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MAMMALS AND THEIR BIOMASS ON A BRAZILIAN RANCH

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Introduction

Biomass data on mammals in the neotropics have been collected primarily in rain forest areas (Eisenberg and Thorington, 1973), whereas the more open vegetation types, which cover vast tracts of South America, have received little attention, the work by Eisenberg et al (1979) in the llanos of Venezuela being a notable exception. The purpose of this paper is to present information on abundance and biomass of mammals on a cattle ranch consisting of a mosaic of pasture, scrub, and woodland, a habitat now representative of many areas in Brazil and neighboring countries.

Between April 1977 and September 1978, I studied wildlife intermittently on the Acurizal ranch (17° 45'S, 57° 37'W) at the western edge of the Pantanal, a swampy plain along the upper Paraguay River in the Mato Grosso states of Brazil. One aim of the project was to measure the impact of jaguar * predation on the prey animals. The cats subsisted on such a wide variety of food (see Schaller and Vasconcelos, 1978a) that it was necessary to estimate abundance of all larger mammals before attempting to evaluate the jaguar's effect on their populations, and these data form the basis of this report. In spite of having been a cattle ranch for nearly 200 years, Acurizal still harbored a moderate amount of wildlife until in mid-1978 ranch hands began to hunt jaguar and other species so persistently that the project had to be prematurely terminated there.

The Environment

Description of study area

The Pantanal, 100,000 km² in size, consists of marshes and seasonally flooded

* Scientific names of most mammals are given in Tables 2 and 3.

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Figure 1. A view of First Valley on the Acurizal ranch, showing mainly pasture and cerrado in the flatlands, deciduous forest on the lower slopes, and grassland on the upper slopes.

grasslands, sparsely dotted with trees, whose expanses are broken by thickets, stands of palm, and patches of deciduous to semi--deciduous forest; there are many shallow ponds, and streams meander sluggishly over the landscape before joining the Paraguay River. The whole area is flat to slightly undulating and lies only at about 100 m above sea level. The Acurizal ranch, 137 km² in size, comprises a strip of land, about 24 km long and 5-10 km wide, between the Paraguay River and the crest of a ridge, the Serra de Amolar, which attains a height of 900 m. Two broad valleys, named here the First and Second valleys, cut into the range. About a third of Acurizal consists of floodplains and these have been wholly under water for most of the year since a severe flood in 1974. Another third of the ranch has relatively level and dry terrain in the valleys and along the margin of the flood plain. Most ranching activities are confined to this area and most wildlife is there too. A final third consists of steep rocky slopes and ridge tops (Figs. 1 and 2).

Climate

The climate is seasonal with nearly half of the average annual precipitation of 1120 mm falling between December and February (Fig. 3). June to September are dry; in 1978, an exceptionally dry year, only 18 mm of rain were recorded at Acurizal during this period (Fig. 4). The rainy season has a marked effect on the water level of the Paraguay River. The water drops gradually some 2.75 m between March and December and then rises abruptly, reaching its highest point again in March (Fig. 3). While the annual change in water level is fairly small, the terrain is so flat that large tracts become inundated.

Mean monthly temperatures remain constant except for a dip during the dry season (Fig. 3), the cool time of year when winds from the south may bring a cold front that drops temperatures close to 0°C. The lowest temperature during the study was 7.7° and the highest 41°C. Average monthly minima ranged from 18° to 24° and maxima from 28° to 34°C.

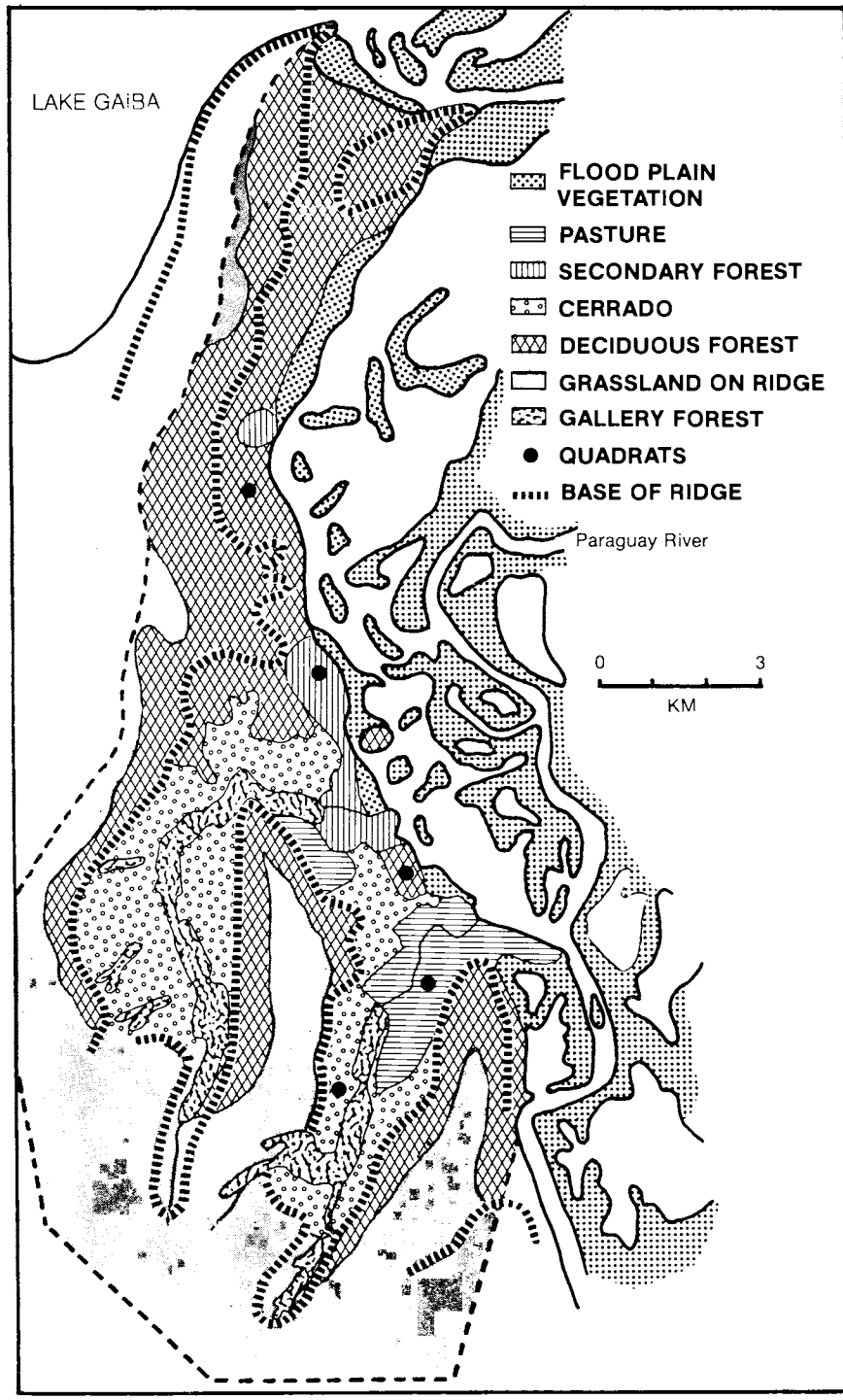

Figure 2. Vegetation types of Acurizal (adapted from Schaller and Crawshaw, 1980).

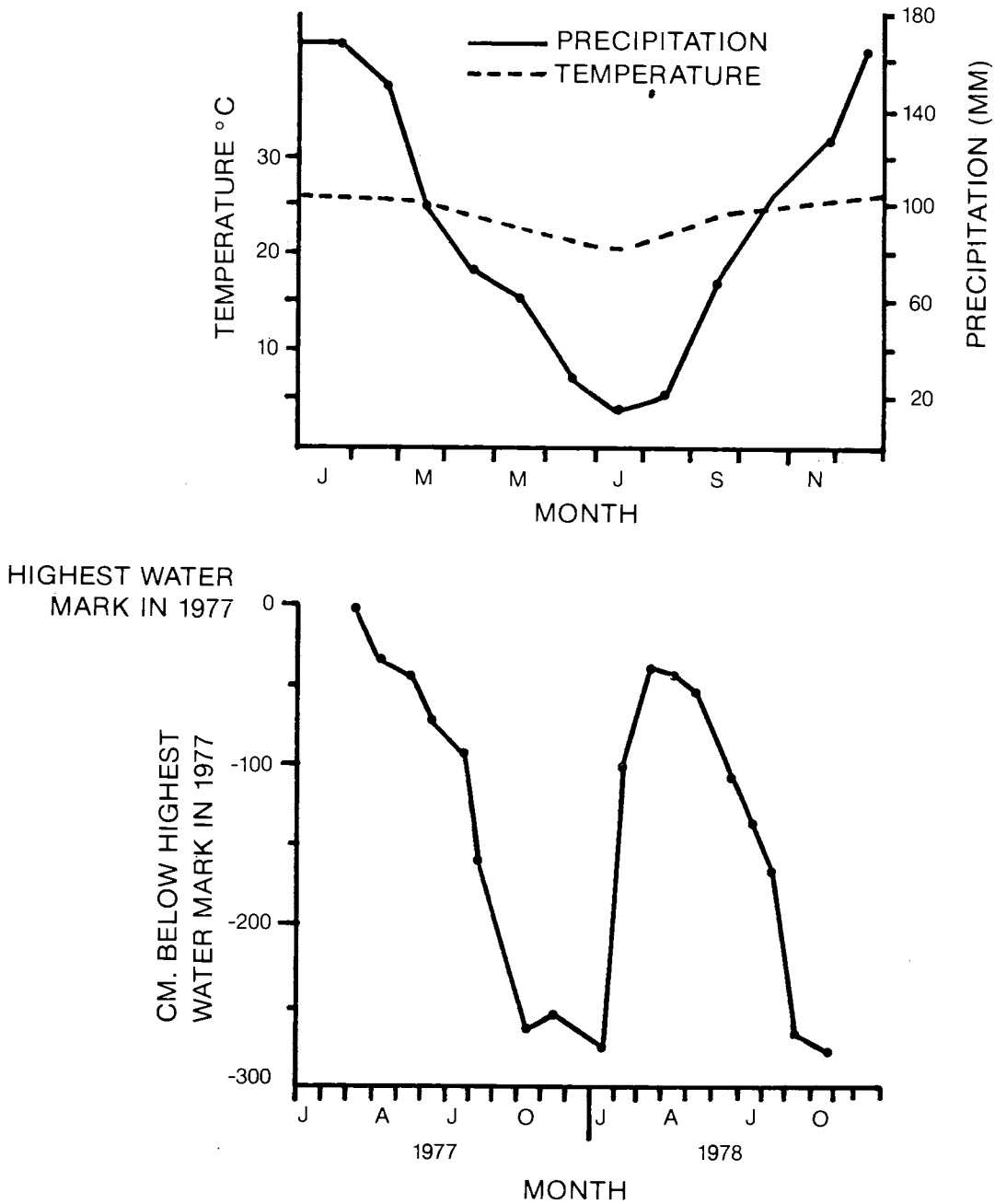

Figure 3. Mean monthly temperature and precipitation at Corumbá, Mato Grosso (after Anon. 1977), and water levels of the Paraguay River at Acurizal in 1977-78.

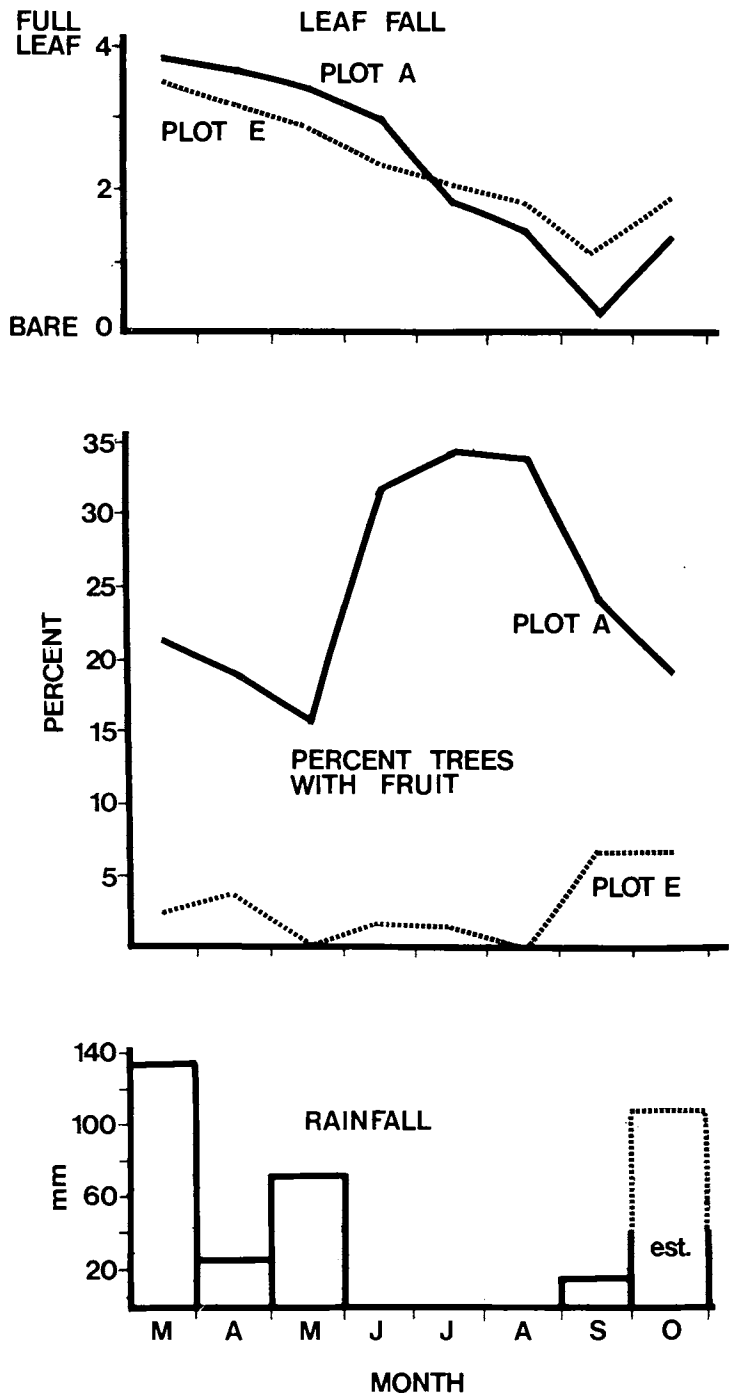

Figure 4. Relative abundance of leaves and percent of trees in fruit at Acurizal from March-October 1978, based on monthly checks of the 160 largest trees on quadrat E and 129 largest trees on A. The rainfall during this period is also indicated.

