savannas and savanna-parklands (*cerrado*). Sanderson et al. (2002) regard these populations as having low probability of long-term survival. These populations, however, are important to biodiversity conservation in general and jaguar conservation in particular because they contribute to species-level genetic diversity, help to maintain functioning ecosystems in the protected areas, and, perhaps most importantly, interact with humans and thus enter into the political and cultural consciousness of the countries in which they occur.

Iguaçu National Park in southwestern Brazil exemplifies an isolated fragment of natural habitat surrounded by intensive human activities. Created in 1939 to protect the world famous Iguaçu Falls, the park currently holds about 80% of the remaining subtropical forest that once covered Paraná state east of the coastal Serra do Mar (Poupard et al. 1981). Today, only about 6% of the state is covered by forest. At the time of the study, the park sustained populations of jaguars, pumas (*Puma concolor*), ocelots (*Leopardus pardalis*), and large ungulates such as collared peccaries (*Tayassu tajacu*), tapirs (*Tapirus terrestris*), and white-lipped peccaries (*Tayassu pecari*).

Jaguar studies in Central and South America (Rabinowitz and Nottingham 1986;

Emmons 1987; Ludlow and Sunquist 1987; Crawshaw and Quigley 1989; Konecny 1989; Sunquist, Sunquist, and Daneke 1989; Crawshaw and Quigley 1991; Emmons 1991; Quigley and Crawshaw 1992; Sunquist 1992) have usually been conducted in large tracts of relatively undisturbed, continuous habitats. By studying jaguars in Iguaçu, we can look at the impact of fragmentation on individuals and populations of a large predator. From April 1990 through December 1994, we collected information on the ecology of jaguars in Iguaçu National Park. In 1991 the project was extended to neighboring Iguazu National Park, located in Argentina and separated from the principal study site by the Iguaçu river. Our objectives were to evaluate the conservation status of jaguars (and ocelots; Crawshaw 1995) in the park in order to determine whether genetic interchange through dispersal occurs between the (sub) populations of the two parks and to describe the dispersal patterns (sensu Shields 1987) of subadults.

## STUDY AREA

Iguaçu National Park (INP) comprises 175,000 ha on the western border of Paraná state, southern Brazil (25°05′ to 25°41′ S and 53°40′ to 54°38′ W), along the international boundary with Argentina and Paraguay (fig. 17.1). The climate in the region is temperate subtropical, with mean monthly temperatures ranging from 25.7°C in

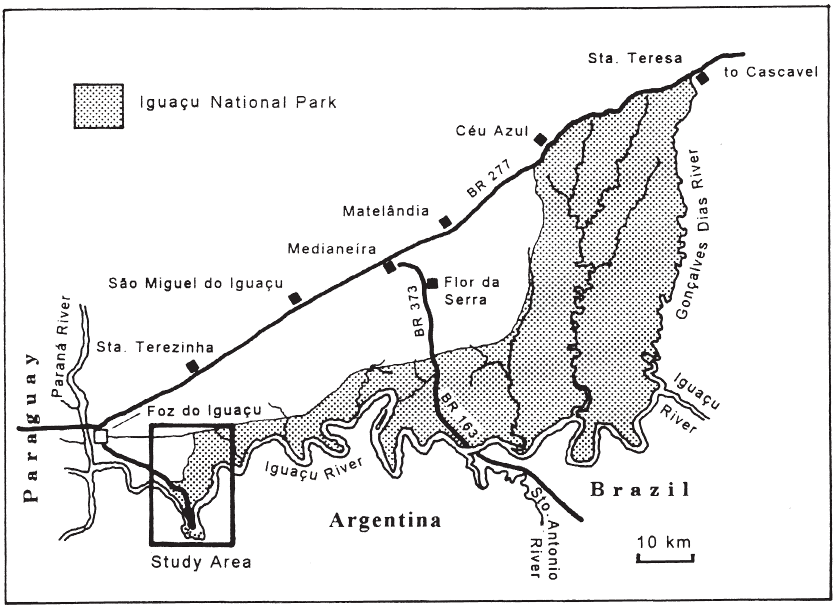

**FIGURE 17.1** Location of Iguaçu National Park and Parque Nacional Iguazu at the border between Brazil and Argentina.

February to 14.6°C in July (Crespo 1982). Mean annual rainfall during the study period (1990–1994) was 1,700 mm, with one peak in May (180 mm) and one in October (240 mm). July and August are the driest months of the year. The vegetation in the park consists of a rather uniform forest cover, with some regenerating patches on the western half, where settlers had cleared or selectively logged the original forest. Four hundred families living in the park were removed and compensated in the late 1970s and early 1980s.

The region's rich soils sustain thriving agribusinesses and small farms, and human population density has increased to about 616 inhabitants/km$^2$ from 31 inhabitants/km$^2$ in the mid-70s (Poupard et al. 1981). On the Brazilian side the park is completely bounded by soybean, wheat, and rice plantations and by cattle pastures; on the Argentinean side it borders the 55,500-ha Parque Nacional Iguazu. Together, the two parks harbor the last large tract of subtropical rainforest that once covered much of the highlands on the west side of the Serra do Mar in southern Brazil. Although contiguous, the two parks are administratively separate.

The shape of the INP resembles that of an "L" turned 90° counterclockwise, with an average width (N/S) of only 5 km in the western half (fig. 17.1). The eastern portion, with approximately 50 km on the N-S axis and 23 km on the E-W axis (roughly 1,100 km$^2$), has the most intact habitat but the highest poaching levels. There is no buffer zone or effective fencing between the park and the private properties along the 136 km of dry boundary of the northern perimeter. Peccaries frequently enter the agricultural areas to feed on crops, while jaguar and puma prey on domestic animals (poultry, dogs, sheep, and cattle). An unpaved road runs along the north border of the western half for less than 60 km. The remaining 304 km of the perimeter is bounded by rivers. Park boundaries are difficult to patrol, and in the same way that wildlife enter agricultural areas, poachers (both subsistence hunters and wealthier landowners who hunt for sport) easily enter the park and place significant pressure on ungulate populations.

The study area encompassed about 80 km$^2$ of the westernmost part of the park, near the falls (fig. 17.2). Access to the falls is provided by a federal highway (BR-469), which ends at the tip of the peninsula that cuts into Argentina. This area is visited by close to one million people a year (mean of 802,587 during the study period 1990–1994), with peaks in the months of January, February, and July. During some national holidays the number of daily visitors may exceed 10,000. Most of the trapping and ground monitoring was conducted along the 8.8-km Poço Preto road (PPR) (fig. 17.2), which had been closed to the public since 1986. Three other trails also were used: Represa (TR; 1.2 km), Bananeiras (TB; 1.5 km), and Macuco (TM; 4.5 km), the latter of which is used for jungle-and-boat tours by a concessionaire.

## METHODS

Jaguars were captured using custom-made wood or iron-bar box-traps, measuring 210 x 80 x 80 cm and baited with live chickens housed at the back of the trap with

