JAGUARS, PUMAS, THEIR PREY BASE, AND CATTLE RANCHING: ECOLOGICAL PERSPECTIVES OF A MANAGEMENT ISSUE

By

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Abstract of Dissertation Presented to the Graduate School of the University of Florida in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

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By

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Jaguar and puma depredation on livestock may be influenced by 1) innate and learned behavior; 2) health and status of individual cats; 3) division of space and resources among jaguar and puma; 4) cattle husbandry practices; 5) abundance and distribution of natural prey. Our study in Los Llanos Altos of Venezuela aimed to establish how all these inter-related elements were related to cattle being lost to cat depredation. Linear foot transects, vehicle transects, point counts, incidental observations, camera trapping, net, hoop trap, funnel trap, haul seine, box trap, and noose captures, and detailed vegetation sampling and mapping were employed to understand the patterns of prey distribution by species and available biomass. Prey distribution was influenced by forest composition, topographical characteristics, and degree of habitat interspersion. Climate, topography, and soils interact to define variation in primary productivity, dictating prey distributions, and large cats use space accordingly. The few preferred prey species were both large and productive. Large reptiles were used less than their high biomass would suggest, presumably a result of access and risk. The biomass of natural prey in the study area was adequate to support the resident large cats without a subsidy of domestic livestock. Selective rather than opportunistic hunting by the cats reinforced that conclusion. However, the distribution of natural prey was far from uniform. Puma were responsible for more attacks on livestock than jaguar, frequently in maternity pastures set in upland areas of relatively low prey availability. The mammalian biomass in the study area rivaled that of the most productive savanna/forest mosaics of the Old World. Up to 97% of that high biomass was represented by grazers introduced from the Old World, the majority being bovid livestock apparently occupying niches left vacant since the megafauna extinctions of the Pleistocene. The closing discussion of management recommendations focuses on Los Llanos Altos of Venezuela, but contains elements applicable to all the savanna/forest mosaics of South America where similar issues may arise.

CHAPTER 1 JAGUAR, PUMA, THEIR PREY BASE, AND CATTLE RANCHING: AN INTRODUCTION

Cattle production is a profitable and relatively non-destructive land use system in the seasonally flooded lowland savannas of Venezuela, Colombia, Brazil, Bolivia, and Guyana. On many large ranches, habitat modification is minimal and wildlife values are high. However, a major source of mortality for jaguars (*Panthera onca*) and puma (*Puma concolor*) is persecution by cattle ranchers who attribute livestock losses to the cats. In some cases these losses to cats are very real (Hoogesteijn et al. 1993). In some situations the problem has been exacerbated by poor herd management (Hoogesteijn et al. 1993), or indiscriminant shooting, which can result in disabled incipient "problem cats" (Rabinowitz 1986). Cattle mortality due to flooding, disease, parasites, and malnutrition may be high, but with adequate records rare, that issue is often obscured (Mondolfi & Hoogesteijn 1986). In some areas, pumas may play a larger role in livestock losses than jaguar (Farrell 1999; Gonzalez-Fernandez In Press; Scognamillo et al. In Press).

Rabinowitz (1986) found healthy adult jaguars reluctant to enter open pastures, despite the presence of potential domestic prey. Domestic animals left untended in forest were quickly dispatched by the same jaguars that avoided human habitations. In the Pantanal, many cattle killed by cats were very lightly managed. In habitat use and behavior they resembled wild prey, and during high water, were forced to use elevated forest areas (Quigley & Crawshaw 1992; Schaller & Crawshaw 1980). Half the cattle killed by cats in the same area were calves (Quigley & Crawshaw 1992). Given the

jaguar's propensity for closed forested habitats and areas near water, restricting calving to open areas with few permanent streams seemed one means for decreasing depredation (Quigley & Crawshaw 1992). The same applied for adult cows; keeping all cattle out of forested habitats should reduce depredation (Quigley & Crawshaw 1992). An analysis of cattle management methods and depredation problems on three Venezuelan ranches by Hoogesteijn et al. (1993) suggested much of the same. Lower depredation rates were hypothesized to result from: 1) exclusion of cattle from gallery forest; 2) adequate distance between calving grounds, young calves, and forested areas; 3) pasturing problem areas with bulls over a year old; 4) maintaining adequate populations of wild prey.

Shaw (1977) hypothesized that the number of cattle taken by puma in Arizona was inversely proportional to the size of the deer herd. Mondolfi and Hoogesteijn (1986) hypothesized a similar relationship for jaguar and puma in Venezuela, where the large cats exploit a more diverse prey base. These speculations were vastly pre-dated by the observation by Roosevelt (1914) that ranches in Brazil that possessed abundant native prey experienced fewer jaguar problems. Eighty years later these ideas had yet to be tested with data.

This dissertation represents part of one team's effort to examine the overlapping variables contributing to the conflicts between jaguar, puma, their prey base, and cattle production in tropical America. Throughout the bio-region in which our study was located there are problems with attacks on livestock by both jaguar and puma (Gonzalez-Fernandez In Press). Jaguar predation on cattle stranded on forest islands amidst flooded savannas, a common situation in the Pantanal of Brazil, was rare in our particular study area (Hato Piñero). This was more a function of sound cattle management than evasion

of jaguar attacks. Adult cattle can forage in water but need a dry place to rest at night. Calves cannot forage in water. Calf survivorship (and hence production and profits) are increased when calving occurs in uplands during wet months. However, every action has a reaction, and throughout the Llanos Altos, and in our study area in particular, the greatest losses to predators were young calves lost to puma in maternity pastures, during the rainy season.