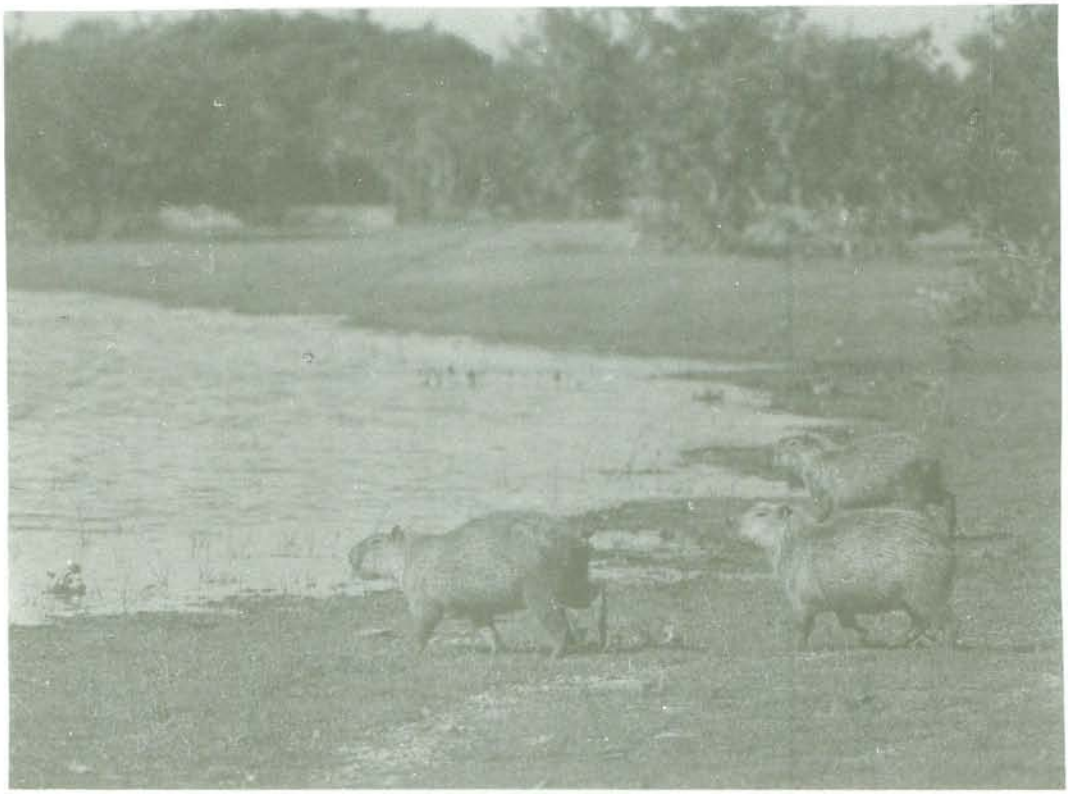

Figure 5. The grassy shoreline at Acurizal is a favored feeding area of capybara.

Vegetation

The main vegetation types at Acurizal are shown in Fig. 2. To obtain data on physiognomy and phenology, 5 one-hectare quadrats were established, one each in pasture, secondary forest, and cerrado, and two in deciduous forest. Every tree of 15 cm DBH or more was numbered, measured, and identified, as well as checked for leaf-fall and fruiting at monthly intervals between March and October 1978. Ground-cover was determined by placing a 50 x 50 cm square at 3 m intervals in transect lines within the quadrats and estimating the percent of area occupied by each plant type. Since a general description of the Pantanal vegetation can be found in Veloso (1948) and Anon. (1977), and a more detailed one has been presented by Prance and Schaller (1982), only a brief outline is given here.

Vegetation types. The whole floodplain was submerged to 1 m or more during the study, only strips of high-lying ground along rivers and channels emerging at the height of the dry season. Rafts of water hyacinths (*Eichhornia azurea* and *E. crassipes*) clog the margins of waterways and bays, and floating mats of vegetation, consisting of rushes and sedges (*Cyperus surinamensis, Scirpus cubensis*) and a variety of herbs and vines, are common. On flooded pastures various shrubs (*Ipomoea fistulosa, Cassia pendula*) and tall herbs (*Oyedaea trachyphyllum*) protrude above the water's surface. There are narrow gallery forests, the trees often no more than 10 m tall except for an occasional emerging *Cassia grandis*. *Inga sp.* is dominant, and *Cecropia sp., Nectandra* sp. and *Pterocarpus rohrii* are prominent. These gallery forests are often so heavily draped with vines (*Cissus* cf. *hassleriana, Mikania periploci-*

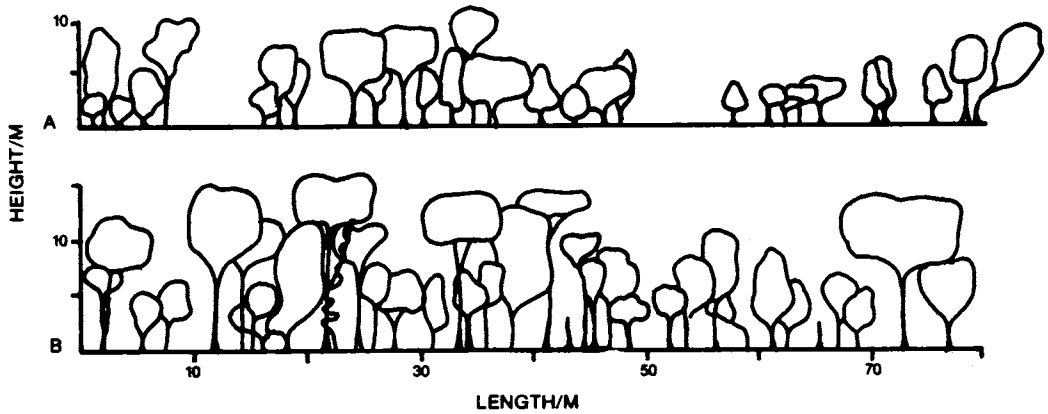

Figure 6. Profile diagrams of all trees (15+cm DBH) along a 80 x 5 mm strip in A) cerrado of quadrat E, and B) in deciduous forest of quadrat B.

folia, Ipomoea alba) that the trees themselves remain barely visible.

At the edge of the flood plain is a strip of scrubby trees (*Rheedia gardneriana, Pithecolobium multiflorum*), shrubs (*Psidium guineense, Senna aculeata*), and thickets of *Astrocaryum* palm beyond which a narrow grassy beach, periodically inundated, marks the transition to high ground (Fig. 5).

A deciduous forest covers much of the lowlands and hillsides (Fig. 2). Trees reach a height of 22 m and the canopy, though uneven, is continuous (Fig. 6B). Two quadrats, one in a selectively felled forest near the bay and one in an undisturbed stand at the base of a ridge, showed that there were 274-275 trees (15+cm DBH) of about 35-40 species per hectare, a low number when compared with the 350 trees of 179 species on an area of similar size in the Amazonian rainforest (Prance et al, 1976). Such small-leafed leguminous trees as *Caesalpinia floribunda, Acacia* cf *paniculata,* and *Acosmium cardenasii* predominate; broad-leafed species, among them *Aspidosperma pyrifolium* and *Simira* cf *hexandra,* are particularly common in the understory. *Attalea* palms are abundant in low-lying, disturbed forest. On slopes, trees are stunted, often no more than 10 m tall, and species characteristic of dry areas (*Albizzia hassleri, Bauhinia* sp) are conspicuous, as are thickets of *Randia* aff. *armata* and other shrubs. Groundcover in the flatlands consists mainly of patches of spiny *Bromelia* and *Ananas,* whereas in hilly terrain there are mostly low shrubs; grasses (*Kyllinga odorata, Axonopus compressus*) and herbs (*Chaetothylax tocantinus, Abutilon aristulosum*) are scarce (Table 1). Over 75% of the ground is bare, covered only with dead leaves.

'Cerrado', a vegetation type typical of central Brazil (Goodland, 1971), is found at Acurizal mainly in the two valleys. Physiognomically, it varies from grassland with scattered trees to woodlands of varying densities. A transect through one woodland quadrat showed that most trees were around 10 m tall and that the canopy was discontinuous (Fig. 6A). There were 189 trees (15+cm DBH) of 22 species on the quadrat, a third fewer species as in deciduous forest, and 2/3 of the trees belonged to 6 species (*Qualea* cf. *parviflora, Q. grandiflora, Caryocar brasiliense, Tabebuia caraiba, Diptychandra glabra, Hymenaea stigonocarpa*). The DBH of 81% of the trees belonged to the smallest size class measured, 15-25 cm, as compared to only 62-64% of the trees in that class in deciduous forest. In spite of shrubs and scrubby trees (*Davilla elliptica, Lafoensia pruniciflolia*) and occasional bamboo thickets, visibility in cerrado is generally good and passage easy, especially since fires sweep across much of this habitat annually. A

Table 1. Tree number and groundcover in 4 vegetation types at Acurizal

QUADRAT (1 ha)	FOREST TYPE	NO. TREE SPECIES (15+cm DBH)	TOTAL NO. TREES (15+cm DBH)	No. Sample Plots	Groundcover					
					Grass	Bromeliad	Herb	Palm	Vine and shrub	Total
A	Deciduous	35	224*	75	3.3	15.0	.1	0	5.9	24.3
B	Deciduous	—	275	80	tr.	0	1.1	0	13.9	15.0
E	Cerrado	22	190	75	21.6	4.2	1.5	4.5	4.4	36.2
C	Secondary	1	1*	75	3.2	37.0	13.9	0	7.0	61.1
D	Pasture	2	2	50	58.0	10.4	tr.	0	0	68.4

* Excludes 50 *Attalea* palms on A and 31 on C.

coarse bunchgrass covers much of the ground, and patches of bromeliads and *Bactris* palm occur (Table 1). As terrain becomes hilly and rocky, trees become scarcer and more gnarled, and species such as *Bowdichia virgilioides, Curatella americana,* and *Miconia* spp. increase in relative abundance. The upper slopes and ridgetops consist of grassland with an occasional cerrado tree.

A gallery forest, with trees up to 25 m high and some over 75 cm DBH, borders the streams in the First and Second valleys. *Mabea fistulifera, Licania octandra, Guarea* sp. and *Myrcia* sp. are some of the trees found in this habitat and not the others; *Attalea* palms are common near water. Since many species are evergreen, this is the only habitat at Acurizal which retains its moist shadiness throughout the year. The ground is virtually bare except for rare herbs such as *Geophila repens.*

Most Acurizal habitats have been modified to promote cattle production. Trees in deciduous forest have been selectively felled for fence posts, thickets in cerrado have been eliminated to increase the grazing area, and blocks of forests have been entirely converted to pasture. Some pastures were subsequently abandoned, and are now covered with a dense growth to a height of 5 m or more, a mixture of *Attalea,* saplings (*Bauhinia* sp.), shrubs (*Chamaecrista nictitans, Psidium guineense*), *Bromelia,* and tall herbs (*Eupatorium squalidum*), all bound with a tangle of vines (*Mimosa sensitiva, Cydista decora*). However, other pastures remain open, broken only by isolated trees (*Vochysia* sp., *Xanthoxylum cinereum*) and islands of bromeliads and brush (Fig. 1, Table 1).