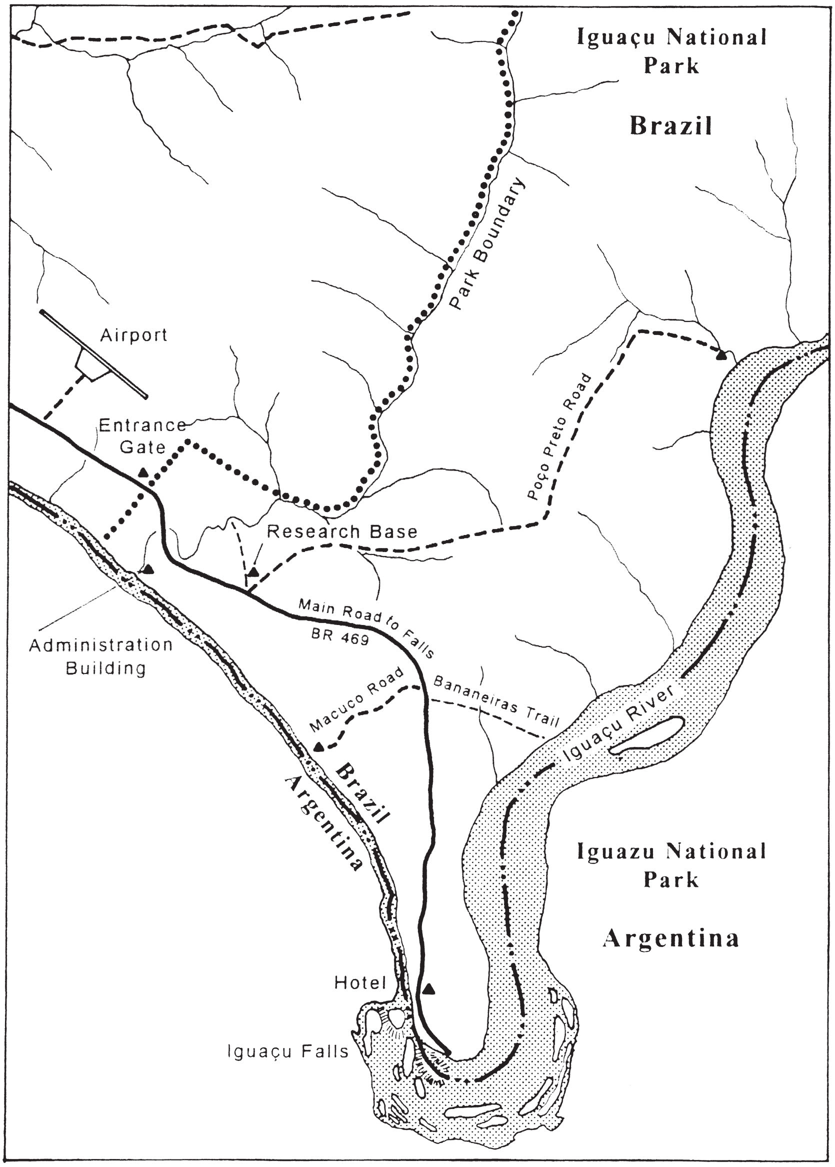

**FIGURE 17.2** Map of Iguaçu National Park study area showing trails used for trapping and monitoring.

wire mesh. Once trapped (or, on three occasions, treed by trained dogs), animals were chemically restrained using a projectile dart shot with a $CO_2$ pistol (Telinject U.S.A., Saugus, CA 91350) or powder rifle (Capchur, Palmer Chemical and Equipment, Douglasville, GA 30133). Animals were anesthetized with either ketamine hydrochloride (Parke-Davis, Detroit, MI) or Zoletil (same as Telazol, or CI-744;

Virbac do Brasil, São Paulo, SP 04021), examined for general body condition, measured, weighed, ear-notched and/or tattooed, photographed, and fitted with radiocollars (150–152 MHz; Telonics, Mesa, AZ 85204). Relative age was estimated mainly on the basis of presence of milk or permanent dentition and tooth color and wear (juvenile, subadult, adult) in combination with other physical characteristics, such as weight, size, sign of previous reproduction (for females), and texture and color of the skin of the heel pads (Crawshaw 1992). Anesthetized animals were kept under observation until ambulatory.

Radio-equipped animals were located from a vehicle with a mounted omnidirectional antenna, or on foot with a directional antenna. Once a signal was heard, locations were obtained through triangulation, using the hand-held directional antenna. Given the limited ground range of the equipment, about 300 m in dense vegetation, a light aircraft was used at approximately 14-day intervals to obtain an unbiased sample of locations. The flyby method described by Mech (1983) was used to define animal locations from aircraft. Accuracy tests performed by project personnel indicated that locations could be described within a circle of 50 m radius (0.8 ha).

Locations were plotted on a 1:25,000 map of the study area, divided into 1.5-ha cells by a transparent grid overlay. Grid coordinates (vertical and horizontal) were assigned to each location. In the latter period of the study (subsequent to 1992), geographical coordinates were also obtained with a GPS (Global Positioning System) receiver (Transpak, Trimble, and Pronav 100, Garmin).

Home ranges were estimated with the Home-Range (Ackerman, Samuel, and Leban 1991) and the Mcpaal software packages(Microcomputer Program for the Analysis of Animal Locations; Stüwe 1985; National Zoo, Washington, D.C.). Comparisons between individuals in this study were made using the Minimum Convex Polygon, corrected upon visual analysis of plotted locations (Harris et al. 1990). Outliers, including locations of dispersing subadult individuals, were omitted from calculations.

Fecal samples were routinely collected along roads and trails, dried in large cardboard boxes with permanently lighted lamps, and stored until analysis. Contents were separated into the various components in running water over a wire mesh sieve and identified to the lowest taxon possible, using a local reference collection of hair, bones, reptile scales, and fruit. Some items were identified at the Capão da Imbuia Museum, in Curitiba, Paraná state. Whenever possible, the predator species that left the scat was identified at the collection site based on tracks and/or other circumstantial evidence. When such identification was not possible, hairs ingested in autogrooming were identified by comparison of cuticle and medullar patterns with hairs of known samples. Hairs were selected from samples by macroscopic characteristics, clarified with xylene, and compared with known samples at 400x magnification.

To correct for differences in prey size in the diet, we multiplied the mean weight of each food item by the number of times it was found in the sample of scats and by the mean number of individuals per scat (as indicated by the number of body parts found), thus obtaining an estimate of biomass consumed for each taxa ($B_{est}$). When available, we used weights from local animals; if unavailable, weights from the literature were used. The relative importance of each prey item was then expressed as the percentage of that item in relation to the combined weight of all items.

## RESULTS

Seven jaguars were captured and radio-collared, including two adult males, one adult female, three subadult males, and one subadult female (table 17.1). One of the adult males (M48) was captured in Iguazu National Park, Argentina; all other animals were captured in INP, Brazil. Five of the jaguars in INP were probably related. Judging from sightings and spoor prior to capture and from subsequent monitoring after radio-collaring, the adult female F17 was presumed to be the mother of M13 and F21 (littermates) and M32 (from a subsequent litter). As the resident adult M33 was probably the father of both litters. There was evidence of the presence of other jaguars in the trapped area—one female and subadult were observed but not captured, and one captured subadult (M34) must also have been the offspring of this unknown female.

### HOME RANGES AND MOVEMENTS

A total of 236 locations (81% aerial) were obtained on the study animals, 142 (60%) for males and 94 (40%) for females. Adult and subadult animals were monitored about equally, with 49% and 51% of locations, respectively. Overall, the mean interval between locations was 10.1 ± 15.2 days (range: 0–102 days).

**TABLE 17.1** Home-range Estimates for Seven Jaguars in Iguaçu and Iguazu National Parks

| AN# | N | MCP (KM$^2$) |
|---|---|---|
| F17 | 69 | 70.0 |
| F21 | 25 | 8.8 |
| M13[a] | 10 | 22.6 |
| M13[b] | 11 | 138.6 |
| M32[a] | 9 | 5.4 |
| M32[b] | 6 | 104.0 |
| M33 | 17 | 25.7 |
| M34 | 21 | 16.4 |
| M48 | 15 | 86.5 |

*Note:* Uses the MCP (Minimum Convex Polygon) method. AN# is the animal's ID number, and N the number of radio locations.

[a] Natal area

[b] Adult home range (incomplete; *see* Dispersal)

Home-range estimates varied considerably for the study animals (Crawshaw 1995; table 17.1), ranging from 8.8 km$^2$ (F21) to 138 km$^2$ (M13). Undoubtedly, some of this variation can be accounted for by differences between sex and age classes. However, cumulative area curves (Odum and Kunzler 1955) indicate that the ranges of most individuals are underestimated because of small number of locations. The only exception is F17, which used a total area of 70.0 km$^2$ during 14.5 months of monitoring and for which an asymptote was reached at fifty locations.

The movements of most of the radio-tagged jaguars were influenced by human activities. Adult male M48 was translocated and released in an area 8 km from his first capture site because of his habit of preying on domestic dogs. Two months later, he was back in his original area and was wounded with a shotgun by a local resident as he was attacking a dog by the house. He was recaptured thirty-nine days later in a trap baited with the remains of another dog he had killed the previous night in an indigenous village, and permanently removed to a zoo after treatment of the wound.