Losses usually were not high. In the region, 70% of the ranches lost less than 0.4% of the herd annually (Gonzalez-Fernandez In Press). Between 1991-1997 in Hato Piñero, 13.3% of all calf losses were attributable to jaguar (1.8%) and puma (11.5%)(Scognamillo et al. In Press). In other ranches in the region, losses were not as skewed (43% problems due to jaguar and 57% due to puma) but overall, the highest losses were still calves taken by puma (Gonzalez-Fernandez In Press). Ranches set in the evergreen moist forests south of the Orinoco River experienced more problems with jaguars (Juan La Vieri pers. comm.). Although the number of cattle lost are usually low, some cats become habituated on cattle and local losses then become unacceptably high to ranchers. In the region, a few ranches had lost between 2.5% and 5% of all calves born to felids (Gonzalez-Fernandez In Press). Such outbursts of chronic losses usually result in dead cats and our study hoped to suggest means for reducing the problem. The study began with the management issue of cat and cattle co-existence, but also addresses questions of broader interest relating to resource competition, foraging theory, and the ecology of the prey species themselves.

The range of the puma spans 110 in latitude (Culver et al. 2000). The species essentially covered the Americas (now extirpated in some regions), from far north to extreme south, but it has yet to appear in southern Alaska. In North America, large ungulates, primarily deer, constitute 68% of the puma's diet by frequency of occurrence; large rodents, lagomorphs, small carnivores, and where present, armadillos, constitute the remainder (Iriarte et al. 1990). Evidence from numerous North American locales (Anderson 1983; Dalrymple & Bass 1996; Hornocker 1970; Kunkel et al. 1999; Logan et al. 1996; Maehr 1997a; Murphy 1998; Shaw 1977) convinced many workers that the puma specializes on deer. The breadth of puma diet appears to have an inverse relationship with latitude due to greater diversity in the tropics. While the food habits of puma have been well-studied in North America and in Chile (Iriarte et al. 1990), in the tropics the subject began as a minor component in jaguar studies (Emmons 1987; Quigley & Crawshaw 1992; Rabinowitz & Nottingham 1986). Very recently, more data have become available. Aranda and Sánchez-Cordero (1996) made observations on jaguar and puma coexistence in southern Mexico based on 37 jaguar scats and 15 puma scats. Taber et al.(1997) examined the same issue in the Paraguayan Chaco based on 106 jaguar scats and 95 puma scats. Nuñez et al. (In Press-a) employed a more comprehensive methodology, using telemetry to study jaguar and puma in west-central Mexico. Their conclusions on food habits were based on 50 jaguar scats and 19 jaguar kills and 65 puma scats and 26 puma kills (Nuñez et al. In Press-b).

In the Peruvian Amazon, puma appeared to use more smaller prey than jaguar (Emmons 1987). The same held true in intact habitats in the northern Paraguayan Chaco (Taber et al. 1997) and in dry forests in western Mexico (Nuñez et al. In Press-b). In the

Pantanal of Brazil, puma attacks on cattle was more skewed towards calves than those by jaguar (Crawshaw & Quigley In Press). The puma is a highly adaptable species whose size and ecology can vary among habitats and latitudes.

Unlike the puma, which is found across a vast stretch of habitats and latitudes, the jaguar is restricted to the subtropics and tropics. In the northwestern United States, where the jaguar is not present, puma are larger than in the tropics and regularly prey on young elk (Cervus elaphus) and adult mule deer (Odocoileus hemionus) (Hornocker 1970; Iriarte et al. 1990; Logan et al. 1996; Murphy 1998). Mule deer weights are double those of capybara and tropical white-tailed deer and triple those of white-lipped peccary (Anderson & Wallmo 1984). In Alberta, Canada, male puma, averaging 75 kg (larger than many tropical forest-dwelling jaguars), take moose (*Alces alces*), including 250 kg yearlings (Ross & Jalkotzy 1996). As mule deer populations dropped in New Mexico during the late 90s, puma turned to bighorn sheep (Ovis canadensis) (Eric Rominger pers.comm.). Chilean puma are also larger than tropical puma, and pursue some large prey, though less than the northern puma (Iriarte et al. 1990). The puma's adaptation to a staggering variety of habitats across latitudes has demanded plasticity in diet. Size differences between leopards and tigers (weight ratio 1:4) are more extreme than between puma and jaguar (Seidensticker 1976), but echoes of their relationship may be found where the New World large cats co-occur. Perhaps puma take a higher frequency of smaller prey when in the company of the larger bodied jaguar? Even this postulate must account for observed variation. In Hato Piñero, the average jaguar weight was 70 kg and that of puma 41 kg. On average Piñero jaguar were 1.7 times the size of Piñero puma. In west-central Mexico, where perhaps jaguar were "making do" in puma habitat, jaguar

were 35-55 kg and puma 25-50 kg, approximately the same size (Nuñez et al. In Press-a; In Press-b).