Phenology. The seasonal climate markedly affects the vegetation. During the rains from November to March, the trees are in full leaf, although a few cerrado species already begin to shed toward the end of this period. April to June is a time of transition when many herbs and vines bloom but forests and pastures dry up until they acquire the brown tinge of dying vegetation. From then until September or October is the dry season during which most trees and shrubs in deciduous forest and cerrado lose their leaves, exposing the ground to the sun, and fires leave many areas bare and black. The land greens and leaves unfurl rapidly with the first heavy rains of October.

Fig. 4 presents the seasonal change in the relative number of leaves on trees in cerrado and deciduous forest. Cerrado had more leaves than deciduous forest at the height of the dry season mainly because one species, *Caryocar brasiliense,* sheds its leaves and bursts into new ones during any month from March to October, some trees doing so twice in that period.

Flowering and fruiting of trees does not show as regular a pattern as does leaf-fall: peak flowering of *Caesalpinia* was in March, *Pseudobombax* in May-June, *Bowdichia* and *Pouteria* in July-August, *Tabebuia*

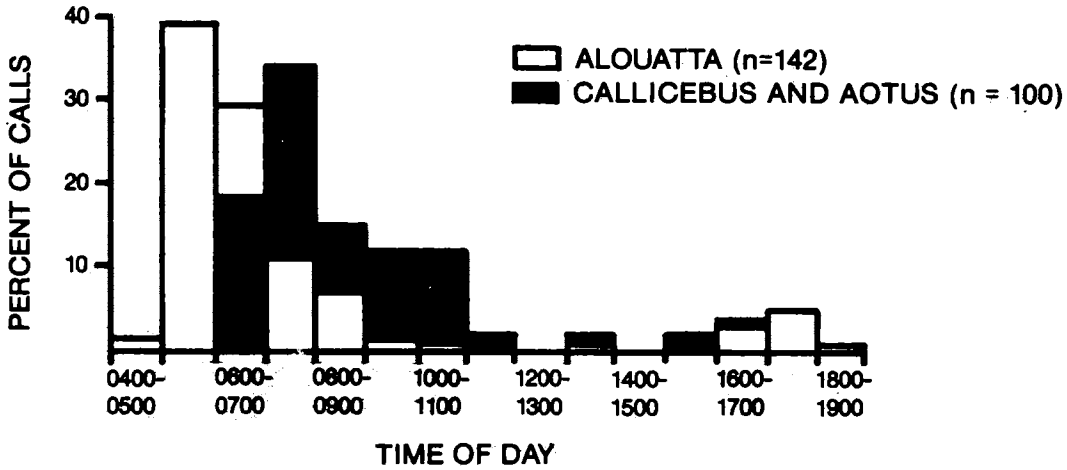

Figure 7. Frequency of calling by *Alouatta* and by *Callicebus* and *Aotus* at various times of day at Acurizal. The *Alouatta* data were collected in June-July 1977, and the other throughout the year.

caraiba in August, *Magonia* and *Simarouba versicolor* in September, and *Acosmium* in October, to mention a few species. *Curatella americana* and *Tabebuia impetiginosa* may be in bloom from May to September but with one or more peaks. Consequently trees are also in fruit during any month, especially since seedpods of leguminous species often remain on trees for several months after they have ripened. Seeds and fruits are more abundant in deciduous forest than in cerrado, as measured by percent of trees with fruit each month (Fig. 4). This difference in availability of seeds as food for animals in the two habitats can also be expressed in another way: 20% of the cerrado trees on quadrat E but 52% of the deciduous forest trees on quadrat A were in fruit at some time between March and October, and the latter figure does not include the 50 *Attalea* palms.

Census Methods

The problems of censusing forest mammals, especially small, cryptic, or nocturnal ones, have been discussed by Eisenberg and Thorington (1973) and Cant (1977). Census methods at Acurizal varied with the species.

Monkeys are known to limit themselves to relatively small home ranges (see Izawa, 1976), and this provided a basis for plotting on a map the distribution of groups observed on the ranch. *Callicebus* was shy, hiding in leafy canopy when it sensed danger, but since groups vocalized loudly it was easy to pinpoint the location of animals. *Aotus* occasionally called in daytime too (it was not heard at night), but its vocalizations sounded to me so similar to those emitted by *Callicebus* that I was unable to distinguish the two. *Alouatta* also called communally but, as Fig. 7 shows, its daily peak of vocalizing was between 0500 and 0600, two hours earlier than that of *Callicebus*.

Numbers of several species, such as brocket deer and armadillos, were estimated on the basis of walking through various habitats and recording every individual seen (Table 4). Such strip censuses covered about 2282 km away from human habitations of which 794 km were along the shoreline, 837 km in cerrado, and 215 km in pasture, all habitats with good to excellent visibility. In addition, 86 km of transects were made in secondary forest, 25 km in gallery forest, and 120 km in deciduous forest. Visibility in forest varies greatly with the season, it being best at the height of the dry season when many trees are almost leafless. Although I estimated

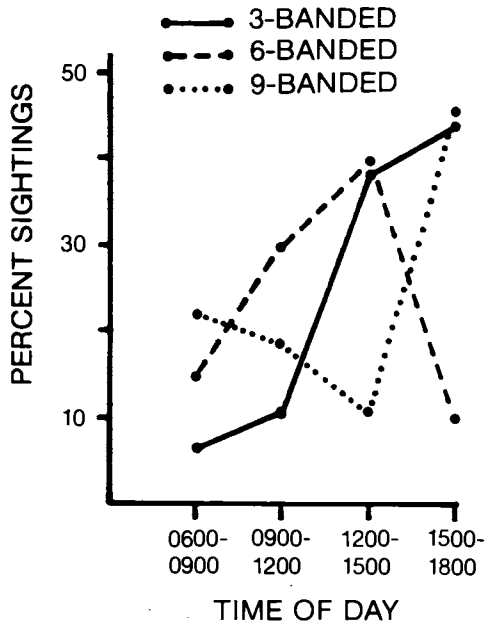

Figure 8. Frequency of sighting 3-banded (n=18), 6-banded (n=20), and 9-banded (n=26) armadillos at various times of day in the Acurizal area.

the distance between myself and any animal sighted, using the figures as an index from which to compute the width of transect strips and hence population size in each habitat, so many biases are involved in gathering data that the results provide only a rough approximation of numbers. For example, a brocket deer may respond by fleeing before being sighted, it may silently sneak away or stand quietly behind a screen of vegetation, or it may crouch motionless, permitting an observer to pass at 2 m. Time of day may have an influence on armadillo sightings (Figs. 8), the 3- and 9-banded species being most active in late afternoon when the 6-banded seems to be least active.

To provide a check on the census results, I made several foot transects during which the number of fresh tapir and brocket droppings and newly dug armadillo holes were counted in a strip 4 m wide. The study on the ranch had to be terminated before all habitats were adequately sampled, but walking distances included 21 km in gallery forest, 14 km in deciduous forest, and 144 km in cerrado.

An attempt was made to estimate the size of the crab-eating fox population by live-trapping, tagging, and releasing 8 individuals, and then determining numbers by using the ratio of tagged to untagged animals sighted. However, the method proved unsuccessful because foxes were seldom observed.

Information on relative densities of rodents and rat-sized marsupials was obtained by sampling different habitats with snap traps for a total of 584 trap nights. Afterwards each of the 5 one-hectare vegetation quadrats were snap-trapped with mouse and rat traps for 4 to 7 consecutive days during the dry season, for a total of 915 trap nights, until it was felt that all residents had been captured. Traps were not set in a grid but at the most promising locations such as in hollow logs and by tangles of brush. Since ants and roaches consumed moist bait within a few hours, whole peanuts were glued on the treadles.

The abundance of several species could only be estimated on the basis of spoor. The size and shape of jaguar and puma tracks, coupled with radio-tracking one cat of each species, provided a reliable figure of population size (Schaller and Crawshaw, 1980). Ocelot, raccoon, and giant anteater were scarce, judging by tracks, and I did little more than guess at actual numbers. Tapir are secretive, seldom permitting themselves to be seen in daytime, but the propensity of individuals to remain in a limited area (Terwilliger, 1978) provided a means of estimating population size, using both location and differences in track dimensions as criteria.

Capybara concentrated along beaches during the dry season to feed on young green grass. Intensive counts were made along 8 km of beach, about 1/4 of the total distance, and numbers were estimated for the remaining area on the basis of sightings and fresh tracks.

Number of Species

Sixty-four species of mammals were recorded at Acurizal (Tables 2 and 3), a list which presents no distributional surprises, most species being widespread in this part of South America. More work on the ranch might also reveal pampas cat (*Felis colocolo*), oncilla (*Felis tigrina*), and grison (*Galictis vittata*), all species which have been reported from the western Pantanal (Allen, 1916; Miller, 1930); the four-eyed opossum (*Philander opossum*) may also occur at Acurizal for I collected it in similar habitat elsewhere in the Pantanal. The giant otter (*Pteronura brasiliensis*) has been virtually exterminated in the area. Some species, such as paca (*Agouti paca*) and cavy (*Cavia aperea*) were unexpectedly absent from Acurizal possibly because the surrounding swamps and hills present barriers of unsuitable habitat.

A third of the species consists of bats. The list is probably incomplete and biased in favor of insectivorous bats which were at times conspicuous, small colonies living in houses (*Myotis*) and caves (*Peropteryx*), and flying at dusk over rivers and bays (*Molossus*). All 6 frugivore species were caught in a mist net at the same fruiting fig tree.

Estimates of Numbers and Densities

Although Acurizal is 137 km² in size, 48 km² consist of inundated flood plain, used only by capybara and about 25 howler monkeys, and 19 km² comprise ridge tops covered with grass and a few trees, a barren habitat with some 6-banded armadillos and little else. These two areas are deleted from further consideration, leaving 70 km² of terrain, of which deciduous forest includes 37 km², cerrado 18 km², gallery forest 6 km², managed pasture 5 km², and young secondary forest 4 km².

Primates

Ten of 24 *Cebus* groups frequented gallery forest, two secondary forest, and the rest deciduous forest. It was difficult to determine group size because members tended to be widely scattered. Counts of seemingly complete groups varied from 3 to 20 with an average of about 8, a figure within the size range of other reports (Izawa, 1976). Of 65 animals sampled, 68% were adult, 14% yearling, and 18% young. A calculated 192 *Cebus* were found in groups, and the total number on the ranch, including solitary animals, was probably somewhat higher, perhaps about 225.

Twenty-one *Alouatta* groups were tallied, 6 in gallery forest and the rest in deciduous forest; in addition, several solitary males and a male group with 6 members were seen. Sixteen groups ranged in size of from 4 to 12 (mean 7.2). An average group contained 1.8 (1-4) black or adult males, 0.6 (0-2) subadult males, 2.4 (1-4) females, 0.8 (0-2) yearlings and 1.6 (0-3) young. Males and females each comprised 33% of the group membership. Since some males were solitary, the population as a

Table 2. Bats of Acurizal

Principal food	Species
Insects	Eptesicus furinalis
	Eumops auripendulus
	Micronycteris minuta
	Molossops temmincki
	Molossus ater
	Molossus molossus
	Myotis nigricans
	Myotis albescens
	Noctilio albiventris
	Peropteryx macrotis
	Phyllostomus hastatus
	Rhynchonycteris naso
	Tadarida laticaudata
Blood	Diaemus youngi
Fruit	Artibeus fallax
	Artibeus jamaicensis
	Artibeus lituratus
	Carollia perspicillata
	Chiroderma villosum
	Sturnira lilium
Nectar	Glossophaga soricina