The movements of M33, a male well past his prime, were likely influenced by an apparent acquired dependency on the live baits in our traps (eight recaptures). This dependency may have resulted from a decrease in his hunting ability, since his condition deteriorated steadily between captures. Similarly, the movements of F21, a subadult female, were influenced by a dependency on the garbage dump at the hotel by the falls and then by a short translocation (circa 5 km) following capture. This dependency was likely developed because of an infection on one of the upper canines, that prevented her from normal hunting. She was treated during capture and had apparently resumed normal feeding three months later when she was killed by a poacher inside the park, as her stomach contained the remains of a collared peccary. Her remains, together with the transmitter, were found buried in the forest. Initially captured as subadults, M13 and M32 were in the process of establishing their adult home ranges when they were also killed by poachers in the park.

## DISPERSAL

Two subadult males, M13 and M32, were monitored during dispersal. After a few long-range movements (> 5 km) outside of his natal area, M13 (at an estimated age of eighteen months) crossed the Iguaçu river into Iguazu National Park, in Argentina, on September 24, 1991. He remained in Argentina until November 9, and was located five times during the interval, with a mean linear distance between locations (MLDBL) of 2.4 ± 2.7 km. On November 10 he was back in INP, where he remained until November 13, with a MLDBL of 2.0 ± 1.4 (0.6–3.8; $N = 4$) km. On November 21 he was found again in Argentina, where he traversed the whole peninsula and on December 1 was found in Paraguay, having crossed the Paraná river at a point where it is > 400 m wide. He was confined to a small island of forest surrounded by farmland. On December 17 he was back once again in his natal area in INP, a linear distance of 16.2 km from his previous location. On January 18, 1992, he was located 33 km northeast of where he was located on January 9.

When he was recaptured on March 13 to change his collar, he weighed 88 kg. He had several open cuts, likely incurred during intraspecific fights, and his upper right canine was broken off almost at the base. Between January 18 and May 16, the mean distance between thirteen locations was 12.9 ± 11.1 km (range 1.0–33.0 km). On May 26 we located the collar at a house by the Iguaçu river, on the opposite side from the Park—M13 had been killed by the owner and his fifteen-year-old son while they were poaching white-lipped peccaries in INP.

During his first nine locations following capture on November 17, 1992, M32 covered an area of 5.4 km$^2$, presumably still in his natal area. After January 21, 1993, the signal of his transmitter could not be found within the study area. After gradually increasing the area searched during flights, he was found on February 22 on the eastern sector of the park, 64 km east of his last location. Assuming he was born in September 1991, his age then was sixteen months. His dispersal may have been precipitated by the removal of his mother, F17, from the park in October.

His next ten locations encompassed an area of 308 km$^2$, with a mean linear distance between locations of 9.0 ± 3.6 km (range 4.4–16.7 km). His movements for the next ten locations decreased to a mean of 3.4 ± 1.2 km (range 1.8–4.9 km) and were confined to an area of 17 km$^2$. In his next ten locations he increased the area used, as a result of two long-range movements (17.5 and 10.2 km) to an area where he was later seen twice (during recapture attempts) with an adult female. Therefore he was already becoming an established adult when he was killed by poachers in June 1994.

## DENSITY

Despite heavy human disturbance within and around the study area, jaguar sign (mainly tracks) was frequently encountered along roads and trails. Six jaguars were captured and radio-tagged in the 80 km$^2$ in a four-year period. Radiotelemetry data on the collared animals and indirect evidence indicated that at least one other adult male and two adult females (uncollared) used the entire area. On April 19, 1990, an uncollared adult male was photographed by an infrared-sensor remote camera. He was never captured and could have been either a resident or a transient. The estimated minimum density of adult animals therefore was 3.7 jaguar/100 km$^2$. Assuming the adult females had, on average, 1.5 young per litter in alternate years, the total estimate for the area would be six animals in the 80 km$^2$, or 7.5 jaguar/100 km$^2$. If applied to the 1,750 km$^2$ of INP, the total density would be approximately 64 adults, or 134 animals, including all ages. However, given that both dispersing subadult males were able to establish home ranges within the park, as well as the high jaguar mortality due to humans, the actual density was certainly much lower.

## DIET

A total of seventy-three jaguar scats was found in INP. Mammals comprised 80% of the 106 items recorded, followed by birds (8.5%), reptiles (6.6%), fruit (3.8%), and invertebrates (1.9%) (table 17.2). Considering only the mammals, peccaries were the prey taken most often (45% of all items), followed by opossum, armadillo, and deer, to mention only those occurring above 10% in the sample. However, if the different food items are corrected by weight, the order of relative importance of these species changes considerably. Peccaries become even more prominent (77%), followed by deer (14%), coati (2.2%), armadillo (2.0%), agouti (1.1%) and opossum (1.0%). Therefore these species alone account for over 97% of the diet derived from the jaguar scat sample. It is noteworthy that these same species are among the most abundant in the study area, judging from our sighting data. However, the propor-

**TABLE 17.2** Food Items Found in Seventy-three Jaguar Scats in Iguaçu National Park, Brazil

| PREY ITEM | WGT (KG) | N | #IND | ITEMS (%) | SCATS (%) | $B_{est}$ (KG) |
|---|---|---|---|---|---|---|
| Peccary (*Tayassu* sp.) | 30.0 | 38 | 1 | 35.8 | 52.0 | 1,140 |
| Opossum (*Didelphis aurita*) | 1.50 | 10 | 1 | 9.4 | 13.7 | 15 |
| Armadillo (*Dasypus novemcinctus*) | 3.30 | 9 | 1 | 8.5 | 12.3 | 30 |
| Deer (*Mazama* sp.) | 22.5[a] | 9 | 1 | 8.5 | 12.3 | 203 |
| Bird (Cracidae, Tinamidae) | 0.65 | 9 | 1 | 8.5 | 12.3 | 5.9 |
| Lizard (*Tupinambis teguixin*) | 1.60 | 6 | 1 | 5.7 | 8.2 | 9.6 |
| Coati (*Nasua nasua*) | 5.50 | 6 | 1 | 5.7 | 8.2 | 33.0 |
| Agouti (*Dasyprocta azarae*) | 3.2 | 5 | 1 | 4.7 | 6.8 | 16.0 |
| Unidentified fruit | — | 4 | — | 3.8 | 5.5 | — |
| Squirrel (*Sciurus aestuans*) | 0.80 | 2 | 1 | 1.9 | 2.7 | 1.6 |
| Invertebrates | — | 2 | 1 | 1.9 | 2.7 | — |
| Rabbit (*Sylvilagus brasiliensis*) | 0.8 | 1 | 1 | 0.9 | 1.4 | 0.8 |
| Paca (*Agouti paca*) | 10 | 1 | 1 | 0.9 | 1.4 | 10.0 |
| Capuchin monkey (*Cebus apella*) | 3.0 | 1 | 1 | 0.9 | 1.4 | 3.0 |
| Tayra (*Eira barbara*) | 5.5 | 1 | 1 | 0.9 | 1.4 | 5.5 |
| Margay (*Felis wiedii*) | 3.0 | 1 | 1 | 0.9 | 1.4 | 3.0 |
| Unidentified snake | 1.00 | 1 | 1 | 0.9 | 1.4 | 1.0 |
| Total |  | 106 |  | 99.7 | 145.1[b] | 1,478 |

*Note:* Wgt equals mean live weight of prey item; N, number of scats in which the item was present; #Ind, number of individuals per scat; items, percentage of total number of items found; scats, percentage of scats containing that food item; and $B_{est}$, estimated total weight of that prey item.

[a] Average of the weights of the two species (*M. americana* and *M. nana*).

[b] Does not add to 100% because of more than 1 item per scat.