Jaguar appear to use waterside habitats when they are available more than puma (Emmons 1987). In such habitats, the jaguar may eat freshwater turtles, caiman, fish, and even sea turtles (Carrillo et al. 1994; Carrillo & Saenz In Press; Emmons 1987; 1989; 1991; Hoogesteijn & Mondolfi 1993). Large aquatic and terrestrial reptiles figured heavily in the diet of Emmon's study animals, leading her to speculate that the large head and great bite force of the jaguar could be an adaptation for breaking through the hard integuements of large reptiles (Emmons 1987; 1989). Aranda (1994) also speculated on the origins of the powerful physique and bite force of jaguars. However, his study area lacked large areas of surface water, and thus large reptiles, and the jaguar's morphology seemed well-suited to killing peccaries, which, though not large (23-35 kg) do have fairly formidable defenses. The current and Recent ranges of *Tayassu tajacu* and *Panthera onca* do coincide (Aranda 1994).

In the Peruvian Amazon, puma did not prey on turtles and crocodilians (Emmons 1987; 1989). In habitats of the Florida Everglades too low in elevation to be prime puma habitat, 11.1% of florida panther (*Puma concolor coryi*) kills were alligators (*Alligator mississippiensis*) (Dalrymple & Bass 1996). In the upland habitats that the panther prefers (Maehr 1997a), and which are more productive for ungulates and panthers, feral hogs (*Sus scrofa*) and white-tailed deer were more dominant food items. Alligator consumption became negligible (Maehr 1997a).

In the xeric habitats of western Mexico and the Paraguayan Chaco, dietary differences between jaguar and puma were subtle (Nuñez et al. In Press-b; Taber et al.

1997). Yet, in western Mexico, the jaguar did show slightly more preference for collared peccary than did puma (Taber et al. 1997). In the Yucatan Peninsula of Mexico collared peccary were the most important prey for jaguar, while brocket deer (Mazama *americana*) and white-tailed deer (*Odocoileus virginianus*) were the most important prey for puma (Aranda & Sánchez-Cordero 1996). In the Peruvian Amazon, jaguars took peccaries more than expected from known densities (Emmons 1987). In the Pantanal of Brazil, jaguar slightly preferred peccary over capybara, while puma took more capybara than any other natural prey (Crawshaw & Quigley In Press). In perhaps the most comprehensive study of jaguar and puma coexistence to-date, Nuñez (In Press-b). found 7 prey items in 50 jaguar scats and 11 prey items in 65 puma scats. The habitat in their west central Mexico study area (90% low deciduous dry forest) may be better suited to puma than jaguar in the same way that the lower areas of the Brazilian Pantanal might be better suited for jaguars than pumas (Crawshaw & Quigley In Press). Including kill data, Nuñez (In Press-b) found more diversity in puma diet than in jaguar diet. Although both species may be flexible (Rabinowitz & Nottingham 1986), the puma would be expected to be more of a generalist, particularly in the presence of a social dominant (Seidensticker 1976).

In the rain forest of Belize, the three most important prey species for jaguar (ranked in descending order by frequency of occurrence) were armadillo (*Dasypus novemcinctus*), paca (*Agouti paca*), and collared anteater (*Tamandua mexicana*) (Rabinowitz & Nottingham 1986). The armadillo, a relatively small animal, represented 54% of all prey identified. There were a total of 16 prey species from 228 samples. Emmons (1987) reported similar breadth in the taxon and size of jaguar prey in the

western Amazon. There were 40 prey items in 25 jaguar feces and 12 in 7 puma feces, item/sample ratios of 1.6 to 1.7 respectively, suggesting both cats have a diverse diet, and that more feces would have yielded yet more prey species. Both studies suggest that jaguar hunt opportunistically in densely forested habitats. In Peru, jaguars even ate snails and skinks (Emmons 1991).

A caution in interpreting jaguar and puma diets across their entire low latitude distributions is that prey diversity varies among study areas. The sub-tropical moist forests of southern Belize have relatively high prey diversity (Rabinowitz & Nottingham 1989). The upper Amazon in Peru is one of the most biologically diverse areas in the world (139 mammal species (Voss & Emmons 1996). In contrast, the llanos of Venezuela are less diverse (75-80 mammal species (Eisenberg & Polisar 1999). The llanos prey base is more diverse than that of temperate study areas (Dalrymple & Bass 1996; Hornocker 1970; Logan et al. 1996; Maehr 1997a; Maehr 1997b; Murphy 1998), but its forest-dwelling prey are a subset of the assemblage native to more constantly humid forests (August 1983; Eisenberg & Polisar 1999; Eisenberg & Redford 1979), that penetrate the savanna via the mesic and structurally complex forest. This is a situation similar to other South American savanna-forest mosaics (Mares et al. 1985; Redford & Fonseca 1986), and typically involves very few endemic mammals (Eisenberg & Redford 1979).

The diverse prey in rainforests may be relatively evenly distributed in comparison to savanna-forest mosaics. Fauna and flora cannot truly be evenly distributed, but contrasts can be expected. In large blocks of high-alpha diversity tropical moist forest, edges are softer and much production (primary, secondary, and tertiary) arboreal

(Eisenberg 1980). In the llanos, edges are abrupt, much production is at ground-level, and oscillating aquatic habitats facilitate an impressive amphibious prey base (capybara, caiman, turtles). Not only is terrestrial production high in the llanos (Eisenberg 1980; Eisenberg et al. 1979), and mean weight of prey high (Hoogesteijn & Mondolfi 1996), the physiognomy of the region with its horizontal beta-diversity should result in a more patchy distribution of resources, even for secondary consumers such as jaguar and puma. These predicted contrasts in the patchiness of prey distributions and subsequently, concentrations of cat food, would in turn predict that the hunting patterns of llanos cats would be less opportunistic and more selective than those of rain forest cats.