Table 3. Mammals (excluding bats) and their biomass at Acurizal

Scientific name	*Common name*	Average Weight (kg)	Source for Weight *	Estimated Number	Total Biomass (kg)
Marsupialia					
Monodelphis brevicaudata	Short-tailed opossum	.06	1	—	—
Marmosa pusilla	Murine opossum	.06	2	—	—
Didelphis albiventris	White-eared opossum	1.25	8	?	—
Primates					
Aotus trivirgatus	Night monkey	.80	2	30	24.0
Callicebus moloch	Titi monkey	.70	1	70	49.0
Cebus apella	Black-capped capuchin	2.10	9	225	472.5
Alouatta caraya	Black howler	4.50	6	180	810.0
Callithrix argentata	Black-tailed marmoset	.32	1	60	19.0
Edentata					
Myrmecophaga tridactyla	Giant anteater	20.00	3	4	80.0
Tamandua tetradactyla	Collared anteater	5.00	1	30	150.0
Euphractus sexcinctus	Six-banded armadillo	3.30	1	400	1320.0
Tolypeutes matacus	Three-banded armadillo	.90	1	300	270.0
Priodontes maximus	Giant armadillo	55.00	2	?	—
Dasypus novemcinctus	Nine-banded armadillo	3.00	10	150	450.0
Lagomorpha					
Sylvilagus brasiliensis	Brazilian rabbit	1.15	1	50	57.5
Rodentia					
Sciurus langsdorffi	Squirrel	.30	1	20	6.0
Oryzomys delicatus	Rice rat	.025	1	—	—
Oryzomys concolor	Rice rat	.06	1	—	—
Akodon varius	Grass mouse	.04	1	—	—
Akodon lasiurus	Grass mouse	.04	1	—	—
Calomys callosus	Vesper mouse	.015	1	—	—
Thricomys (Cercomys) apereoides	Spiny rat	.20	1	—	—
Proechimys sp.	Spiny rat	.045	1	—	—
Coendou prehensilis	Prehensile-tailed porcupine	2.6	2	?	—
Hydrochaeris hydrochaeris	Capybara	30.00	1	110	3300.0
Dasyprocta punctata	Agouti	3.00	1	75	225.0
Carnivora					
Cerdocyon thous	Crab-eating fox	5.20	1	20	104.0
Chrysocyon brachyurus	Maned wolf	23.00	3	Transient	—
Nasua nasua	Coati	3.00	1	150	450.0
Procyon cancrivorus	Crab-eating raccoon	10.00	1	6	60.0
Eira barbara	Tayra	4.00	2	6	24.0
Lutra platensis	LaPlata otter	9.00	est.	Transient	—
Felis pardalis	Ocelot	8.00	1	4	32.0
Felis yagouaroundi	Yagouaroundi	5.00	7	2	10.0
Felis concolor	Puma	48.00	1	2	96.0
Panthera onca	Jaguar	70.00	1	4	280.0
Perissodactyla					
Tapirus terrestris	Brazilian tapir	150.00	5	45	6750.0
Artiodactyla					
Tayassu tajacu	Collared peccary	18.00	4	55	990.0
Tayassu pecari	White-lipped peccary	28.00	1	110	3080.0
Mazama gouazoubira	Gray brocket	15.00	1	120	1800.0
Mazama rufa	Red brocket	26.00	11	120	3120.0
Ozotoceros bezoarticus	Pampas deer	40.00	1	6	240.0
Blastocerus dichotomus	Marsh deer	80.00	1	8	640.0

*1) This study (see Table 5); 2) Eisenberg and Thorington (1973); 3) Walker (1975); 4) Neal (1959); 5) Anon. (n.d.); 6) Pope (1966); 7) Guggisberg (1975); 8) Crawshaw (1977); 9) Kühlhorn (1954); 10) Layne and Glover (1977); 11) Gardner (1971)

whole had more males than females. This was also noted in another area, on an isolated hillock covered with deciduous forest. On it were 24 *Alouatta* in 5 groups of which 42% were males and 33% females. These statistics are similar to those reported by Pope (1966) for a population in Argentina. The total Acurizal population was about 180.

Callicebus is locally distributed, mainly in deciduous forest but also in bamboo with emergent trees and in the strip of scrub forest bordering the flood plain. Evidence for 17 groups was found. Excluding 2 solitary individuals, groups contained 2-5 (mean 3.3) members, a size range typical of the species (Mittermeier and Coimbra-Filho, 1977). The known population comprised 58 animals, and, assuming that a few were overlooked, the total perhaps reached 70. Only 5 groups of *Aotus* were seen, 3 in deciduous forest, one in secondary, and one in scrub forest. Group size was similar to that of *Callicebus*. As noted earlier, the calls of the 2 species sounded alike to me. I located groups 14 times after first hearing them and of these 12 were *Callicebus* and 2 *Aotus*. If calls are a valid index of abundance, the former is more common. I would guess that about 30 *Aotus* inhabit the area.

Of 7 *Callithrix* groups, 6 were in deciduous forest and one in secondary forest. Average group size was 5.6 (3-12). The ranch population probably did not exceed 60 animals.

Monkeys were found only in forest types with continuous canopy, although *Cebus* occasionally penetrated cerrado along drainage lines and crossed pasture to reach isolated food sources. The small variety and seasonal scarcity of fruit in cerrado (Table 1, Fig. 4) probably also deterred monkeys from settling in this vegetation type. Suitable monkey habitat comprised about 35 km^2 of which gallery forest, with only 6 km^2, harbored 28% of all *Alouatta* and 42% of *Cebus*, a density of 24 monkeys per km^2. Deciduous forest, excluding the upper slopes which are seldom if ever frequented by monkeys, had a density of 15 monkeys per km^2. The highest density was noted in

Table 4. Terrestrial mammals sighted during strip censuses in various habitats at Acurizal

	Beach	Pasture	Secondary Forest	Cerrado Forest	Gallery Forest	Deciduous Forest	Total * No. instances	No. animals
Collared anteater	1	2		3	1	2	9	9
3-banded armadillo	1	1	1	16		1	20	20
6-banded armadillo	1	1	1	8	1	7	19	19
9-banded armadillo	4		1	6			11	11
Rabbit				1			1	1
Squirrel			2		1	2	5	7
Agouti			2		2	5	9	9
Coati	4			4	3	7	18	78
Crab-eating fox	2	1	1	4			8	8
Tayra				1		2	3	3
Tapir	1		1	2	1	1	6	6
White-lipped peccary	4		1		1		6	100+
Collared peccary	1		1	5	3	1	11	32
Pampas deer				1			1	1
Marsh deer	2			1			3	3
Gray mazama	11		4	6		3	24	29
Red mazama	1		4	2	2	4	13	13
Unidentified mazama			1	3	2	2	8	8

* As these data indicate, the only group-living terrestrial mammals at Acurizal are the coatis and peccaries.

a 0.6 km² isolated patch of deciduous forest bordering the bay. A detailed census revealed 44 monkeys of 5 species, including 15 *Callicebus* and 12 *Callithrix,* or 73 monkeys per km². A forested hillock, 0.7 km² in size, in another part of the Pantanal harbored 24 *Alouatta* and 4 *Cebus,* or 40 monkeys per km².

Edentates

The giant anteater was seen only once, after the termination of the study. The usual sign of its presence was an occasional set of tracks or a digging in valleys and along the bay. Probably no more than 4 individuals inhabited the ranch. Collared anteaters were encountered 9 times, usually on the ground early in the morning as they returned from foraging along pastures and in cerrado to the protection of gallery and deciduous forests. I was unable to estimate population size and arbitrarily use a figure of 30.

The giant armadillo was either very rare or recently extinct on the ranch: I found only a few old holes in cerrado and gallery forest. The 3-banded armadillo tended to be in open woodlands — 80% of 20 sightings were in cerrado — where it preferred flat terrain no doubt because its carapace prevents it from climbing over rocks. The 6-banded armadillo was widely distributed, in all vegetation types, as long as there was some soil in which to dig. The 9-banded armadillo appeared to be confined to low-lying forests, being especially noticeable in secondary forest and along beaches bordering it, where 45% of sightings were made. This species occurs throughout the wet parts of the Pantanal, in contrast to the other three which prefer drier areas. To obtain an idea of relative armadillo abundance in different habitat types, I counted burrows made by the 6- and 9-banded species in the 5 one-hectare quadrats: low-lying deciduous 58, hilly deciduous 1, secondary 76, cerrado 48, pasture 0. The results from the two species are combined because it was sometimes not possible to distinguish burrows. (The 3-banded armadillo does not dig burrows.) Based on 50 sightings, the relative abundance of the 3 species in decreasing order were 6-banded (40%), 3-banded (38%), and 9-banded (22%). At the nearby Bela Vista ranch, a 90 km² island covered with vegetation similar to that of Acurizal but with more extensive tracts of secondary forest, 88% of 17 sightings were of 9-banded and 12% of 6-banded, indicating that proportions of the different species may vary considerably in various parts of the Pantanal.

To estimate armadillo numbers on the basis of sightings is biased because animals may be underground, or, in dense vegetation, may hide at the approach of an observer. Strip transects 20 m wide gave a calculated .48 six-banded armadillo per km² in cerrado, .59 in secondary forest, 2.0 in gallery forest, and 2.9 in deciduous forest; for 3-banded armadillo the respective figures were .96, .59, 0, and .42. Nine-banded armadillo in cerrado had a computed density of .36 per km². While these figures may reflect relative abundance, the actual figures are too low. I also attempted to estimate combined numbers of 6- and 9-banded armadillo by counting burrows dug the previous night in a 4 m wide transect on the assumption of one burrow per animal per day except when two diggings were side by side. The results showed 7.0 per km² in flat cerrado, 11.9 in gallery forest, and 17.9 in deciduous forest.

Assuming that the burrow counts were on the correct order of magnitude, a total of 105 six- and nine-banded armadillos occurred in the 15 km² or flat cerrado, 216 in the 12 km² of low-lying deciduous forest, 72 in the 6 km² of gallery forest, and an estimated 48 in the 4 km² of secondary forest, a total of 441. Based on sightings, the 9-banded is confined to the flatlands where it is half as abundant as the 6-banded, or

a total of 221; however, sightings were so infrequent in deciduous forest that the species seemed uncommon there, and I doubt if more than a total of 150 inhabited the ranch. To the calculated 291 six-banded in the flatlands, must be added those living in hilly cerrado and on slopes, an estimated total of 400 on the ranch as a whole. Based on encounters in cerrado, 3-banded armadillos were slightly more abundant than the combined 6- and 9- banded, which, according to burrow counts, had a density of 7 per km^2. A calculated 120 three-banded occurred in the 15 km^2 of this habitat, possibly too low a figure judging by the frequency with which tracks were seen. Relative number of sightings in deciduous forest suggested that 3-banded were 6 times less common than the other two species, or a total of 36 in 12 km^2, again too conservative a calculation. Secondary forest had a calculated 48 three-banded, and gallery forest none, if sight records are indicative. The total estimate is 204, but I believe that 300 is more realistic.

The 41 km^2 of low-lying terrain, including pastures which are used by armadillos for foraging, support about 741 armadillos of 3 species, or about 18 per km^2.

Rodents, rabbits, and marsupials

The cricetid rodents *Akodon, Calomys,* and *Oryzomys* were confined largely to thickets at the edge of pastures, ravines, and forest roads, and *Proechimys and Thricomys* to deciduous forest but with a few also in cerrado and those parts of the gallery forest which escape flooding. The small marsupial *Monodelphis* was trapped in deciduous forest and *Marmosa* was twice caught in or around huts. Sample traplines in various vegetation types produced one animal per 48 trap nights, and intensive trapping on one-hectare quadrats one per 102 trap nights, indicating a sparse population of small rodents and marsupials. The highest density was found in deciduous forest where 2 *Thricomys* and 1 *Monodelphis* were caught on one quadrat and 4 *Thricomys* on another.

Squirrels were encountered in all forest types except cerrado but they were everywhere rare. Only 7 were seen and the total number probably did not exceed 20.

A total of 30-35 capybara frequented 8 km of shoreline and adjacent parts of the flood plain, and, based on sightings and tracks, the total population was about 110. Agouti were surprisingly uncommon. I saw them only 9 times, and heard their distinctive alarm bark several more times, always in low-lying forests, bamboo thickets being especially favored. Calculated densities, based on census strips 25 m in width, were 3.2 agouti per km^2 in gallery forest, 1.7 in deciduous, and .9 in secondary for a total of 43. However, some animals were no doubt overlooked during the strip counts and the actual number is perhaps about 75.

Rabbits were rare: I observed one in cerrado and trapped two at the edge of deciduous forest. The population probably did not exceed 50.

Ranch hands informed me that the porcupine is present but extremely rare. I examined the remains of one on a neighboring ranch.

Locals informed us that an opossum with white ears occurs in the area. A piece of skin with a foot provided the only evidence that opossums inhabit Acurizal; I never even saw their distinctive tracks.

Carnivores

Three jaguar were wholly resident and two part-time in early 1978. Assuming that the latter two equalled one resident, 4 jaguar used the ranch on a permanent basis. Tracks indicated that 3 or possibly 4 puma included Acurizal in their travels, but an average of only 2 probably frequented the area at any one time. Although the two

species used all vegetation types, they were separated spatially to some extent in that puma seldom entered the deciduous forests in the northern half of Acurizal (Schaller and Crawshaw, 1980). I live-trapped a male ocelot in cerrado and a female in deciduous forest, and tracks were seen occasionally in other areas, but the scarcity of spoor suggested that no more than 4 ocelot were on the ranch. A settler killed a yagouarundi that preyed on his chickens, my only direct evidence for this species at Acurizal.

I never met the nocturnal crab-eating raccoons, but their tracks occasionally followed beaches and cattle trails in cerrado for several kilometers. Probably no more than 6 inhabited the ranch. By contrast, another procyonid, the diurnal coati, was the most abundant carnivore at Acurizal. It was encountered 18 times in all forest types. Groups contained up to 13 members, and average group size, excluding 3 solitary animals, was 5.3, and including solitary ones 4.3, with 44% of the members comprising large young. Strip censuses 40 m wide in low-lying deciduous forest revealed a density of 1.5 groups or 6.2 individuals per km^2, a total of 74 coati in the 12 km^2 of forest. In gallery forest there were 13 individuals per km^2, a total of 78 in 6 km^2. This high density probably represented a dry season concentration near water from which groups foraged out into the surrounding habitats. It was my impression that a figure of 150 coati is a realistic population estimate.