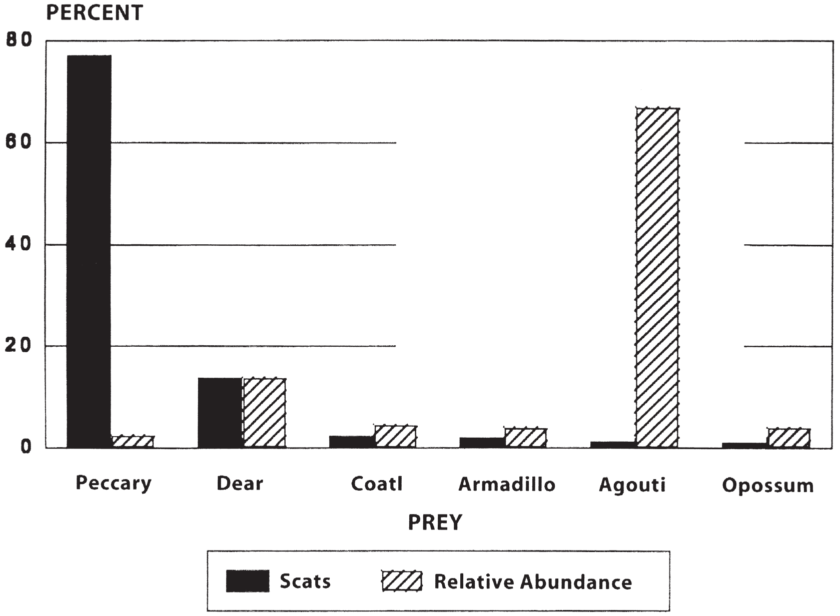

FIGURE 17.3 Percentage of corrected prey taken by jaguar in Iguaçu National Park, compared with relative abundance derived from sighting data.

tion in which they are taken indicates different levels of selectivity by the jaguar (fig. 17.3). Peccaries were taken much more often than the relative abundance estimate would predict, whereas agoutis were taken much less. Deer were the only species taken in equal proportion to their relative abundance.

## MORTALITY AND RELATIONSHIPS WITH HUMANS

We lost all seven radio-tagged jaguars in a three-year period (Crawshaw 2002). Three were poached inside the park (M13, M32, and F21), two had to be removed from the park because of livestock depredation habits (F17 and M48; the latter had already been wounded), and two disappeared prematurely and were suspected of having been killed (M33 and M34). In addition, three other uncollared jaguars were known to have been killed during the study period, one for livestock depredation outside the Argentine park, one shot by a poacher, and one cub killed by a vehicle at the INP boundary.

Complaints of livestock depredation by jaguars were common during the study period, especially in the last two years. Incidents included predation of twenty-two sheep in a ten-day period, and of thirty-six calves and cows in a three- to four-month period (Crawshaw 2002). Most people attributed the increase of instances to an increase in the population of jaguars in the park. However, the fact that two subadult males (M13 and M32) could establish adult home ranges within the INP indicates that there were still open spaces in the population (perhaps because of the high mortality of adults).

Other hypotheses can be postulated. Prior to the project, there was little response from park and wildlife authorities to predation complaints because of a lack of technical information and expertise on the subject. Therefore there was an unspoken policy between ranchers of resolving the situation by eliminating the problem animal. With knowledge of the project and of the critical status of the species, some of the more conscientious ranchers tended to report losses rather than to eliminate the animal. The widely publicized arrest of two poachers that killed radio-equipped jaguars also must have acted as a deterrent, with a widespread belief that all jaguars in the park were being radio-monitored.

## DISCUSSION

Although conservation programs for large carnivores—quintessential charismatic megafauna—are successful in attracting funding (Weber and Rabinowitz 1996; Sanderson et al. 2002,), conservation successes on the ground are more difficult to achieve for several reasons. First, carnivore conservation projects must work with or change the negative attitudes of local peoples toward animals that pose real or perceived threats to livestock and human lives. Ranchers often consider all large carnivores as potential threats to their stock and shoot them on sight (Hoogensteijn 1993; Kellert et al. 1996; McNammee 1997).

Second, it is increasingly difficult for conservation units to provide the huge land areas required to maintain viable populations of top predators. When protected areas are surrounded by ranchlands, animals moving in and out of the area or living near its boundaries are susceptible to being killed by humans. They also suffer high mortality rates on roads because of collisions with vehicles.

Third, adequate prey bases must be maintained in and around protected areas to sustain carnivore populations. Carnivore management therefore involves management of ungulate and other larger herbivore populations, which are often the target of subsistence hunters and poachers. These issues are common to carnivore conservation worldwide, e.g., wolves in North America, tigers in Asia, and jaguars in South and Central America.

Despite its island nature and the extreme loss of habitat in the region, it is not habitat loss per se that is affecting jaguar populations in Iguaçu National Park. Rather, mortality related to the high human densities that accompany fragmentation have the greatest impact on jaguars. If such mortality could be controlled, viable jaguar populations could still persist. This viability presupposes, however, the maintenance of an abundant prey base. Polisar (2000) demonstrated a strong negative correlation between the availability of natural prey and the level of predation by pumas and jaguars on cattle in the Venezuelan Llanos.

In INP loss of white-lipped peccaries because of poaching and harassment by humans may pose one of the greatest threats to jaguar viability. Peccaries, especially white-lipped, were prominent in the diet of jaguars at Iguaçu. Assuming a jaguar needs about 5% of its body weight (4.0 kg) as the mean daily food intake (Emmons 1987), it would require approximately 1,460 kg per year. Using the percentages of the main food types in the scat sample, it would require the equivalent of thirty-eight peccaries, nine deer, six coatis, ten armadillos, five agoutis, and ten opossums to fulfill one individual jaguar's annual food requirements. The total figure for the entire park jaguar population (approximately seventy animals) would be 102,200 kg of required prey, of which 81,000 kg would presumably be provided by peccaries alone.

Our density estimate for white-lipped peccaries in the study area was about seventy individuals (in one herd that apparently split in subgroups occasionally) in the 80 $km^2$, or 0.9 individual/$km^2$. However, we knew of the recent killing of at least eight members of this herd when they invaded crops at a neighboring property. Fragoso (1994) found home-range sizes of 21.8 and 109.6 $km^2$ at Maracá Island Ecological Reserve, Amazonia, with densities ranging from 1.2 to 8.1 peccaries/$km^2$. Assuming a conservative estimate of 1.5 peccaries/$km^2$ for the 1,750-$km^2$ park, the resulting estimate would be 2,625 animals, or a total biomass of 78,750 kg (weight estimated as 30 kg, as opposed to 35 kg of adults, to account for young and subadult animals).

Collared peccary densities ranged from 1.0 to 3.3/$km^2$ in Maracá (Fragoso 1994). For Manu National Park in the Peruvian Amazon, Emmons (1987) estimated a density of 5.6 individuals/$km^2$ for the two species combined. Based on our sighting data in Iguaçu, collared peccaries were either scarcer than white-lipped or less conspicuous or both (36% for collared peccaries and 64% for white-lipped; N = 33 group sightings). Mean number of individuals per sighting was two for collared and twelve for white-lipped. Using this sighting ratio to estimate collared peccary density, as compared to white-lipped, the total estimate for the INP would be roughly 1,575 animals, or a biomass of 34,650 kg (mean weight of 22 kg). Therefore the estimated combined adult biomass of the two species would be approximately 113,400 kg for the entire park, or about 65 kg/$km^2$. To this figure should be added the potential yearly productivity, estimated at about 50,750 kg, for a total of 164,150 kg. The 81,000 kg required by the total jaguar population would thus comprise roughly half of the available peccary biomass. By itself, this level of predation would already be unsustainable, even in the short run. However, to this figure should be added competition from poachers, who also hunt selectively for peccaries (Becker 1981; Jorgenson and Redford 1993; Townsend 1995a) and the control exerted by neighboring farmers when peccaries raid their crops.