The aggregate of management and ecological questions that this component of Hato Piñero project addressed follows. Do jaguar and puma have adequate natural prey to survive without a subsidy from livestock? How much natural prey biomass is available to the large cats? Are prey distributions even or patchy? Do prey distributions vary seasonally? Do habitat characteristics affect prey distributions? If so, what habitat characteristics are important? Do the large cats hunt opportunistically, taking prey in relation to abundance? If diets demonstrate selective hunting, which prey are preferred by jaguar and which by puma? How do the diet of jaguar and puma differ in terms of prey body sizes and overall diet breadth? What are the relationships between felid attacks on livestock and the seasonal distribution of livestock? Are attacks on livestock related to local prey availability? What can be done to reduce the frequency of large cat attacks on livestock?

Chapter 2 introduces the study area, describing it in some depth. It also presents summaries of vegetation analyses, concentrating on forest floristics and physiognomy.

Since the most important prey of the large cats were likely to be herbivores, it was important to clarify forest types and evaluate the relative ability of those types to sustain prey. Chapter 3 focuses on the distribution, abundance, and biomass of potential prey. While Chapter 3 contains many subtopics of interest, it also serves to set the stage for the section that follows it. Chapter 4 is a broad, yet condensed synthesis of the availability of prey, the selective patterns of the large cats, and how those both relate to cat attacks on livestock. Ecological theory and Paleontological perspectives assist the interpretations. Chapter 5 contains comments and recommendations, both general and specific, relating to ways in which conflicts between large cats and cattle ranchers can be reduced. These recommendations address the immediate region in which we conducted this study, under the premise that large-scale gains in conservation are constructed of, and constrained by, the sum of local advances. Despite that perspective and presentation, elements of the recommendations are quite applicable to the complete range of savanna/forest mosaics present in South America.

CHAPTER 2 STUDY AREA:TOPOGRAPHY AND VEGETATION RELATIONSHIPS ON A CATTLE RANCH IN LOS LLANOS ALTOS, ESTADOS COJEDES, VENEZUELA

Introduction

Hato Piñero is a working 80,000 ha cattle ranch/wildlife preserve located between 8 40' and 9 00 N and 68 00 and 68 18 W(Miller 1992) in the southeast corner of Estado Cojedes in north-central Venezuela. The northern boundary of Piñero lies among hills that rise to 396 m above sea level (Farrell 1999). The western boundary is formed by the Cojedes and Portuguesa rivers, the southern and eastern boundaries by the Chirgua and Pao rivers (Fig. 1). Smaller streams (caños) run through this basin. The lowest elevations are approximately 65 m above sea level in the open esteros in the southern part of the ranch. The landscape can be characterized as a complex mosaic of interdigitated forests and open areas with vegetation types based on interactions of elevation, substrate, and hydrology. The ratio of open to forested areas is roughly 50:50 depending on interpretation (Fig. 2). Many of Piñero's forests follow stream beds, but relatively large blocks of semi-deciduous forest not adjacent to stream beds are a characteristic of this region, termed Los Llanos Boscosos (the forested plains) (Velasco & Ayarzagüena 1995). Only in the far southern reaches of Piñero is broad savanna laced with narrow strips of gallery forest, a landscape characteristic of areas further south in Los Llanos Bajos. The estimated 407 ha of open water in the study area during the late dry season is in stark contrast with the almost 80 % of the ranch shallowly inundated in the middle of the rainy season.

The hyper-seasonal environment (Thorbjarnarson 1991a) of the llanos is a result of interactions between climate and soils. Piñero receives an annual average of 1468.8 mm of precipitation, with the majority falling between the beginning of May and the end of November. The dry season runs from December 1 through April. For faunal analyses, I designated the wet and dry seasons as May 16-November 30 and December 1-May 15, respectively. This was based on 1996 and 1997 rainfall patterns (Fig. 3), patterns of leaf flush and fall, and seasonal shifts in animal distributions. The clay soils in the plains cause surface water to accumulate starting in June and reaching peak levels in July and August (Fig. 4). This flooding is relatively shallow (Fig. 5). The deepest water encountered on foot transects was about 1m (waistline), and the deepest ever encountered about 1.5 m (belly deep for horses). Although up to 80-90% of the surface area of some forests are shallowly flooded following strong July rainfalls, the average is less (Fig. 4) and contrasts in micro-elevations important. Islands of damp land remain in most low elevation forests, even when surrounded by a shallow sea of flooded savanna.

Many savannas retain water through January, as does the evergreen forest (Fig. 4). As the dry season progresses, mid-day temperatures in the sun may exceed 40 C. Vast areas of surface water contract, forcing impressive concentrations of caiman, turtles, and fish in shrinking aquatic habitats. The same savannas that are 100% inundated during the rainy season are burnt by the ranch workers (llaneros) during March to improve forage. Forests occupied by fish and frogs in July are bone-dry by March, the hard clay soil covered with leaf-litter from the bare trees above. The shallow, phosphorus and calcium poor, granite derived soils and gravels in the hills are highly permeable and

dry rapidly (Ramia 1993). These edaphic characteristics create extreme drought in the dry season, and the vegetation in the high hills is clearly fire-adapted.