Crab-eating fox preferred open habitats. Although they traversed gallery and deciduous forests, their main activity centered along beaches, pastures, and cerrado. Nine foxes were trapped (of which one died), and these comprised 2 adult males, 2 adult females, and 5 yearling females. Three foxes were tagged around First Valley and one was subsequently caught again and 2 untagged ones were observed; three foxes were also tagged around Second Valley and later one marked and 2 unmarked foxes were seen in the area; two foxes were caught in the north and subsequently one was retrapped 4 km away and two untagged ones were seen. Thus at least 11-14 foxes were known to frequent the ranch, and the total probably reached 20. The maned wolf was only a transient. I saw tracks twice and a ranch hand killed one prior to the study.

Tayra were seen once in cerrado and twice in deciduous forest, and the population probably did not exceed 6. No La Plata otter resided at Acurizal, but one was seen by a ranch hand in 1977.

Ungulates

Tapir were most abundant in gallery forests and the drainage lines radiating out from them, and in low-lying deciduous and secondary forests; they frequented other habitats as well, it being common to see their nighttime tracks along beaches and in cerrado. The preference of tapir for gallery forest was evident from counts of fecal sites, deposits being placed singly or in clusters of up to 10, sometimes in shallow water. Strip censuses 4 m wide revealed 1.1 such sites per km in gallery forest, .14 in deciduous forest, and .01 in cerrado. Evidence from tracks suggested a population of about 45 tapir at Acurizal.

Two large white-lipped peccary groups with overlapping ranges roamed the deciduous and secondary forests near the margin of the bay. Exact group counts were difficult to obtain in the dense undergrowth, but 3 times I saw between 20-35 and sounds of others indicated that there were perhaps 40-45. An occasional group of about 10 peccary moved into gallery forest, but it was not clear if these were subgroups or distinct groups. The total population probably did not exceed 110. Collared peccary were somewhat separated spatially from the white-lipped peccary: the former favored gallery forest and the drainage lines leading to the deciduous forests on the hillsides

whereas the latter was usually in the flatlands near the bay. Herd size of collared peccary at Acurizal ranged from 1-7 (mean 3.3), but at nearby Bela Vista a herd of 12 was seen. Since these peccary were difficult to spot in thickets, strip censuses were biased. A tally of skulls also gave skewed results. A total of 43 white-lipped and 8 collared peccary skulls were found, but the former species was not five times as abundant; instead, it preferred the vinicity of beaches where skulls were readily found. It was my impression that collared peccary were half as abundant as white-lipped, or about 55.

Of the 4 deer species at Acurizal, the pampas deer was the rarest. Only one was seen and the total number on the ranch probably did not exceed 6. Marsh deer prefer swamps with shallow water, now a scarce habitat in the area. In 1977 about 12 marsh deer were at Acurizal but one female was killed by dogs, another by jaguar, a third died of unknown causes, and a male was shot by a ranch hand.

The two brocket deer species inhabited the same vegetation types but they were ecologically separated to some extent: gray brocket favored thickets and the dense margins along open areas, whereas red brocket tended to be in the interior of forests. Thus, 46% of 24 gray brocket sightings were along the beach, 25% in cerrado, and 12.5% in deciduous and gallery forests, in contrast to 13 sightings of red brocket whose respective percentages were 8, 15, and 46. The two species were considered together during the strip censuses because a fleeting glimpse was sometimes not enough to identify the species. Based on a transect strip 25 m wide, gallery forest had a density of 6.4 deer per km^2, secondary forest 4.2, and deciduous forest (excluding upper slopes) 3.0, or a total of 139 deer in 38 km^2 of suitable habitat. Cerrado was not included in these computations because transects tend to skirt thickets of bamboo and bromeliad into which brockets retreated in daytime and were thus overlooked.

The accuracy of the strip census can be checked by another method. North American deer defecate on the average of about 13 times a day (Neff et al, 1965). The New York Zoological Society has two pair of red brocket in outdoor enclosures. Curator M. MacNamara generously counted fecal piles of one pair for 7 days and the other for 3 days. The first defecated at the rate of 6.5 (3-8) times per animal per day and the second at 7.6 (5-9.5). In addition to the piles of typical pellets, the deer made small mushy deposits, the first pair at the rate of 26.5 (15-41.5) per animal per day, the second at only 1.6 (0-2.5). With part of their intestinal wastes devoted to mushy deposits, brocket show a lower daily pellet count than do other deer. A 21-km transect, 4 m wide, in gallery forest revealed 5 fresh pellet groups, some associated with older piles, for brocket tend to defecate repeatedly at the same site. At an average of 7 pellet groups per animal per day, there were 8.5 brocket per km^2. A 14-km pellet group count in deciduous forest revealed a density of 2.6 brocket per km^2. Both densities are similar to the strip census results of 6.4 and 3.0 animals per km^2, respectively, in these habitats.

In addition to the earlier estimate of 139 brocket, there were a few residents in cerrado and an unknown number of fawns, which apparently remain hidden while their mothers forage. The total population is estimated at 240, divided equally between red and gray brockets.

Biomass

The literature contains few precise weights for the species discussed in this report, and I supplemented published information by weighing animals captured,

Table 5. Weights (in kg) of adult male and female mammals from the Pantanal

Species	Male		Female	
	Sample size	Weight	Sample size	Weight
Titi monkey	1	.80		
Black-tailed marmoset	1	.38		
Collared anteater	2	4.8, 5.0	1	5.0
3-banded armadillo	6	1.08 (1.0-1.15)	4	1.05 (1.0-1.1)
6-banded armadillo	4	3.6 (3.0-4.0)	7	4.0 (3.3-5.0)
9-banded armadillo			1	4.7
Brazilian rabbit	2	1.0, 1.5		
Squirrel			1	.3
Agouti			1	3.6
Capybara	8	41.8 (29.5-56.8)	5	36.8 (28.9-45.9)
Crab-eating fox	4	6.4 (6.0-7.0)	4	6.2 (4.8-6.8)
Crab-eating raccoon	1	10.2	1	10.0
Coati	2	4.3, 5.5		
Ocelot	1	9.0	1	5.5
Puma	1	54.5		
Jaguar[1]	6	95.0 (80-119)	3	78.0 (73-85)
Collared peccary	1	18.5		
White-lipped peccary[1]	1	34.0	1	33.0
Gray brocket[2]	3	16.3 (14.0-18.0)	2	18, 20
Marsh deer[1]	5	108.6 (89-125)		

1) Data from A. de Almeida (pers. comm.)
2) Data collected in Paraguay (R. Wetzel, pers. comm.)

shot, and found dead on roads. Table 5 presents the adult weights on which some of the biomass data in Table 3 are based. When possible, the latter have been adjusted to take into account the composition of a population. In assessing biomass of a species, it is at times useful to distinguish between crude biomass, which encompasses the total area, and ecological biomass which considers only suitable habitat (Eisenberg and Seidensticker, 1976).

Bats

Bats ranged in weight from the tiny *Micronycteris* (10 gm) to the robust *Phyllostomus* (75 gm), but most were intermediate (20-40 gm). The only locally abundant species was *Noctilio* which at the northern tip of Acurizal aggregated by the hundreds over water. No attempt was made to census bats. In terms of mammalian biomass they contributed only a few percent of the total.

Primates

The average weight of 10 *Cebus apella* males was 2.9 (2.4-3.6) kg and of 9 females 2.3 (2.0-2.9) kg (Kühlhorn, 1954). With about a third of the Acurizal population being subadult, the total biomass was estimated at 472.5 kg. According to Pope (1966), *Alouatta caraya* juveniles weigh 1-4 kg, females 4-6 kg, and males 6.5-9 kg. More precisely, 4 adult males weighed 6.4, 6.6, 8.3 and 9.8 kg, respectively, and 3 females 3.1, 5.6, and 5.8 kg (Krieg, 1948; Kühlhorn, 1954). As with *Cebus*, about a third of the population consisted of subadults, and the total biomass

was 810 kg. The other 3 monkey species contributed only a further 92 kg (see Table 3). The total monkey biomass was 1374.5 kg, a crude biomass of 19.6 kg per km^2 and an ecological biomass, based on 35 km^2 of suitable forest, of 39.3 kg/km^2. The highest biomass — 96.9 kg/km^2 — was found in an isolated stand of deciduous forest.

Edentates

The average weight of 16 six-banded armadillos was 3.3 (0.7-5.0) kg and of 14 three-banded it was 0.9 (0.2-1.2) kg. The sources for weights of other armadillo species are indicated in Table 3. The 3 species have a combined biomass of 2040 kg, with the 6-banded contributing two-thirds. The two anteaters add another 230 kg, raising the total for the myrmecophagous species to 2270 kg, a crude biomas of 32.4 kg/km^2. Only the 6-banded appeared to venture into the hills, and, taking solely the flatland populations, the ecological biomass is 51.6 kg/km^2.

Rodents, rabbits, and marsupials

Snap-trapping in two 1 ha plots of deciduous forest produced a small rodent and marsupial biomass of 0.6 and 1.03 kg, respectively, an average of 0.82, or a total of 81.5 kg/km^2. The 12 km^2 of this habitat supported a biomass of 978 kg. Only one rat with an estimated weight of 0.2 kg was caught in the 1 ha cerrado plot. Judging by sample trapping in other cerrado areas of Acurizal, the average biomass was even lower than on the plot, perhaps about 0.15 kg/ha or a total of 270 kg for the cerrado as a whole. One 15-year-old secondary forest plot produced no rodents, but a few were caught in similar habitats elsewhere. A plot in heavily grazed pasture with islands of brush had one .02 kg mouse. Thirty-six trap-nights in gallery forest produced nothing at Acurizal, and, in another part of the Pantanal, 104 trap-nights in a 1 ha plot caught one .33 kg *Philander*. Pasture, secondary forest, and gallery forest had a low biomass, perhaps no more than 0.1 kg/ha or a total of 120 kg in 12 km^2. I have no data on densities in deciduous forest on the hill sides, and arbitrarily put the figure at 0.15 kg/ha on the lower slopes and 0.10 on the upper, or 310 kg in the 25 km^2. The total small rodent and marsupial biomass is calculated at 1678 kg or 24 kg/km^2.

The capybara had a biomass of 3300 kg, more than for any other species except tapir, even though its habitat was confined to a narrow strip on and near the shoreline.

The agouti had a biomass of 225 kg and the rabbit of 57.5 kg, a combined crude biomass of 4.04 kg/km^2 and ecological biomass of 12.84 kg/km^2. Squirrels contributed only 6 kg to the Acurizal biomass.

Carnivores

Among the six species of small carnivores, the coati had the greatest biomass. Given an adult weight of 5 kg (Kaufmann, 1962) and a population with 44% young, the average coati weighed about 3 kg, or a biomass of 450 kg. The average weight of 9 trapped foxes at Acurizal was 5.2 kg and the total biomass on the ranch 104 kg. A captive tayra male weighed 5.3 kg and female 3.9 kg (Poglayen-Neuwall, 1978), and the weights for raccoon and ocelot are given in Table 5. These species contributed only 126 kg. Puma and jaguar had a biomass of 376 kg. Thus, the carnivores had a total biomass of 1056 kg, a crude one of 15.1 kg/km^2 and an ecological one almost as great, for the animals roamed over much of the area.

Ungulates

I have been unable to find reliable weights for free-living tapir; the average

weight of 8 captive adults (3 male, 1 female, 4 unsexed) was 172 (112-200) kg (Anon, n.d.). The average animal at Acurizal was estimated to weigh 150 kg, giving a total biomass of 6750 kg, or a crude biomass of 96.4 kg/km^2.

A male white-lipped peccary from the Pantanal weighed 34 kg and a female 33 kg (T. de Almeida, pers. comm.). I hand-reared a female and her weights at various ages were as follows: 1.5 months — 2.8 kg, 4 months — 7.2 kg, 6 months — 12.3 kg, 11 months — 20 kg, and 26 months — 29 kg. In Surinam, I weighed 3 adults, males at 24 and 27 kg and a female at 19 kg, suggesting that the species is somewhat smaller there. Of 99 peccaries sampled at Acurizal, 16% were young of the year. Collared peccary are smaller than white-lipped. One Pantanal male weighed 18.5 kg. The average weight of males in Arizona was 19.9 kg and of females 20.7 kg (Knipe, 1956). None of the 32 collared peccaries I saw at Acurizal were young of the year. The white-lipped had a biomass of 3080 kg and the collared of 990 kg, a combined 4070 kg, or a biomass of 58.1 kg/km^2.

The literature appears devoid of precise pampas deer weights, and I arbitrarily assign the figure of 40 kg. The average male marsh deer weighs 109 kg (Table 5) but there is no information on females. Both species were on the verge of extinction at Acurizal and had a biomass of only about 880 kg.