At the time of the study we predicted that, given the pronounced selection for white-lipped peccaries by jaguars (Crawshaw and Quigley 1984; Aranda 1994; Fragoso 1994; this study) and even allowing for some error in our estimates for this species in INP, white-lipped peccaries would not withstand current predation levels (both from jaguar and from humans) and would become extinct in the park within the foreseeable future. In this event jaguars, as an adaptable species, would likely gradually switch to smaller, abundant prey, as was probably the case in Belize (Rabinowitz and Nottingham 1986). Despte their initial abunddance, white-lipped peccaries did indeed disappear from the park in 1995 (Azevedo and Conforti 1998). Continued monitoring of the cat population is needed to determine the effect of this extinction on jaguar populations.

## MANAGEMENT AND CONSERVATION

When one first looks at INP from the air and realizes its condition as an island, thoughts of inbreeding depression and genetic deterioration (Ralls and Ballou 1983; Ralls, Harvey, and Lyles 1986; Lacy 1992) come to mind, especially applied to species such as the jaguar. However, data presented herein suggest that inbreeding may not be a serious consideration in jaguar conservation in Iguaçu, as long as a corridor with undisturbed areas is maintained in Argentina. Dispersing subadults of both jaguar and ocelot (Crawhaw 1995) can, and do, eventually cross between countries and ensure gene flow between populations.

Some 12,000 km$^2$ of subtropical forest remain in the Argentinean province of Misiones (J. C. Chebez pers. comm.). A total of 4,140 km$^2$ (34.5%) of this area is protected to some degree, forming an almost continuous corridor, about 200 km in length, linking INP to Turvo State Park in the state of Rio Grande do Sul, also in Brazil (Ministerio de Ecologia y Recursos Naturales Renovables 1993). Turvo State Park protects the last known population of jaguar in that state and represents the southern limit of the species in Brazil (Crawshaw and Pilla 1994). Jaguar populations in the province of Misiones, Argentina, may well represent the southern limit of the species in South America.

Even though an alternative, staple prey base and the habitat for jaguar may be preserved, problems with their coexistence with humans will likely tend to escalate if present conditions persist. Direct competition from poachers taking its main prey (peccaries, deer, and paca) will tend to increase the frequency of livestock depredation around INP. Jorgenson and Redford (1993) showed extensive overlap in the prey taken by big cats and humans in several areas in the Neotropics that resulted in the decline of populations of the former. Results from Townsend (1995a) for lowland Bolivia also show the negative impact of human hunting on the same species of prey taken by jaguar in INP.

The large areas occupied by individuals, the narrow shape of INP, and the lack of effective deterrents will always lead jaguars to the periphery of the park in search of food. It is difficult to deter cats from feeding on livestock once they become habituated to this food source. This habituation is especially critical for females with cubs, who tend to pass this acquired behavior to their offspring (Ewer 1973; Crawshaw and Quigley 1984). The considerable economic impact that livestock depredation imposes is amplified for low-income landowners, and it is unreasonable to expect these small farmers and ranchers to accept jaguar predation without retaliation. Indeed, jaguar killing for livestock depredation control is presently one of the main mortality factors for the species throughout its remaining range (Rabinowitz 1986; Crawshaw and Quigley 1991; Quigley and Crawshaw 1992; Hoogesteijn, Hoogesteijn, and Mondolfi 1993). In this study two adult males from Argentina were shot because of livestock depredation. In addition to animals killed by ranch owners, an unknown number of jaguars will continue to be killed by poachers hunting for other species in the park. Such was the case with the two radio-tagged subadult males, M13 and M32.

The picture gleaned from some hard-won facts on the ecology of jaguar in the present study is not a very encouraging one. There were problems with almost every individual that was radio-monitored: cats that were shot because they killed animals outside the park or because they came too close to a poacher who was killing their prey inside the park; animals that became dependent on food scraps from humans; and animals that had to be removed because of acquired bad habits toward humans or their property. However, given the sheer size of INP and the fact that the habitat and some very productive prey species will remain, jaguars may just have a chance to endure there. Still, for jaguar survival in the park, three conditions have to be quickly met:

1. The park needs a completed and maintained road around its dry perimeter.
2. This road will help with the next requirment: more efficient control of poaching. Poacher control also demands the efforts of park police and a fence (combining conventional wire netting and electric) that would not only serve as a deterrent for poachers entering the park but also decrease the chances of animals (both carnivores and herbivores) from searching for food outside the park.
3. The final requirement is a permanent corridor with undisturbed habitat in the province of Misiones, Argentina.

Reinforced by this project and a similar study in Turvo State Park (Crawshaw and Pilla 1994), close ties between IBAMA, Argentine environmental authorities, and some NGOs (such as Fundación Vida Silvestre, Argentina; WWF-U.S.; WWF-Brazil; and the Sociedade de Preservação da Vida Silvestre, or SPVS) are beginning to develop. These organizations are working toward (a) the maintenance of a corridor of subtropical forest in Misiones, linking Iguaçu and the Parque Estadual do Turvo, in Brazil (WWF-U.S. 1991) and (b) the developmnet of a Trinational Corridor (Argentina, Brazil, and Paraguay) that will eventually link Morro do Diabo State Park in São Paulo state, as the limit to the north, with Parque Estadual do Turvo in Rio Grande do Sul state, as the southern limit (M. Di Bitetti pers. comm.). A further small step in crosscountry collaboration may allow for a metapopulation approach (Gilpin 1987; Guerrant 1992; Pádua 1993; Forys 1995) for the management and conservation of jaguar populations in the area.

As with for the wolf recovery program in the United States (Mech 1995), the maintenance of a permanent local program of environmental education is essential to jaguar conservation efforts. This program should emphasize the importance of Iguaçu not only for the conservation of natural resources, including the large predators, but also to the local economy in terms of tourism. Through this program close contact should be kept with neighboring landowners in order to help solve problems when they arise. One of the objectives of the recently created National Predator Center (IBAMA 1994) is to promote some form of compensation for losses inflicted by predators. This compensation may be accomplished by cuts in federal, state, or municipal taxes or by direct reimbursement using funds raised by NGOs. A similar attempt is underway in northwestern Argentina (Perovic 1993), and there is a law project in the parliament of Misiones province, Argentina, to implement a mechanism of compensation through provincial tax cuts. As a consequence of the reported jaguar depredation problems in the vicinity of Iguazu National Park and other areas, a management-conservation action plan is beginning to be implemented in Misiones (Chebez 1995).

Ultimately, the fate of the jaguar in INP and, for that matter, of any large predators constrained within relatively small, isolated parks and reserves, remains in the hands of the people who live around these areas and who coexist with these species. However, it is the responsibility of managing agencies to resolve local conflicts that are inevitable in the interface between the natural and the man-modified worlds. Only through the integration of applied research, implementation of management recommendations derived from these findings, involvement of NGOs, and participation of local communities through environmental education programs will these species have a chance to survive.

# 18

# A Long-Term Study of White-Lipped Peccary (*Tayassu pecari*) Population Fluctuations in Northern Amazonia

## ANTHROPOGENIC VS. “NATURAL” CAUSES

JOSÉ M. V. FRAGOSO

White-lipped peccaries (white-lips—*Tayassu pecari*) are among the largest of Neotropical forest mammals, reaching weights of about 50 kg (Sowls 1984; Fragoso 1998a). They can form groups with more than 100 animals, and anecdotal reports exist of groups with 1,000 and even 2,000 individuals (Mayer and Brandt 1982; Mayer and Wetzel 1987; Fragoso 1994). Occasionally, herds and even entire populations have disappeared from areas where they were usually found, leading some researchers to hypothesize that white-lips are migratory, probably in response to variations in food supply (e.g., Kiltie 1980; Kiltie and Terborgh 1983; Sowls 1984; Bodmer 1990; Vickers 1991). This hypothesis has been supported by the stories of several Amerindian groups, who tell that local disappearances of white-lipped peccaries are normal and that the herds return after a given time (e.g., Vickers 1991).