The predominant races of cattle among Piñero's 14,000 head were cebú (nelore, brahma, guzerat, gir) (*Bos indicus*). Other races were criollo (*Bos taurus*), senepol, romosinuano, and various hybrids. A herd of approximately 150 water buffalo (*Bubalus bubalis*) was maintained in the southern savannas. Approximately 420 horses, mules, and burros fulfilled working and breeding needs. Most cattle were moved from flooded areas to higher drier pastures during the wet season. Artificial insemination resulted in calving peaks from July through September (Fernando Corrales pers.comm.).

Cattle ranching is the dominant land use in the llanos. Land is far from equitably distributed among the populace. Powerful landowners hire men to manage cattle and horses, and women to cook. Wages hover around the minimum required. Despite any ramifications this has for social mobility among rural folk, the landscape is relatively intact considering the profits generated, and the llaneros proud of their heritage and skills. Hunting has been banned in Piñero. As a result, most wildlife is common and visible, giving support to a profitable on-premises ecotourism lodge. Poaching does occur on ranch perimeters, and to a lesser degree, within the ranch in several less frequented areas. Sampling investments were lower in such areas to avoid potential disruptions in study design and execution.

On two sides of Piñero, neighboring large ranches also contain good wildlife habitat and reduced levels of hunting (Hato Socorro to the northwest, Hato Corralito to the northeast). Caño Caujaral enters Piñero through a valley bisecting the northern hills. Visits to the caño where it ran through Hato Mata Clara (north of Piñero), ultralight

aircraft reconnaissance, and satellite imagery all testified to the dense strip of forest surrounding the caño as it extended north of the ranch. These factors of connectivity are what has allowed jaguars, white-lipped peccaries, and tapir to persist in the agricultural matrix of los llanos altos.

Piñero possessed a high degree of horizontal habitat heterogeneity. This was predicted to influence prey distributions, and correspondingly, large felid intra-specific and inter-specific partitioning of space and resources. A classification of forest types was critical for mapping purposes and to evaluate the relative utility of habitat types for potential prey. The remainder of this chapter describes 1) quantitative and qualitative vegetation sampling in forests, savannas, and pastures; 2) forest classification; 3) some aspects of forest phenology; 4) mapping efforts and spatial analyses of the study area; 5) plant resources available to prey in different habitat types; and 6) all of the above in relation to work conducted by colleagues in the same region.

Methods

The 26 transects established to evaluate faunal distributions and abundance were also used to record quantitative floristic and physiognomic data. Reconnaissance trips by vehicle, foot, and ultralight aircraft were used in planning transect design. A vegetation map, created by Dr. Francisco Delascio's (Venezuela National Herbarium & Botanical Garden) interpretation of 1989 Landsat Thematic Mapper imagery assisted planning, although reconnaissance also indicated that it needed additional detail. The numbers of transect lines and their length were as follows: dry hill forests [4, 9.8 km]; semideciduous forest not adjacent to permanent water [3, 5.5]; semi-deciduous forest near permanent caño or prestamo [4, 7.51]; interspersions of semi-deciduous forest and savanna, ecotone crossed perpendicularly [2, 4.5]; semi-deciduous forest edge, parallel to pasture [1, 2]; small flooding savannas and managed pastures near forest [5, 5.65]; large flooding savanna, close to forest [2, 4]; large open flooding savanna away from forest [2, 4.7]; higher elevation, non-flooding pastures [3, 3.55] (Fig. 2). This design took in a representative cross-section of habitat types, and facilitated evaluations of the effects of proximity to water, habitat interspersion, and distance to cover on animal distributions.

Structural characteristics of transects were recorded at 100 m intervals. Variables recorded in forests were: substrate; canopy height; canopy closure; mid-story closure; shrub-level closure; two densiometer readings; distance to and DBH of nearest overstory trees in four quarters; distance to permanent water; distance to ecotone; and habitat and elevation categorizations. The variables recorded in savannas, pastures, and calcettas (pockets of savanna in forest) were: distance in quarters to nearest tree; height of preceding; distance to ecotone; distance to permanent water; and habitat and elevation categorizations. GPS locations recorded on transects or at nearest open area facilitated mapping.

During the first week of every month, for twelve months, phenology observations of marked individuals of 29 tree species important as food for prey were recorded along 3-5 trails in forests. This was complemented by published phenology data on 14 tree species from nearby Caño Benito (Ortiz 1990), observations of animals feeding in our study area, and data presented in (Monasterio & Sarmiento 1976) and (Robinson 1986).

With help from Venezuelan National Botanical Garden/Herbarium staff (Dr. Francisco Delascio and Rafael Ortiz) forest composition was sampled along an altitudinal cross section of Piñero's forests. All trees and vines over 4 m in height were identified

and enumerated in 10 x 50 m plots. Understory species were assigned a cover classification in each plot. The 35,000 m² sampled ranged from hilltop chaparral to seasonally flooded evergreen forest. The majority of plots were placed at 100 m intervals along four transects with rich data on animal observations. Eleven plots not along the foot transects represented potential intermediate types. These plots lacked the physiognomic data collected along transects. Qualitative observations of relative species composition were recorded for several types of savannas and pastures and some additional forest areas of interest.