Adult gray brocket average about 17 kg in weight (Table 5). One female red brocket in Peru scaled 35 kg (Gardner, 1971), the only weight record for this species I could find. Average weight is here given arbitrarily as 26 kg. The two brockets totalled 4880 kg, a biomass of 69.7 kg/km^2.

The total mammalian biomass in the 70 km^2 was 26,587 kg or 380 kg/km^2. Ungulates contributed 62.5% to this figure (Table 6) and capybara 12.4%. Next, with 8.5%, are the edentates which are terrestrial except for the scansorial *Tamandua*. Small rodents, rabbits, agoutis, and marsupials comprise 7.4% of the total. The arboreal species—primates and squirrels—contribute only 5.2%. And lowest in terms of biomass are the carnivores with 4.0%. These biomass figures cannot be extended to the periodically flooded parts of the Pantanal. Tapir, 6-banded armadillo, and small rodents are, for example, rare in such habitats, as are most terrestrial species, except capybara.

The livestock at Acurizal has as yet not been considered. The ranch supported about 1500 cattle, as well as a few horses, sheep, pigs, and dogs, all of which foraged within the 70 km^2 used by wildlife. Given an approximate average weight of 175 kg for a head of cattle, the total biomass was

Table 6. A summary of biomass of wild non-volant mammals at Acurizal

Species	No. species	Total biomass	Biomass kg/km^2	% of total
Primates	5	1375	19.6	5.2
Edentates	5	2270	32.4	8.5
Capybara	1	3300	47.1	12.4
Agouti and rabbit	2	282	4.0	1.1
Squirrel	1	6	0.1	tr.
Rats, mice, and small marsupials	9	1678	24.0	6.3
Small carnivores	6	680	9.7	2.6
Large carnivores	2	376	5.4	1.4
Tapir	1	6750	96.4	25.4
Peccaries	2	4070	58.1	15.3
Deer	4	5800	82.9	21.8
Total	38	26,587	379.7	100.0

262,500 kg, or 3750 kg/km², a figure 10 times greater than that for the native mammals.

Factors affecting the biomass

The Acurizal biomass of 380 kg/km² is low when compared with that of other areas on other continents having similar habitat and species diversities. For example, Seidensticker (1976) found that the forests and grasslands of Chitawan National Park in Nepal harbored an ungulate biomass alone of 1756 kg/km². With 7 ungulate species occurring both at Acurizal and Chitawan, an explanation for the low biomass in the former area is needed. Several factors are responsible.

Habitat modification

Five times in this century — in 1905, 1920, 1932, 1959, and 1974 — exceptionally high floods inundated large parts of the Pantanal, and in 1980 the water still had not receded to normal levels after the last flood. Small terrestrial mammals are eliminated from the inundated areas, except for those finding refuge on islands on high ground. No mouse or rat in the Pantanal is arboreal, although *Thricomys* climbs fallen trees. Such species as white-eared opossum, collared anteater, coati, tayra, and ocelot are scansorial, climbing trees to forage or sleep. Arboreal species include only the 5 primates, squirrel, porcupine, and probably murine opossum, a total of 19% of the non-volant species listed in Table 3. For comparison, 36% of the non-volant species in Malaysia are arboreal (Muul and Liat, 1978).

Intensive cattle management converts forest to pasture, it changes a complex habitat to a simple one, and at the same time eliminates most forest mammals. A patchwork of pasture and thicket may harbor a few rodents, armadillos and gray brockets, but short-cropped grasslands, deprived of cover, support little wildlife. Only a few km² of Acurizal have so far been denuded, but current emphasis on increased cattle production on this and some other ranches can only affect wildlife adversely.

Fire may have an impact on various small mammals in cerrado and other open habitats by depriving them of cover and food (see Crowner and Barrett, 1979). From July until the first rains in October, dry grasses in many parts of the ranch are burned off to encourage a flush of green grass for livestock. Such fires burn not only over the hills and across cerrado but also into deciduous forests where a litter of dry fallen leaves provides fuel. Fires penetrating bamboo and other thickets, which often have not been burned for several years, produce such an inferno that few rodents may be able to survive.

Hunting

Capybara, 6- and 9-banded armadillos, and all ungulates are hunted for food by ranch hands and squatters, the pampas deer having been almost exterminated as a result. Foxes are shot because they occasionally kill chickens, and otter and ocelot are taken for their fur. Puma and jaguar prey on cattle, and, in addition, jaguar skins are valuable trade items. Three jaguar were shot and one was captured at Acurizal in 1974 and two more were killed in 1978; one puma was also shot. The impact of hunting on most species was difficult to measure, but there is no question that those animals which are sought for their skins have been seriously affected.

Disease

Capybara were abundant at Acurizal until the 1974 flood. Deprived of their favored

habitat on the flood plain, the animals crowded onto the remaining beach where disease soon decimated them, according to the local inhabitants, and they were still affected in 1978. Judging by symptoms, the capybara suffered from equine trypanosomiasis (*Trypanosoma* sp.). The population also failed to reproduce adequately: it was rare to see young at Acurizal whereas about 40% of a population in another area consisted of this age class. On a ranch in the llanos of Venezuela, in a habitat similar to the Pantanal, Ojasti (1973) recorded an average capybara biomass of 270 kg/km^2, with a maximum of 6240 kg/km^2 when the animals concentrated in the dry season, figures probably reached at Acurizal too before flooding and disease decimated the population.

Aerial surveys every year between 1976 and 1979 revealed such a low annual increment of marsh deer fawns that the Pantanal population appeared to be declining. The reason for such poor fawn production remains unknown but a disease, such as brucellosis, appears a likely cause (Schaller and Vasconcelos, 1978b).

Two 6-month-old white-lipped peccary young were found dying near each other at Acurizal. Both were emaciated and anaemic and an autopsy of one revealed pneumonia. An adult gray brocket was found similarly thin and anaemic.

Predation

Jaguar subsist on a wide variety of wild mammals in the Pantanal. I found kills of capybara, marsh deer, tapir, both peccaries, La Plata otter, and *Aotus* monkey. M. Dantas (pers. comm.), a long-time hunter, also recorded predation on 9-banded armadillo, *Alouatta*, agouti, coati, and ocelot, and other hunters told me of kills of raccoon and both anteater species. Azara (1837) listed the porcupine as prey in Paraguay. Puma are also catholic in their tastes, with, for example, Miller (1930) recording pampas deer, collared anteater, and brocket as prey in the Pantanal, and J. Schweizer (pers. comm.) 6-banded armadillo. Both large cats appear to consume the whole spectrum of available mammals, except perhaps mice, rats, and small marsupials, although Enders (1935) lists the *Proechimys* rat as a puma food item in Panama.

The biomass of puma and jaguar at Acurizal was 376 kg and the prey biomass, excluding small rodents, was 24,533 kg (Table 6), or 1 kg of predator per 65 kg of prey. In several African national parks the ratio of large predators to their ungulate prey was about 1:100 (Schaller, 1972), suggesting at first glance an unusually large number of puma and jaguar in relation to their prey resources. However, wild mammals contribute only a fraction of the available biomass, cattle alone providing 10 times as much. Although jaguar readily prey on fully grown cattle weighing 250 kg or more and puma too may dispatch a 2-year-old, both prefer calves, an age class which may be poorly represented because attempts to manage livestock in much of the Pantanal can best be characterized as feeble. There were only 12 calves to 100 cows at Acurizal, and other ranches in the area had a similarly low calf:cow ratio. Between dusk and dawn, free-ranging cattle tend to cluster at specific sites, a habit which probably prevents puma and jaguar from easily selecting victims. Still, cattle are locally abundant, stocking densities being generally one head per 3-5 ha, except in densely wooded or deeply flooded parts.

Vertebrates other than mammals may also provide the big cats with food. M. Dantas told me that he has encountered jaguar with the remains of jabiru stork (*Jabiru mycteria*), white-necked heron (*Ardea cocoi*), and currasow (*Crax fasciolata*), and A. de Almeida (pers. comm.) once followed a jaguar to where it had raided a duck nest of its eggs. Puma prey on rhea (*Rhea americana*) according to

Miller (1930). Large lizards (*Dracaena, Tupinambis, Iguana*) provide potential food, and I found the remains of a tortoise (*Geochelone*) which apparently had been killed by a jaguar. Paraguayan caiman (*Caiman crocodilus*) are locally abundant, of substantial size, the average adult male weighing 40 kg, and readily eaten by jaguar (Miller, 1930). One night count along 3 km of Acurizal beach revealed 71 caiman of various sizes within 50 m of shore. The anaconda (*Eunectes notaeus*) is another jaguar food item (Rengger, 1830), although the Pantanal species is fairly small, the largest I saw weighing only 40 kg.

I found it difficult to assess the relative importance of the potential prey species in the diet of jaguar and puma. Since most prey is small, the carcass is eaten rapidly and the kill site may be abandoned the same night. Remains are difficult to find in the dense undergrowth into which cats characteristically retreat to eat, and feces are seldom encountered. A. de Almeida (1976) and R. Mason (pers. comm.) examined 17 jaguar stomachs in the Pantanal and noted that 7 were empty, 7 contained cattle, 1 capybara, 1 coati, and 1 fish. At Acurizal I found the following fresh jaguar kills: 12 capybara, 1 marsh deer, 1 collared peccary, and 5 cattle of which 3 were cows and 2 calves; ranch hands showed us the remains of 4 more calves and a 2-year-old. One collared anteater was killed but not eaten. A radio--collared female jaguar was contacted on 35 days over a period of 2½ months on the Bela Vista ranch and was known to have killed a calf, a capybara, and probably a dog (Schaller and Crawshaw, 1980); she also attacked a calf but it escaped in spite of a fractured neck vertebra. During this period, other jaguar in the same area preyed on a dog and lacerated a foal. However, predation on domestic animals is more easily observable than on wild ones, and such unsystematic records tend to be biased in favor of the former. Cattle, capybara, and peccaries probably provided jaguar with the bulk of their food at Acurizal, as perhaps in many parts of the Pantanal. I have no precise data on puma, but according to local informants they generally prey on the same mammals as jaguar.

The effects of predation on the prey populations was difficult to measure, but, given the low densities of several species such as giant anteater and marsh deer, the loss of even a few individuals could have had an appreciable impact. Each of the 3 main prey species was probably affected somewhat differently by the big cats:

Jaguar and puma are persecuted for their depredation on cattle. Indeed, cattle probably are the jaguar's main food, although kills account for only a small percentage of the animals dying annually. In the Poconé district, which contains the largest remaining jaguar population in the Pantanal, cattle are said to have declined from 700,000 to 180,000 since the 1974 flood as a result of drowning, disease, and starvation. Between July and October, during the height of the calving season at Acurizal, I found 10 freshly dead young of which only one had been killed by jaguar, the others having died of malnutrition and disease.

Jaguar at Acurizal killed 20-23% of a sample population of 30-35 capybara within two months in 1977 (Schaller and Vasconcelos, 1978a), and disease also affected the animals. The relative impact of the two mortality factors can be deduced from skulls found in the field. Since jaguar usually kill capybara with a bite in the head — 82% of fresh kills had tooth marks on the skull — death due to predation can in most instances be separated from that due to other causes, mostly disease. Twenty-six of 70 skulls comprised definite kills, and, when to this total some undetected kills are added, it becomes apparent that predation and disease affected the population about equally. Table 7 presents the ages of capybara at death, based on the sequence with which cranial sutures ossify (Ojasti, 1973).

Table 7. Relative age at death of capybara at Acurizal, based on skulls found, expressed in percent

Age class	Predation	Mainly disease deaths	Poaching
I	0	2.3	0
II	0	0	11.1
III	3.8	2.3	0
IV	7.7	9.0	11.1
V	26.9	31.8	16.1
VI	61.5	54.5	61.1
Sample size	26	44	18

Age classes I and II consist of young fewer than 12 months of age, class III of subadults about 12-18 months old, and classes IV to VI of adults, class VI being the oldest with all sutures closed. The age structure of animals dead from predation, disease, and poaching is similar, the small number of young being especially noticeable. As pointed out earlier, the Acurizal population had a low reproductive success. The evidence suggests that disease coupled with poor reproduction reduced a large capybara population to a level where predation could have a significant impact and that the combination of the 3 factors was still operating in 1978 to further depress the population.

Peccary skulls from Acurizal showed a characteristic age-related mortality pattern, as shown in Table 8. A tame white-lipped peccary had all her deciduous teeth at the age of 2 months, her first molar erupted at 6 months, the permanent canines at 11 months, the second molar at 13 months, the permanent incisors at 14-18 months, and the third molar at 24 months. As Table 8 indicates, mortality before the age of 24 months (classes I and II) was low, most animals dying in middle age. Of the 43 white-lipped peccary skulls, 2 young were known to have died of disease and 10 adults of predation, judging by tooth marks and punctures on the occipital and parietal bones; the cause of death of the others was unknown, but it probably was also attributable to jaguar and puma in most instances. Among the 8 collared peccary, 7 were definite kills. Collared peccary have only one or two young per litter (Knipe, 1956), and white-lipped ones do too. Given a low birth rate and a considerable predation pressure, the big cats probably removed a substantial part of the annual increment. The collared peccary may be especially vulnerable because predators have a greater chance of locating one of its many small herds than they do one of the few large herds characteristic of the white-lipped.