Further support for the migratory hypothesis was provided by Kiltie (1980) and Kiltie and Terborgh (1983), who using a mathematical model based on step length and number of animals, demonstrated that a herd could cover an area of more than 200 km$^2$. On the basis of this model, they hypothesized that herds may be nomadic and lack fixed home ranges. Some researchers have interpreted the results of this model as support for the hypothesis of white-lipped peccary migrations (e.g., Vickers 1991), which has come to be considered a fact by many biologists working with white-lips (e.g., Mayer and Brandt 1982; Sowls 1984; Bodmer1990; March 1993). During fifteen years (1988–2003) of studying white lips in the northern Amazon region of Brazil, however, I have not found support for this hypothesis (Fragoso 1994, 1998a, 1998b, 1999, unpublished data), and have proposed that local disappearances are in fact in situ population declines caused by mortality and/or reproductive failure.

This article describes the disappearance of white-lipped peccaries from the northern portion of Roraima state, Brazil, an area of primary rainforest unimpacted by peoples of western descent, including colonists. The area is part of continuous rainforest that extends for about 1,500 km to the west, perhaps the same amount to the south, and hundreds of kilometers to the north of the study region (see below). To the east it borders the naturally occurring cerrado and savanna biome of the Guiana shield region. The Yanomami peoples, one of the least Westernized of native South American groups, inhabit much of the study area (Ricardo 1996). I consider three alternative hypotheses to explain the disappearance of white-lips in this area: (a) out-migration; (b) overhunting by humans; and (c) local in situ population decline resulting from an epidemic caused by an introduced pathogen.

## METHODS AND STUDY AREA

Maracá Island Ecological Reserve is located at 3°25′ N latitude and 61°40′ W longitude, on the northern margin of the Amazon basin in the state of Roraima, Brazil. The riverine island was created by the bifurcation of the Uraricoera River, a tributary of the Rio Branco in the Amazon watershed. The 110,000 ha of rainforest, isolated savannas, and wetlands that make up the reserve are protected by IBAMA (Brazilian Institute of the Environment and Natural Resources) as a site for research and forest conservation. The river provides an incomplete barrier between Maracá and the surrounding forests. In the dry season it is bridged by stepping-stone islands, and white-lips and other animals are frequently sighted swimming the river at all times of year (J. Hemming pers. comm.; J. Thompson pers. com.).

The Yanomami Indigenous Reserve starts almost at the margin of Maracá and extends westward for more than 300 km. It covers 9,400,000 ha of rainforest, montane forest, transitional forest, and some savannas and woodlands. Elevations range from 100 m above sea level in the Amazonian lowlands to 2,000 m in the Parima and Pacaraima mountains that divide the Amazon and Orinoco watersheds. To date the flora and fauna of these two study sites have not been affected by Western peoples, with the exception of the recent invasion by artisanal gold miners (*garimpeiros*) of some parts of the Yanomami reserve (MacMillan 1995; Milliken and Ratter 1998).

### POPULATION CENSUSES AND COUNTS ON THE EASTERN END OF MARACÁ ISLAND

Data on abundance and density of white-lipped peccaries on the eastern end of the island were collected during three separate periods. From June 1 to June 28, 1988, density transects were walked on a permanent trail system covering approximately 60 km (Fragoso 1998b). For each encounter the distance and angle of the herd to the transect line were noted along with the number of animals in the herd, and the information was used to calculate density using the King and Webb method (Schemitz 1980). Between June 1988 and June 1989, all individuals and herds encountered on the entire trail system during 227 days of walks were counted. All transect walks began between 7:00 and 8:30 A.M. and continued until 5:00 or 6:00 P.M., with a break between 11:00 or 11:30 A.M. to 1:00 or 2:00 P.M. On some days transect walks occurred only in the morning or afternoon. From January 1991 to December 1992, these transects were repeated in the same manner in the same area on 220 days.

## RIVER SEARCHES

To assess the status of white-lipped peccaries in the central and western portions of the island, I traveled along 200 km of the north channel (Santa Rosa Channel) of the Uraricoera River and its tributary the Uraricaá during ten days in September 1991. During the trip I interviewed gold miners and Xiriana-Yanomami and opened four 5-km-long trails oriented toward the center of the island along which I searched for white-lips and their sign (tracks, rooted areas, feces, and hair). The transect start points were spaced to maximize coverage of the island: two near the center of the island (separated by approximately 5 km) and another two also separated by about 5 km near the westernmost point of the island. All interviews were informal and included the following questions: (a) when was the last time you or someone you know saw white-lipped peccaries or their sign, (b) when was the last time you or someone you know killed a white-lipped peccary, and (c) how many individuals were killed during hunts?

## RADIO TELEMETRY

From January 1992 through January 1993, I radio-tracked seven white-lipped peccaries belonging to the only two herds using the eastern portion of Maracá island (region around the research station) and described their seasonal movement patterns and home range use (Fragoso 1994, 1998a, 1999). From June 1995 to May 1997, I again radio-tracked the two herds, which were still the only ones occupying this region of Maracá (Fragoso unpublished data).

## INTERVIEWS IN THE MACUXI INDIGENOUS AREA NEAR MARACÁ ISLAND

To the southeast and northeast of Maracá, the Macuxi indigenous people live in widely spread communities. To assess the status of white-lipped peccary populations immediately east of the island, I interviewed four Macuxi Amerindian hunters from a community (Boqueirão) located approximately 20 km southeast of the Maracá study area. Between 1991 and 1992 I repeated the interviews with fifty hunters from Boqueirão and Mangueira, a neighboring Macuxi community located approximately 15 km to the southwest of Maracá. These were the nearest villages in these directions from Maracá.

### INTERVIEWS AND SEARCHES IN THE YANOMAMI AREA

To assess the status of white-lipped peccaries in the Brazilian Yanomami area, I spent twenty-one days hunting with Yanomami hunters in April 1993, using the Paapiu area approximately 180 km southwest of Maracá as a base. I also interviewed representatives of thirty-eight Yanomami communities located throughout the reserve, including Yanomami people, indigenous health workers, Western teachers living in indigenous communities, and FUNAI (National Indian Foundation) personnel. These interviews were repeated with representatives of between thirty-five to fifty communities during the Yanomami Peoples Assemblies (which brings together Yanomami representatives from almost all villages) in 1996, 1997, and 1998. I collected information from at least one individual from each community represented at the assemblies. When one village was represented by more than one person, community members conferred before responding to my questions and then provided one community answer.

All interviews were informal and included the following questions: (a) when was the last time you or someone you know saw white-lipped peccaries or their sign and (b) when was the last time you or someone you know killed a white-lipped peccary? Because most Yanomami do not count beyond the number two (the exceptions are a few individuals with Western educations), I approximated the date of the last hunt by estimating the age of a child in the community who was said to have been born in the same year as the hunt.

### DOMESTIC LIVESTOCK AND DISEASE

To assess the health of domestic livestock in Roraima state, I reviewed files kept by the Roraima Department of Agriculture in 1996. Complete yearly records were available dating to the early 1970s. In Roraima almost all domestic livestock, including cattle, sheep, goats, pigs, horses, chickens, turkeys, guinea fowl, and ducks are free ranging.

## RESULTS

### EASTERN END OF MARACÁ ISLAND

Transect data showed that white-lipped peccaries were extremely abundant at Maracá in June of 1988, reaching densities of 139 to 542 individuals per km$^2$ (Fragoso 1998b). Herds were encountered 478 times during the 227 search days between June 1988 and June 1989; however, within this time period no peccaries were sighted after March 1989.

During the January 1991 to December 1992 study period, herds were encountered only thirteen times despite a search intensity similar to that in the 1988–1989 study period (220 search days: 103 days in 1991 and 117 in 1992). Thus abundance and density fell sharply between the first and the second study periods; herd encounter rates indicate that the decrease occurred in or shortly before March 1989. Radio telemetry data collected from 1991 to 1992 indicated that the study area supported between 1.4 and 8.3 individuals per km$^2$.

## RIVER SEARCHERS AND RADIO TELEMETRY

No white-lipped peccaries or their sign were found on the four 5-km-long transects cut in the central and western part of the island. Neither were animals or their sign found in the forest along the northern river channel toward the Yanomami Reserve. Fifteen gold miners interviewed during the river trip stated that they had not seen or killed white-lipped peccaries since 1989.