The existing vegetation map was improved through the following: 1) GPS locations along transects and roads and areas in question; 2) overlaying the map and my modifications on topographic maps and a plotted February 27, 1990 (dry season)Landsat TM Scene classified in Bands 3, 4, and 5; 3) finalizing classifications (pooling for simplicity in spatial analyses) and drawing polygons; 4) scanning into a TIF file; 5) digitizing in ESRI's ARCVIEW 3.1 to obtain habitat-specific area estimates and a product for presentation.

Forest plots were classified using hierarchical cluster analyses using furthest neighbor linkages and squared euclidean distances (SPSS 1999). These were based on tree species frequencies in each plot. Analyses were run with 1) all plots and all species; 2) 59/70 plots with rare trees removed (occurring in 2.857%< of plots) and structural parameters added (mean height of canopy trees, mean DBH of canopy trees substrate and elevation classifications); 3) all plots, no structural data and rare and common species (occurring in 4.28%< or >50% of the plots) removed. Following classification, data from clustered plots were pooled for composition comparisons and assessment of relative food

availability. The list of plants used as food for the more important prey came from observations presented in (Barreto et al. 1997; Brokx 1972; Danields 1991; Delascio-Chitty & Branger 1996; Delascio-Chitty & Stergios 1996; Moskovits & Bjorndal 1990; Robinson 1986; Robinson & Eisenberg 1985). In addition, we substantially supplemented the literature using observations made by project personnel throughout the study period, and complemented by personal observations supplied by llaneros.

<u>Results</u>

Forest Types

The most definitive results from cluster analysis came from transect plots, in which floristic differences were complemented by physiogonomy, and rare species were screened out (Fig.6). Evergreen Forest/Bosque Siempre Verde (BSV), a small forest patch on loam soils in a valley subjected to prolonged flooding was unique due to the dominance (over 56% of all trees) of *Vochsyia venezuelana* Vochysiaceae (Table 1). Mixed Dry Forest/Bosque Seca Mezcla (BSM), so-named because it was a hillside (50% high hillsides, 50% low hillsides) mix of hill and lowlands elements, was, despite relatively high diversity, dominated alternatively by *Protium heptaphyllum* Burseraceae and *Erythroxylum orinocense* Erythroxylaceae (both over 25%)(Table 2).

Species area accumulation curves run on subsets of the Semi-Deciduous Forest Type 1/Bosque Semi-Deciduo Type (BSDT1) type (Fig. 7) indicate that, in relative homogeneous forest (La Candelaria) one might expect a leveling out at around 6 plots (3000 m²). The Caujaral Norte transect (also BSDT1) differed. Located parallel to the Caño but at varying distances, mild topographical irregularities due to past and present seasonal feeder streams resulted in higher diversity. Although the BSV and BSM types were based on only three plots each, these small forest patches were clearly distinct. (Table 1, Table 2, Fig. 6). The Atypical Bosque Seca Mezcla (ABSM) was located in the shaded fold of a high hill, and was sometimes used by *Cebus olivaceous*, uncommon for that elevation. Topographical irregularities and subsequent variation in exposures allowed elements from lower elevations to penetrate these higher sites. BSM plots were 50% on high hillsides, 50% on low hillsides, and the substrates were 75% rocky and 25% gravel.

Dry Forest/Bosque Seca (BS) could be divided into two sub-types based on elevation (Table 3, Table 4). Dry Hill Forest/Bosque Seca de Cerros (BSC) occurred at lightly higher elevations (40% high hillsides, 60% hill bases, substrates 60:40 rocky/gravel (Table 3). Hill Base Dry Forest/Bosque Seca de Falda (BSF) occurred along the base of hills (100% hillbase, 62.5:37.5 gravel/rocky substrates (Table 4)).

Dry Savanna with Chaparral/Sababa Seca con Chaparros (SS/CH) could be broken down to that occurring on high ridges (SS/CH Alta: 60% ridge top, 20% high hillsides, 20 % low hillside, 60% gravel, 40% rocky (Table 5)) and low ridges (SS/CH Bajo: 50% hillside, 50% hillbase, 50% gravel, 50% rocky (Table 6)). No trees in these plots equaled or exceeded 4 m in height, which excluded them from cluster analyses while establishing their uniqueness.

The greatest number of plots were in Bosque Semi-Deciduo. This apparent sampling bias echoed the spatial dominance of BSD in Piñero. Bosque Semi-Deciduo 1 (BSDT1) was wide-spread (Table 7). Bosque Semi-Deciduo Tipico 2 (BSDT2), more prone to inundation, occurred relatively close to Caño Caujaral.(Table 8) All BSDT plots were on hard clay-based soils. Other variants of BSD included: (BSDG=Galeria) directly

adjacent to Caño Caujaral; (BSDS=Seca) typical of non-flooding plains below hills; and (BSDQ=Quebrada) in ravines among the high hills in the northwestern part of the study area (Tables 9,10,11). The latter three sub-types of BSD were less strongly defined . Lacking physiognomic data such as tree height and DBH, the classifications were more variable (Fig. 8). Nonetheless, the quebrada (BSDQ) forests, the hill base forests (BSDS), and the gallery forests (BSDG) were set amidst other BSD plots (Fig. 8). The CER11-13 plots, that accompanied them in the same section of the dendrogram were BSC plots that classified poorly until they received the added variables of tree height and DBH. The gallery forest directly adjacent to Caño Caujaral did differ in composition from that further from the stream (Tables 7, 8, 9). Along the west shore of Rio Pao standard BSD continued up to the edge of the steep river banks.