Seasonal changes in food abundance

While such factors as burning and predation may affect some species it does not explain, for example, the low rodent biomass in forests which are seldom if ever burned or the relative scarcity of primates even though they are not killed for food by local people and predators probably do not often catch them. Changes in food abundance may have an influence on population in an environment as seasonal as at Acurizal where, for instance, many trees are leafless in September and certain flying insects reach a peak of abundance in January. Before assessing the possible impact of changes in food abundance it is necessary to outline briefly the food habits of the mammalian species.

Primates. The howler monkey is largely vegetarian, subsisting on fruits, young leaves, buds, and flowers (Smith, 1977). In contrast, *Cebus* eat a greater variety of foods than do any other New World monkeys (Mittermeier and Coimbra-Filho, 1977). I observed them eating seeds and fruit of *Bumelia obtusifolium, Tabebuia impetiginosa, Hymenaea stigocarpa, Attalea, Bromelia,* and *Salacia elliptica* as well as flowers of the vine *Combretum lanceolatum,* to mention a few plants. One dropped a partially eaten frog, confirming Izawa's (1978) observation that this monkey eats

Table 8. Relative age at death of peccaries at Acurizal, based on skulls found, expressed in percent

Age class	Tooth characteristic	White-lipped peccary	Collared peccary
I	Deciduous canine; m^1 erupted	9.3	0
II	Permanent canine; m^2 erupted	0	12.5
III	m^3 erupted; little wear m^1	14.0	12.5
IV	Moderate wear m^1	39.5	12.5
V	m^1 worn flat	18.6	37.5
VI	m^2 worn flat	9.3	12.5
VII	m^3 worn flat	9.3	12.5
Sample size		43	8

small vertebrates such as lizards, frogs, and bats. The diets of *Aotus* and *Callicebus* include fruits, seeds, insects and other invertebrates, and an occasional small vertebrate (Krieg, 1930); one *Callicebus* stomach at Acurizal contained 90% seed pulp and 10% *Atta* ants. Krieg (1930) found that *Callithrix argentata* eat insects and vegetable matter. The stomach of one animal at Acurizal was full of beetle remains, and R. Hansen (pers. comm.) observed there 4 marmosets apparently searching for insects beneath dry cow patties.

Edentates. On several occasions a giant anteater in the Pantanal used its snout to push soil from newly constructed parts of a *Cornitermes* mound but it seldom fed for more than 10 seconds, probably because fire ants (*Solenopsis*) living in the same mound soon swarmed over the disturbed area. Anteaters were also observed to feed on *Acromyrmex* and *Solenopsis* ants and on *Anoplotermes* termites. One dropping consisted solely of the remains of *Camponotus* ants, and the stomach of an animal killed by a car was full of *Acromyrmex* ants. Collared anteaters often forage on arboreal ant and termite nests (Lubin et al, 1977), and I also observed this anteater on the ground eating *Syntermes* termites. Mathews (1977) found that one stomach from Mato Grosso contained various termites (*Cornitermes, Velocitermes, Nasutitermes, Parvitermes*), all of them ground-living species.

As noted by Redford (in press), armadillos range in their food habits from generalized omnivores through insectivores to specialized ant and termite eaters. All 3 types occur at Acurizal. The 3-banded is the most specialized feeder. Of 4 stomachs examined, one was empty, one contained *Syntermes molestus* and 1 spider, one was full of *Camponotus* ants, *Syntermes,* and several grubs and spiders, and the fourth had a few ants and termites and much sand. Several individuals fed in daytime on *Syntermes molestus,* a species which does not construct mounds. The 9-banded armadillo feeds on insects and other arthropods, including spiders, millipedes, and scorpions, as well as on snails, frogs, and lizards, animal food making up 90% of its diet (Fitch et al, 1952). The 6-banded is an omnivore. Although Table 9 shows that this armadillo may eat insects, spiders, leeches, and small vertebrates, vegetable matter, especially tubers and fruit, provided the bulk of its diet: 7 of the 10 stomachs contained more than 90% by volume of plant food. I also observed this species eating the fruit of *Bromelia* and large chunks from a turnip-like tuber.

Rodents, rabbits, and marsupials. The stomachs of most trapped mice and rats were examined and all contained seeds and fruits; none contained grass. Agouti are mainly fruit and seed eaters too (Smythe, 1978); one stomach at Acurizal contained only *Attalea* fruit pulp. I saw one squirrel carry an *Attalea* nut, and the stomach of

Table 9. Food habits of 10 six-banded armadillos from the Pantanal

Food item	Frequency of occurrence
Acrocomia palm fruit	1
Fleshy tuber	1
Unidentified plant fibers	5
Ananas fruit	1
Ficus fruit	1
Unidentified fruit pulp	3
Unidentified seeds	1
Beetle	2
Grasshopper-cricket	2
Insect larvae	3
Insect pupae	3
Ant (*Ectatoma* and others)	3
Spider	1
Leech (*Hirudinea*)	1
Frog	1

another was full of unidentified fruit. By contrast, the capybara is a herbivore, primarily a grasseater although it also consumes water plants, forbs, and the leaves of shrubs (Ojasti, 1973). *Cyperus haspan, Panicum decipiens* and P. *laxum, Paspalum conjugatum* and P. *repens, Eleusine indica, Hymenachne amplexicaulis* and *Digitaria adscendens* are some of the grasses and sedges eaten by capybara in the Pantanal, and this basic diet is supplemented with herbs (*Vernonia brasiliensis, Aeschynomene fluminensis, Heliotropium procumbens, Hymenache amplexicaulis*) and water plants (*Echinodorus paniculatus, Pontederia cordata*).

The rabbit is the only other herbivorous small mammal at Acurizal.

The two small marsupials are largely insectivorous, but the fact that I trapped *Monodelphis* with peanuts indicates that seeds may also be eaten. *Didelphis* is omnivorous (Enders, 1935).

Small carnivores. The coati eats a wide assortment of invertebrates and small vertebrates, as well as fruit (Kaufmann, 1962). A list of animals found in 2 coati stomachs gives an indication of food habits in the Pantanal: 1 fish, 2 snakes (probably *Typhlops*), crabs (*Dilocarcinus*), millipedes (*Myriapoda*), sowbugs (*Isopoda*), tarantulas (*Arachnida*), slugs (*Mollusca*), cicadas (*Cicadidae*), beetles (*Coleoptera*), cockroaches (*Blattidae*), crickets (*Orthoptera*), earwigs (*Dermaptera*), ants (*Odontomachus, Ectatomma, Camponotus*), termites, and insect larvae and pupae. I have also observed coati feed on the fruits of *Ficus* and *Copernicia* palm, and on a toad (*Bufo*). The crab-eating raccoon eats insects, crabs, small vertebrates and fruit (Cabrera and Yepes, 1960); one stomach examined during this study contained only fruit pulp.

The crab-eating fox subsists on small rodents, frogs, lizards, crabs, insects and fruits (Brady, 1979). Table 10 shows the food habits of this species at Acurizal and at Fazenda Jofre, a ranch in the northern part of the Pantanal. The diet of foxes in the two areas is quite different, the animals at Acurizal eating mostly fruit and those at Jofre mainly crabs, small vertebrates, and capybara, the last-named scavenged as well as captured in the case of young ones. Of 4 stomachs examined in the northern Pantanal, one contained several frogs and fruit, a second frogs and crabs, another bird and beetle remains, and the last 2 fish, 3 frogs, and fruit. I have no data on food habits of maned wolf from the Pantanal, but an analysis of droppings collected in the cerrado habitat of Brasilia National Park showed that small rodents and *Solanum* fruit predominated (Table 10).

The tayra is omnivorous, eating a variety of fruit (Kaufmann and Kaufmann, 1965) and such vertebrates as lizards, agouti, and small monkeys (Galef et al, 1976).

The small cats are mainly carnivorous, with the ocelot, for example, preying on rats, agoutis, rabbits, young brocket, coatis, and snakes (Enders, 1935). A. de Almeida (pers. comm.) found fish in the stomach of an ocelot, and once observed one of these cats with a howler monkey kill.

Ungulates. Although tapir eat fruit, flowers, and grasses, leaves provide the bulk of

Table 10. Frequency of occurrence (in %) of food items in the droppings of *Cerdocyon* fox and maned wolf

Food item	*Cerdocyon* fox		*Maned wolf*
	Acurizal	Fazenda Jofre	Brasilia National Park
Capybara	5.6	42.8	
Small rodent	8.3	19.0	77.9
Bird	5.6	14.3	17.6
Reptile	2.8		
Armadillo			8.8
Unidentified hair	2.8		
Crab	5.6	61.9	
Insect	2.8		
Ananas fruit	33.3		
Bromelia fruit	50.0		
Acrocomia palm fruit	22.2		
Ficus fruit	2.8		
Solanum grandiflora fruit			82.4
Unidentified seeds	13.8	4.8	
Grass		9.5	2.9
Soil	2.8		1.5
Sample size	36	21	68

their diet (Terwilliger, 1978), a fact confirmed by examining droppings at Acurizal.

The two peccary species appear to have similar food habits in that both eat predominantly fruits and seeds. *Ficus, Attalea,* and *Astrocaryum* were commonly eaten fruits and so was *Talisia esculenta* in season. The fruits and tender leaf bases of *Ananas* and *Bromelia* were also favored items. A tame white-lipped peccary was a selective feeder, plucking only certain grasses and sedges (*Setaria geniculata, Cyperus surinamensis*), herbs (*Gomphrena celosioides*) flowers (*Eichhornia* spp). Both species frequently root, but I was only once able to detect what they had eaten, the roots of *Maranta* cf *arundinacea,* except when they raided gardens for manioc tubers. One stomach of each species revealed only fruit pulp, fibers, and a few finely chewed leaves.

One marsh deer male browsed extensively on the shrubs *Aeschynomene sensitiva* and *Discolobium pulchellum,* and on the vine *Rhabdadenia pohlii.* A. de Almeida (pers. comm.) examined 3 rumens and found mainly leaves, especially those of the water lily (*Nymphaea* sp). However, two rumens at Acurizal contained more grass than browse. Judging by its habitat preference, the pampas deer subsists mainly on grasses and herbs. The rumen of one gray brocket from Acurizal contained green grass, *Enterolobium* seeds, and the seeds of an unidentified legume; and that of another, examined by A. de Almeida, leaves, grass, *Pseudobombax* flowers, and fruit. The red brocket appears to have a similarly mixed diet: one rumen contained small green fruit, dry leguminous seeds, and chewed plant stems.

Discussion

This summary of food habits reveals several trends in resource use. One is that terrestrial mixed browsers and grazers, the tapir and deer, contribute most to the biomass (47%). Low shrubs and trees are abundant, and, even though many are bare of leaves in the dry season, grass and fruit help these herbivores through times of leaf scarcity. Another trend is that, with the exception of the semi-aquatic capybara, primary grazers are absent. Grass is scarce in secondary and deciduous forests but cerrado has a dense cover (see Table 1), indicating that a niche exists for a wholly terrestrial grazer, especially one adapted to coarse, siliceous grasses. The absence of

grass-eating rats and mice affects the biomass, for such rodents, with their abundant food, generally occur at higher densities than do seed-eating rodents whose food supply is dispersed and seasonally erratic (Dalby, 1975). If good grazing exists near water, the capybara can achieve a high density and biomass, as noted earlier. However, the capybara population at Acurizal appeared to be cyclical, depending on flood and disease levels, and during this study it was at a low point. Arboreal folivores are as rare as grazers, the howler monkey and porcupine being the only species which have to some degree specialized on this food source. These two species provide only 3% of the total biomass, in contrast to the Barro Colorado rain forest in Panama where three species — the howler and 2 sloths — comprise 71% of the total biomass (Eisenberg and Thorington, 1973). The seasonal availability of most leaves (Fig. 4), as well as rare leaf-killing frosts, make the Pantanal marginal for arboreal folivores. In 1975 a frost killed an estimated 80-90% of the crown foliage in the gallery forests of Emas National Park adjoining the Pantanal, and I encountered there a male howler monkey walking in grassland, 1 km from the nearest forest, as if in search of food.

Nearly 2/3 of the non-volant species at Acurizal subsist on or supplement their diet with seeds and fruits. All small rodents, including squirrel and agouti, specialize on this food, and it also contributes substantially to monkeys, 6-banded armadillo, peccaries, and several small carnivores. At least some *Ficus, Attalea, Bromelia,* and a few other plants are in fruit for much of the year, making them particularly important food sources. These species grow best on sandy alluvium near water, and it is perhaps not fortuitous that many forest mammals reach their greatest density in those areas too. Other fruits are seasonal. For example, *Talisia esculenta* ripens only in March and April, and at that time cattle, tapir, and peccaries, among others, eat the fallen fruit. Most fruits and seeds ripen not only seasonally (Fig. 4) but also vary in abundance from year to year. In 1977 and 1979 such leguminous trees as *Caesalpinia* and *Acacia* had more seeds than in 1978. Many seeds remain hanging in the trees when dry but with parrots and other birds, monkeys, and insects harvesting them, only a small percentage ultimately becomes available to terrestrial mammals. Among them are cattle which compete for seeds and fruit with the native mammals and perhaps indirectly help affect their density.