Radio telemetry data indicated that white-lipped peccaries have fixed home ranges, regularly use the same feeding sites (that is, they return to the same sites in subsequent years), and do not change their home range from season to season (Fragoso 1994, 1998a, 1999). The continuation of the radio telemetry study in 1995–1997 indicated that two herds continued using the same areas (Fragoso unpublished data). Herds were smaller in 1991–1992 (39 and 130 individuals per herd) than in 1995–1997 (70 and 200 individuals). Home-range size for the small and large herds increased from 21 and 109 km$^2$, respectively, during the 1991–1992 study to approximately 200 km$^2$ in 1997 for the herd with 200 individuals. The increase in home-range size over time as herd size increased and the fact that the large herd always had a larger home range than the smaller herd indicate that home-range size is related to herd size. Radio-collared individuals belonging to these herds were sighted up until November 2002 (J. M.V. Fragoso pers. obs.; G. de Oliviera pers. comm.).

The important point here is that from 1991 to 2002 the area continued supporting only the same two herds. During both tracking periods home ranges were spatially stable (no seasonal or yearly disjunctions in use of areas) within and among years. In other words, herds showed no sign of migratory behavior. They did not maintain two spatially distinct home ranges between seasons or years or between El Niño and non-El Niño years (the El Niño years of 1992 and 1997 caused marked declines in rainfall in the area, according to the climate records of the meteorological office of the Boa Vista, Roraima International Airport).

## MACUXI INDIGENOUS AREA NEAR MARACÁ

If the white-lipped peccary population on Maracá and its surroundings had declined, then there should also have been a reduction in the number of peccaries killed by humans. In 1988 the four Macuxi hunters interviewed near Maracá each killed between three and five peccaries per month (Fragoso 1998b). In the year between December 1990 and December 1991, however, the fifty hunters interviewed in the same region jointly killed only seven white-lips.

## YANOMAMI AREA

No data are available on white-lipped peccary harvests in the Yanomami area prior to 1990. Still, all the Yanomami interviewed, as well as persons associated with the Yanomami, reported that white-lipped peccaries were common prior to 1989. The anthropologist Bruce Albert who worked extensively in this region supported this report. He stated that during his Ph.D. fieldwork white-lips contributed up to 70% of the meat consumed by some Yanomami communities.

In 1993, during twenty-one days of hunting with Yanomami from five communities in the Paapiu area, no white-lips or their sign were encountered. Interviews with persons representing thirty-eight communities scattered throughout the Yanomami Reserve in 1996 and 1997 indicated that most of them had not seen white-lipped peccaries since 1989 or 1990 and some of them not since 1987.

At the 1998 Yanomami Assembly Davi Yanomami reported the return of one herd of white-lips to Ballalawu, a community located on the Parima mountain range that divides Venezuela (Orinoco drainage) from Brazil (Amazon drainage). In 2000 Marcos Wesley da Silva, the education coordinator for the nongovernmental organization Commission for the Creation of the Yanomami Reserve reported that from 1999 to 2000 hunters from Ballalawu had killed white-lips on two separate hunts spaced apart by approximately three months. Indigenous hunters from the communities of Auaris located in the Pacaraima mountains, (approximately 250 km to the northwest of Ballalawu) also noted the reappearance of white-lips in 2000 and reported killing multiple animals. In the Ballalawu case the interviewees reported that, when following the sign left by white-lipes, they concluded that the herd(s) had come up over the mountains from the Orinoco drainage (Venezuela) and was (were) moving into the valleys and lowlands of the Amazon drainage. The Auaris informants did not provide information on the directional movement of herds; however, Auaris sits near the top of Pacaraima mountain range, which forms the northern barrier separating the Orinoco and Amazon drainages.

In 2001 white-lips were again killed at all the aforementioned indigenous communities and at Demeni (far southern region of the Yanomami reserve) and close to the communities of Catrimani (near the southeastern extreme of the Yanomami reserve). Essentially, these communities form an outer ring along the western and southeastern boundaries of the Yanomami reserve. In these regions the reserve borders (and forms part of) the greatest extent of contiguous forest of the Amazon basin. This forest extends for about 1,500 km up and over the Pacaraima and Parima mountain ranges to the Andes Mountains. To the south it extends over mountains of 1,000 to 1,500 m above sea level for about 800 km until encountering the main channel of the Amazon River.

## DISCUSSION

At Maracá Island Ecological Reserve and in the surrounding Macuxi and Yanomami indigenous areas, white-lipped peccary populations either disappeared or decreased drastically to the point that even expert indigenous hunters could not find them. On Maracá the disappearance or decrease occurred approximately in March 1989. The sudden lack of white-lip sightings on the island and the reduction in white-lip harvests by indigenous peoples suggest that the phenomenon occurred throughout the contiguous forest and adjacent cerrado-savanna biome (with islands of forest) of the northern region of Amazonas and Roraima states in Brazil.

Here I consider three hypotheses that could explain the disappearance of white-lipped peccaries. The first hypothesis is that the white-lips migrated out of the study area. Most of the data collected do not support this hypothesis. The area over which disappearances took place is too extensive, and the vegetation, topography, and rainfall patterns too varied for the entire region to have become uninhabitable by white-lip herds searching for food. Rainfall ranges from 1,500 mm of rain per year in the east to over 2,000 mm in the west of the disappearance range (Barbosa 1997). This variation results in a diversity of biomes and plant associations, ranging from evergreen lowland rainforest to shrub-dominated areas, cerrado, savannas, and montane forest. Tree species identity also changes markedly from east to west: on Maracá alone, for example, 70% of the species that occur on the eastern end of the island are absent on the western end (Milliken and Ratter 1989).

If white-lipped peccary herds migrated seasonally or nonseasonally in search of food, they should have stopped once they encountered new plant communities or biomes with their potential for new and perhaps abundant food resources. At Maracá fruit availability does not seem to have varied greatly between the 1988–1989 and 1991–1992 sample periods (Moskovits 1985; Nunes 1992; Fragoso 1994). Even if fruit availability declined in some habitats due to changes in rainfall patterns (such as those caused by the El Niño Southern Oscillation, ENSO), many white-lip foods become superabundant in ponds and streams as they dry (many of these dry out only during El Niño years) (Fragoso 1999, pers. obs.).

Thus the hypothesis that the white-lips migrated is not supported because (a) fruit and seed availability did not vary between two critical time periods, (b) the white-lips should have appeared in some portion of the study area (110,000 ha on Maracá, 9 million ha in the Yanomami area), and (c) after a season or two, migrating animals should have returned to their original territory as seasons changed. Furthermore, if migrations were linked to major changes in rainfall patterns rather than seasonal changes, the white-lips should have returned when rainfall patterns normalized. Note, however, that white-lips did not return to the Yanomami area after the El Niño event of 1991–1992, and on Maracá they appeared to be unaffected by that El Niño event and those of 1997–1998 and 2002–2003 (Fragoso unpublished data). The herd with thirty-nine individuals in 1991 now contained ninety-seven animals in January 2003, and in March 2003 it split into two herds, one with twenty-seven and the other with seventy individuals (J. M. V. Fragoso and K. M. Silvius pers. obs.).

The radio-tracking data provides additional evidence against the migration hypothesis: during the years that two herds were tracked visually and by radio, they used their large home ranges in a regular fashion and gave no sign of migratory behavior (Fragoso 1994, 1998a, 1998b, 1999, unpublished data). They did not leave the area even when food availability was low in some portions of their home range. Their home ranges provided herds with a sufficient food in the appropriate spatiotemporal pattern (Fragoso 1999) to support population increases from 1991 to 1997 and possibly until 2002.

The only other published study that used radio telemetry to evaluate white-lip herd movements tracked thirty-six individuals in Corcavado, Costa Rica, from 1996 to 1998 and also found that herds did not migrate (Carrillo, Saenz, and Fuller 2002). White-lips did not exhibit migratory behavior at Corcavado even when rainfall decreased dramatically from one year to next because of an El Niño event. The decreased rainfall correlated with a drop in fruit production in the area; however, as in Fragoso's 1999 study the Corcavado white-lips responded by expanding home-range areas to include more habitats rather than by migrating (Carrillo, Saenz, and Fuller 2002).