The physiognomic characteristics of 8 forest types are presented in Table 12. Tree height and girth increased with decreasing elevation and increasing moisture as did canopy cover, mid-story and understory. Strata in physiognomic data collection were not limited by the 4 m criteria used in floristic sampling. Tree spacing was positively correlated with tree height and DBH (large trees cannot be clustered tightly together). The BS forests tended to have a high density of small stems. At the far end of the moisture gradient, DBH and tree height declines where flooding persisted. The deeply shaded BSV forest was full of slender stems forming a dense canopy.

Vines species in forest types are presented in Tables 13 through 20. Understory species (including the "stunted" canopy of the SS/CH types) of all forest types are presented in Tables 5, 6 and 21 through 28. The understory was best developed in the BSDT types, which provided food options for major felid prey at all levels (Table 12).

The entire community of the SS/CH types is compressed into Tables 5 and 6. Those partially open habitats did have woody species, and stratification, but all were less than 4 m in height.

The relative abundance of important food items in the forests types is presented in Tables 29 through 37 [trees], Tables 38 through 41 [vines], and Tables 5, 6 and 21 through 28 [understory], and summarized in Figs. 9 and 10. Vines of food importance appeared scarce in BSDS, BSDT2, BSDG, and BSV. The low numbers of plots in BSDS require caution regarding that conclusion for that habitat. SS/CH types appeared to be poor providers, a result of their incomplete ground cover and reduced vertical development. BSDT was rich in comparison, with abundant under story. Although the greater number of plots in BSDST1 has to be considered, the habitat did have multiple productive levels. Its greater area provided more food options overall. The BS forest type was less extensive than BSDT1 , and presented fewer food options (partly but not entirely an artifact of area). BS still possessed considerable food value for prey, confirmed by numerous animal sightings in those hilly areas. The altitude/moisture gradient relationships of the forest types were as follows: SS/CH Alto; SS/CH Bajo; BSC; BSM; BSF; BSDQ; BSDS; BSDT1; BSDS2; BSDG; BSV.

Forest Phenology

The introduced mango (*Mangifera indica*) was a common and seasonally important food (Table 42), but restricted to well-drained sites. Jobo (*Spondias mombin*) fruit fall was superabundant during the rainy season in some sections of BSDS and BSDT1. It also was relatively widespread (Tables 3, 4, 7,10,11,42). Annonaceae species, also fruiting in the rainy season, occurred in nearly every forest type (Table 42). Corozo palms (*Acromia aculeata*) occurred in better-drained sites, palma llanera

(Copernicia tectorum) in wetter sites (Table 42). Bromelia chrysanta and B. pinguin were confined to low elevation BSDT1 & 2. The Marantaceae were also confined to BSD (Tables 24, 25, 42). The tubers of these were used by peccaries in all seasons. The above ground portion of the plant was luxuriant in the rainy season, but collapsed in the dry, when peccary excavations for the tubers were most noticable. Guacimo (Guazuma tomentosa) fruits were also superabundant when in season (January through April) and used very heavily by peccaries. This species, common to BSD, thrives in gaps, thus becoming most abundant along pasture edges and roadsides, rather than the forest interior. *Ficus* sp. were uncommon in BSD (Table 33), but relatively common in BSV (Table 37). *Copernicia* was never abundant in BSD (Tables 33, 34), completely absent in the semi-deciduous forests near Rio Pao, and common in seasonally flooded savannas. Lycania pyrifolia fruited in the rainy season (Table 42). A narrow strip of forest along a seasonal caño in a valley in the northern hills was frequented by collared peccaries (Tayassu tajacu) during the rainy months. Though species poor, this forest was rich in Annona jahnii, A. purpurea and L. pyrifolia (Table 42). Another forest, in the same valley, lining permanent caño, was considerably more diverse.

Savannas

The pastures and savannas of Piñero varied widely in terms of floristics, degree of seasonal inundation, proximity to forest, extent of woody vegetation, and proximity to permanent water. Measurements taken on the most wide-open savanna transect in the south resulted in a mean distance to tree in the open area (MDTR) of 548 m, a mean distance to ecotone (DIE) of 765 m, and a mean distance to water (DIH) of 1772 m respectively. The average for all four transects in the large savannas in the south were: MDTR 280 m; DIE 490 m; DIH 956 m. The average for six transects in small savannas

with forest nearby (a common arrangement in Piñero) was 115, 116, and 437 m respectively. The values for the savanna transect with the highest deer densities and perhaps overall highest open area prey densities were: MDTR 93 m; DIE 87 m; DIE 147 m. All the preceding were savannas that are shallowly flooded for seven months of the year. The average values for the four transects in pastures in higher, drier areas were: MDTR 50 m; DIE 66 m; DIH 460 m. These pastures tended to be set in relatively narrow valleys. The bands of BSDS and BS lining them were usually also narrow, with SS/CH above. The values for distance to permanent water in the high dry pastures was approximately equal to that in small seasonally flooded savannas. In the small seasonally flooded savannas the water sources were occupied by caiman and frequented by capybara.