Insects, especially ants and termites, are an abundant and fairly predictable resource. A casual midday collection in a hectare of pasture yielded 11 ant and 2 termite species, including *Camponotus* and *Cornitermes,* both important edentate foods. Several mammals have either specialized on insects and other invertebrates or added them to the diet including the edentates, small marsupials, 4 monkey species, as well as fox, raccoon, and especially coati. It is difficult to express such species in terms of biomass because some also feed on fruits and vertebrates, but about 8-10% can probably be attributed to the presence of this food source.

Small terrestrial vertebrates were relatively scarce. Rodent density was low and so was that of frogs (mainly *Leptodactylus ocellatus* and *L. labyrinthicus*) and lizards (*Ameiva ameiva, Mabuya frenata, Tropidurus torquatus*), to name two potential resources. Consequently species which normally prey on such vertebrates were either rare (small cats) or subsisted mainly on fruit and invertebrates (fox). The large cats probably remain unaffected by fluctuations in native prey populations, as long as livestock provides a buffer.

Thus, in the seasonal environment of Acurizal most species either have a flexible diet or specialize on a relatively stable and predictable resource.

Comparisons with other neotropical areas

Species diversity in tropical forests is at least double that of temperate forests, the number of mammals rising from 15-16 in Alaskan taiga to 31-35 in forests of the eastern United States to about 70 in Panamanian rain forest (Fleming, 1973). Much of this increase is due to the number of bats which in tropical Surinam, for example, comprise 43% of 143 species (Husson, 1973). The Pantanal lies in an area of transition between the Amazonian rain forest and the more temperate and arid habitats farther south, and it is instructive to compare species diversity in the Pantanal both with rain forest to the north and the scrubby thorn forests of the Paraguayan Chaco to the southwest to see how climate and habitat have affected it. Eisenberg et al (1979) studied diversity and biomass of mammals at two Venezuelan sites. One area, in the Guatopo National Park, is hilly and covered with semi-deciduous and deciduous forest, much of it in an early stage of succession. The other, Masaguaral in the llanos, with its mosaic of deciduous forest, stands of palm, and seasonally inundated grasslands, is ecologically similar to the flood plain of the Paraguay River. A composite of these two areas resembles Acurizal, making comparisons especially interesting.

Table 11 lists the number of species in selected localities, but the results are comparable only in general terms. The rain forest samples are, for example, based on areas ranging in size from a few km^2 to many thousands: species diversity on the small Barro Colorado island is half that of Surinam. My tally for the Pantanal is incomplete, especially with respect to bats and rodents. And man has affected diversity in certain localities by eliminating species, notably the big cats.

Rain forest harbors the greatest number of bat species and the Chaco the least, the Pantanal being intermediate. The increased variety and availability of fruits and insects account for the diversity in rain forest (Fleming, 1973), as does probably the great vertical stratification of the habitat, providing more feeding and roosting areas. Rain forest also tends to have more small rodent and marsupial species than do the other habitats, again probably a reflection on the constant nature of and great variety in the food supply, especially for scansorial species. The Pantanal harbors as many kinds of primates as some rain forest areas even though trees are only half as tall and half as diverse, and food resources are more seasonal; however, under the more severe conditions of the Chaco, primate species have been reduced to one. Edentates reach the greatest diversity in the two extreme habitats, rain forest and Chaco, with the Pantanal intermediate. Rain forest harbors two leaf-eating sloth species and the Chaco an unusual number of insectivorous armadillos, each foraging type adapted to a specialized and predictable food supply. There are as many carnivores and ungulates in the Pantanal as in rain forest, indicating that the latter does not encourage diversity of such mammals (Eisenberg and McKay, 1974). Carnivores and ungulates in the Chaco are as diverse as elsewhere.

In comparing the number of non-volant species in the Venezuelan study areas with the Pantanal, it is apparent that the former are relatively impoverished. This is especially true for Masaguaral where half as many species were recorded as in the ecologically similar Pantanal. In part this paucity can be explained by the small size of the area. Yet in the llanos as a whole there are still only 42 species (Eisenberg and Redford, 1979). Primates, Carnivora and Artiodactyla are orders poorly represented at Guatopo and Masaguaral, and among Edentata the armadillos show a notable lack of diversity. Climate, structural complexity of habitat, and seasonal patterns

Table 11. Number of mammalian species in several neotropical areas (excluding Cetacea and introduced rodents)

	Belem area, Brazil (Pine, 1973)	Surinam (Husson, 1973)	Barro Colorado, Panama (Eisenberg and Thorington, 1973)	Guatopo N. P. Masaguaral ranch Venezuela (Eisenberg et. al. 1979)		Chaco, Paraguay (Wetzel and Lovett, 1974; Myers & Wetzel, 1979)	Acurizal ranch, Pantanal, Brazil (This study)
Principal vegetation Size of area	Rain forest ?	Mostly rain forest 157,500 km²	Rain forest 16 km²	Hilly deciduous to semi-deciduous forest 926 km²	Llanos, pasture forest mosaic 28 km²	Mostly thorn forest 247,000 km²	Pasture-forest mosaic 137 km²
Chiroptera	not recorded	62	34	29+	42	12	21+
Marsupialia	9	10	6	7	2	4	3 (+2)*
Primates	6	8	5	3	2	1	5
Edentata	10	10	5	5	3	10	6
Lagomorpha	1	1	1	1	1	1	1
Rodentia	18	29	13	13	11	13**	11 (+2)
Carnivora	17	16	6	8	7	10	10 (+6)
Sirenia	1	1	0	0	0	0	0
Perissodactyla	1	1	1	1	0	1	1
Artiodactyla	4	5	3	2	2	5	6
Total non-volant species	67	81	40	40	28	45	43 (+10)

* Figures in parentheses indicate number of additional species recorded in the area but not at Acurizal
** R. Wetzel (pers. comm.) recently found 3 more species

of food distribution offer no facile explanation for the differences. Leaving aside man's possible extirpation of several species, some differences can possibly be ascribed to historical vagaries in distributional patterns. For example, the Venezuelan study areas lie within the expected range of coati and white-lipped peccary yet neither species occurs there. The mammalian species in both llanos and Pantanal show little or no endemism, being derived from habitats surrounding their respective river basins, and part of the greater diversity in the latter area can perhaps be attributed to the greater variety of habitats from which the species were drawn.

Table 12 presents biomass of selected mammals in several neotropical areas. Detailed comparisons are not possible, for most censuses lack precision and different authors may use different weights for the same species in computing biomass, but several trends are discernable. Rain forest has the highest biomass, the 4431 kg/km^2 on Barro Colorado being over 4 times higher than any other area. However, it is not known how representative this small island without a normal complement of predators is of rain forest as a whole. The biomass of several species in a Colombian rain forest tract was much lower than that of the same species on Barro Colorado (Table 12). In that area the Bari Indians derived 18% of their meat intake from wild mammals (Beckermann, 1975). A mountain rain forest in Guatemala held an estimated biomass of 1200 kg/km^2, excluding small mammals (Hendrichs, 1977).

Over 2/3 of the biomass on Barro Colorado consisted of arboreal species, mainly primates and sloths. As Eisenberg et al (1979) pointed out, arboreal species contribute much less to biomass in other habitats, terrestrial herbivores, especially ungulates and capybara, replacing them in importance. Still, primates provide 37% of the biomass at Masaguaral West, an area with few terrestrial mammals because of periodic flooding, 13% at Masaguaral East, and 18% at Guatopo. In view of these figures, the primate biomass at Acurizal is low, even the ecological biomass reaching only 97 kg/km^2 in the area of highest density. Since primates are not hunted at Acurizal, the low biomass is probably related to food availability during the dry season.

Masaguaral, Guatopo, and Acurizal are similar in that total biomass is relatively low, on the order of 1000 kg/km^2 or less, with the last-named reaching only 380 kg/km^2. The Acurizal figure does not reflect the carrying capacity of the land, human interference, habitat changes, and disease having depressed the biomass. In contrast to Masaguaral, and probably to Guatopo as well, Acurizal is heavily hunted, and ungulate and carnivore numbers are thereby affected. Small rodents are scarce in periodically flooded areas, both in the llanos and Pantanal, but the low biomass at Acurizal, most of which lies above the flood plain, can perhaps be attributed in part to burning which destroys cover and food. Masaguaral East has a capybara biomass of 300 kg/km^2. The capybara is also the dominant species in the wet parts of the Pantanal, but disease decimated the species at Acurizal after severe floods inundated its favored habitat. One Pantanal area, 20 km^2 in size, had a capybara biomass of 338 kg/km^2, a figure similar to that of Masaguaral East. Thus, under more favorable circumstances, Acurizal could have a biomass comparable to that of Masaguaral and Guatopo, although primates, *Didelphis*, agouti, and certain small carnivores may normally be scarce because of a limited food supply.

The data from Acurizal make it clear that land clearing has an adverse impact on most native mammals. By converting forest to pasture the carrying capacity of areas is lowered in terms of wildlife, except that capybara and marsh deer may benefit in the vicinity of water. However, livestock

Table 12. Crude biomass in kg/km² of selected mammals in several neotropical areas

	Masaguaral West[1)]	Masaguaral East[1)]	Guatopo[1)]	Barro Colorado[2)]	Colombia rainforest[3)]	Acurizal[4)]
Primates	176.3	136.0	167.0	401.3	16.3	19.6
Anteaters	11.2	11.2	22.8	?		3.3
Armadillos	19.0	38.0	23.0	?		29.1
Sloths	absent	absent	7.5	2657.3		absent
Didelphis	53.0	53.0	51.0	66.9		tr.
Small marsupials	5.3	6.0	11.0	38.8		
Small rodents	20.0	9.0	77.5	172.6		24.0
Squirrel	6.7	4.3	6.3	4.8	1.4	0.1
Coendou	17.5	17.5	9.8	?		tr.
Agouti	3.0	80.0	126.0	178.3	12.6	3.2
Capybara	8.7	300.0	34.2	absent		47.1
Small carnivores	54.1	49.9	37.0	114.6		9,7
Large cats	?	1.0	1.1	absent		5.4
Tapir	absent	absent	157.2	152.8		96.4
Collared peccary	?	195.0	34.2	146.5	6.0	14.1
White-lipped peccary	absent	absent	absent	absent	9.5	44.0
Mazama deer	absent	absent	78.8	19.1		70.3
Total Biomass kg/km²	479.0	1086.0	946.0	4431.0	not recorded	380.0

1) Eisenberg et al 1979; 2) Eisenberg and Thorington 1973; 3) Beckermann, 1975; 4) This study.

depends on pasture and many ranchers now manage their land intensively to increase cattle production. Masaguaral and Acurizal both support many cattle — a biomass of 7600 kg/km² in the former (Eisenberg et al, 1979) and 3750 kg/km² in the latter — as well as moderate wildlife populations, indicating that the two can coexist as long as an area retains a mosaic of habitats. With human pressures increasingly affecting wilderness in the neotropics, large ranches are becoming important reservoirs of wildlife. Owners of such ranches should be encouraged to preserve original habitats and the species they contain. While this may have a slight effect on cattle production, alternative means of exploiting the land, such as harvesting capybara commercially (Ojasti, 1973), could compensate an owner for any loss of income from cattle.

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Summary

Sixty-four species of wild mammals were recorded in deciduous forest, cerrado, and other vegetation types at Acurizal, a ranch located in the Pantanal area of southwestern Brazil. The total biomass of these species was about 380 kg/km² of which tapir contributed 25%, deer 22%, peccaries 15%, capybara 12%, edentates 8.5%, primates 5%, and carnivores 4%. Livestock had a biomass of over 3750 kg/km², a figure 10 times greater than that of the native mammals. The low biomass of wild mammals can be attributed to habitat modification (periodic floods, conversion of forest to pasture, annual grass fires), hunting for meat and hides, disease, especially in capybara, and seasonal changes in the abundance of fruit, leaves and other food. An analysis of food habits revealed several trends in resource use: terrestrial mixed browsers and grazers — tapir and deer — contributed most to the biomass; primary grazers were absent, except for the semi-aquatic capybara; and arboreal folivores were rare, comprising only howler monkey and por-

cupine, with 3% of the total biomass. Nearly 2/3 of the non-volant species, including various carnivores, subsist at least partly on seeds and fruit, and many species also eat insects and other invertebrates. In the seasonal environment of Acurizal, most species either have a flexible diet or specialize on a predictable resource. Biomass data from the Pantanal are compared with those from other neotropical areas, especially with the ecologically similar llanos of Venezuela.

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