The second hypothesis, that white-lipped peccary populations were reduced by overhunting, is also difficult to support. White-lips disappeared in 1989 from many areas, whereas the influx of gold hunters into the Yanomami area began in 1983 and reached its peak in 1987 (MacMillan 1995). One would expect overhunting to impact the populations much more rapidly, given that approximately 40,000 gold miners were living and hunting in the area. Furthermore, ten of the Yanomami communities that reported losing white-lips in their hunting areas (Yanomami hunting areas are somewhat larger than the home range of a white-lipped peccary herd; Good 1989) were not invaded by gold miners. If hunting by invaders had caused the loss of white-lips, these noninvaded areas should not have been affected. Additionally, while some illegal hunting by gold miners may have occurred along the northern margin of Maracá, white-lips disappeared from the eastern portion of the island at the same time as in the Yanomami Reserve. This part of Maracá was heavily patrolled by over 100 biological workers of the Maracá Research Project of the Royal Geographical Society and the National Institute for Research in the Amazon (INPA) from the beginning of 1987 to 1989 (Milliken and Ratter 1998).

The third and final hypothesis is that mortality from an epidemic caused a decline in white-lipped peccary populations at the regional level. The following observations support this hypothesis:

1. White-lip populations in noninvaded areas of the Yanomami reserve disappeared.
2. The factor that affected the white-lip populations must have been something that can affect individuals dispersed over an enormous area. Such a widespread agent

is a characteristic of epidemics in other mammal populations (Crosby 1986; Young 1994).

3. A researcher working with primates on Maracá at the time of the disappearance found the bodies of five white-lipped peccaries at one site (A. Nunes pers. comm.), and her description of the carcasses indicates that they were not killed by humans or other predators.
4. In 1989 there was an epidemic in free-ranging domestic pigs on ranches adjacent to Maracá and the Yanomami reserve. The disease, undocumented and unidentified by veterinarians, killed over 50% of newborn piglets and caused a higher than normal mortality in adult pigs (J. Alves, local rancher, pers. comm.).
5. In 1989 there was a documented outbreak of foot and mouth disease in cattle on these same ranches (J. Alves pers. comm.). Further, the largest outbreak of foot and mouth disease documented for Roraima state occurred in 1989 (records maintained by the Roraima Department of Agriculture).
6. Both the pig and cattle disease outbreaks occurred at the same time that white-lips disappeared on Maracá and in the Yanomami area.
7. When gold miners entered the Yanomami area, they brought with them domestic pigs as a source of food (Fragoso pers. obs.).
8. White-lipped peccaries live in herds of more than 100 individuals, the number of animals necessary to maintain an epidemic in a reinfection cycle (A. Dobson pers. comm.).
9. Where they cooccur, free-ranging or feral domestic pigs and white-lips share use of wetland areas.
10. Because white-lipped peccaries are not territorial, they do not maintain exclusive use home ranges, and herds occasionally come together (Fragoso 1998a). This socioecology would allow the rapid dissemination of a disease among herds and across the entire population.

Disappearance patterns similar to those described here have been reported for white-lipped peccaries in other areas. For example, white-lips disappeared from Manu National Park, Peru, from 1981 to 1992 (L. Emmons and J. Terborgh pers. comm.), from the Siono-Secoya area of Ecuador from 1975 to 1985 (Vickers 1991), and from the Yuqui area in Bolivia in 1985 (Stearman 1990). In all these cases researchers working in the areas interpreted the disappearances as migrations. It should be noted that in all cases white-lips remained absent from the areas for approximately ten years. Such long periodicity is not normal in migratory ungulates, but it is typical of mammal populations that exhibit boom and bust cycles (Krebs and Myers 1974). Note the reappearance of white-lips in the Yanomami area from 1997 to 2000 after having been absent for about eight to eleven years.

I suggest that what has been described as white-lipped peccary migrations may in most cases have been in situ population declines. Such population cycles are probably a normal characteristic of this species' life history. I propose, however, that the characteristics that make white-lips susceptible to endemic diseases also make them susceptible to exotic diseases to which they have no resistance and which can cause more marked population declines with a longer recovery time than that of cycles caused by endemic diseases. The relationship between white-lips and domestic livestock may thus be similar to that between native Amerindian populations and the humans that migrated, together with their diseases, from the Old World.

Most of this report was first presented at the wildlife meeting in Iquitos, Peru, in 1995 and included data collected up until December 1992. As described above, I continued working at Maracá and in the Yanomami area from 1994 to the present (2003), tracking the same herds on the eastern end of Maracá in 1995–1997 and visiting Maracá and/or the Yanomami region in 1998, 1999, 2000, 2001, and 2002 for at least one month each year. Two herds are still using what appear to be the same home ranges in 2002 (Fragoso pers. obs.). This constancy means that the same herds have remained in the same general area for at least eleven years. During this time period herd size has increased, and the largest herd has expanded its home range to the north and west, but both herds still use the same areas they used in 1990–1992 and have not been absent from the study site during the entire period. In addition, the increase and splitting of the smaller herd in 2003 suggests that on Maracá populations are at or nearly at their high points and may once again enter a decline. If true, herds splintering off from the main groups should begin dispersal movements out of their natal home ranges, as discussed below.

On the basis of my extended observations, especially the increase in herd size and the apparent movement of white-lipped peccaries from the Orinoco basin into the Amazon basin, I propose the following scenario for the large scale spatiotemporal ecological dynamics of white-lip populations:

1. White-lip herd disappearances are the result of epidemic outbreaks of disease (either endemic or exotic) that kill off most individuals.
2. In areas where there is hunting by humans, this activity may extirpate white-lips that survive the epidemic.
3. Where there is/was no hunting, populations decline, but enough individuals survive to allow the slow repopulation of an area. At Maracá this has been a thirteen-year period from 1989 to the present, but abundance/density levels have yet to attain the levels observed in 1988–1989.
4. Where hunting may have extirpated populations, initial reappearance is slower (eight to twelve years in the Yanomami area), and this reappearance occurs through a process of recolonization by herds dispersing from very distant areas (hundreds of kilometers) that travel across major geographical barriers (e.g., mountain ranges).

White-lip abundances in the Yanomami reserve are only now approximating the levels observed on Maracá in 1990–1992. Of interest is how long it will take for white-lip populations in the Yanomami area to return to pre-1989 levels, when they formed up to 70% of the meat consumed by many Yanomami communities.

If the above scenario is correct, then white-lip populations fluctuate synchronously across very large spatial and temporal scales (perhaps decadal time scales). I predict that white-lip populations in both the Yanomami reserve and Maracá will continue increasing and should eventually attain the very high densities observed prior to 1989. At high densities herds will fission and subherds disperse away from the very large resident parent herds. Subherd dispersal will move individuals away from their natal home range toward areas unoccupied by other herds. This type of movement is best described as a population-level dispersal event and not as a migration. Note that this process may already have started at Maracá. There is evidence that herds have begun dispersing across the rivers, as they did prior to 1990. From December 2002 to March 2003, a herd was observed on numerous occasions on Nova Olinda island (G. de Oliviera pers. comm.), an approximately 1000-ha island that lies between Maracá and the mainland. White-lips did not use this island from 1991 to 1997.

Dispersal of this type is probably responsible for the recolonization of the Yanomami reserve by white-lips. This type of dispersal may also explain the cross-river movement of white-lips observed from Maracá in 1987–1988 during the period of peak population densities (J. Hemming, J. Thompson, and G. de Oliviera pers. comm.) and records of white-lips crossing the savannas of northern Roraima (J. Alves and G. de Oliviera pers. comm.). These dispersal events may also be what indigenous peoples refer to when they say that the "white-lips eventually return." There are many valid definitions of migrations (see Baker 1978), but all necessitate returning to the start point. Dispersion means movement away from a source, most likely without return. At the metapopulation level white-lip populations appear to be linked across scales of thousands of square kilometers. Maintaining white-lip metapopulation dynamics at this scale will continue to be a major challenge as the Western colonization zone penetrates deeper into the Amazon forest.