Brachiaria humidicola, an introduced species from Africa was the most common grass in better drained pastures. The small seasonally flooded savannas were sometimes dominated by *Thalia geniculata* (Marantaceae). Other important species in those habitats were *Sporobolus jacquemontii* and *Panicum laxum* (Graminae), *Sida acuta* and *Wissadula periplocifolia* (Malvaceae), *Eleocharis elegans* (Cyperaceae), *Ipomea carnea* (Convulvaceae), and *Cassia reticulata* (Leguminosae). Less common were *Hymenache amplexicaulis*, *Cynodon dactylon* and *Paspalum fasciculatum* (Graminae), and *Hydrolea spinosa* (Hydrophyllaceae). The most common grasses in SS/CH were *Andropogon angustatus* and *Trachypogon plumosus*. *Ipomea* was common in the large savannas in south-central Piñero. The broadest savannas in the south were dominated by *Paspalum fasciculatum*. The latter has reasonable protein content, but low palatability for cattle. Buffalo (*Bubalus bubalis*) handle its high cellulose/lignin content well, and also use Cyperaceae. Cattle best use *P. fasiculatum* sprouts following a burn.

Brachiaria humidicola is a trampling-resistant invader with slightly better forage quality than native grasses. In general, all forage protein contents decline by 70-75% during the dry season, but this loss can be reduced by fertilizing. The *Trachypogon* in the hills is poor forage. Neither it nor the *Andropogon* are good ground cover. *Thalia* is a poor forage invader, forming impressive and tall cover during the rainy season. When its tall (3m) stems dry and fall during the dry season grasses can emerge from the rows of rubble. *Copernicia* was common along the fringes of small and large seasonally flooded savannas and also scattered in varying densities throughout the open areas away from edge. *Cassia reticulata* fringed many of the smaller seasonally flooded savannas (pers.obs., Rafael Hoogesteijn and Francisco Delascio pers.comm.).

Vegetation Map

The pooled vegetation types when preparing the map (Fig. 2) were as follows: SS/CH; BS; BS/AP; BSD; BSV; M; PS; SI (Table 43). The BS classification pooled all Bosque Seca sub-types. AP represented Agro Pecuaria (cultivated crops). The BSD classification pooled all BSD sub-types. M represented Mangera, which is a local term for a large grove of mango trees (abandoned orchard). PS represented Pasto Seca (high dry pastures). SI stood for Sabana Inundable, and pooled all flooding savannas, both large (low interspersion indices) and small (high interspersion indices). Many times they actually were the same savanna. The interconnectivity of habitats in Piñero was such that a polygon of wide-open savanna in the east, curved around the far south, swept through the southwest as even broader savanna, and also formed short narrow peninsulas of savanna every place where it curved back into BSD. Animal densities and compositions varied throughout, but, in some respects, it was all the same savanna. Similar situations arose with BSD.

A simplified areal summary of habitats in the 63,227 ha study area west of Rio Pao is as follows: seasonal flooded savanna (sabana inundable = SI) 24,699 ha; nonflooding high pastures (pasto seco = PS) 1,806 ha; evergreen forest (bosque siempre verde = BSV) 48 ha; low-elevation moist semi-deciduous forest (bosque semi-deciduo = BSD) 21,434 ha; mango (*Mangifer indica* = M) groves > 7 ha; mid-elevation, hillside dry semi-deciduous forest (bosque seca = BS) 4,986 ha; and on top of high hills and low ridges, (sabana seca con chaparros) = SS/CH 9,648 ha (Table 43).

Discussion

The composition of semi-deciduous forest in Hato Piñero in Estado Cojedes differed from that in Hato Masaguaral in adjacent Estado Guarico (Robinson 1986; Robinson & Eisenberg 1985; Troth 1979). In Masaguaral's semi-deciduous forest, *Copernicia tectorum* was the most abundant tree, *Genipa americana* the second most abundant, and, collectively, *Ficus* sp. were quite common (Robinson 1986). All three of these important food-producing plants were far less common in Piñero's forests (Tables 33, 34). The nearly year-round availability of *Ficus* fruits alone at Masaguaral (Robinson 1986) suggests an explanation for later-discussed differences in mammal densities between the two study areas. That these two sites, both in the north-central llanos could be so different is hardly surprising. The variation inside Piñero alone was impressive. *Copernicia* was common in the southern stretches of BSD where increased flooding also resulted in lower stature forests. Soil characteristics (low Magnesium content) excluded it entirely from the forests leading to Rio Pao (pers.obs., Rafael Ortiz pers.comm.).

Barreto et al.(1997) considered its seeds in *Tayassu pecari* feces in that area evidence of long distance movements. In fact, the palm was common in the savannas just west of the Pao forest, from where we once encountered the group of peccaries returning.

The soils in Pinero's low elevation savannas (and adjacent forests) were relatively rich (eutrophic) (Ramia 1997). Those in the high hills are poorer (oligotrophic) (Ramia 1993). In the hills, the line between savanna and forest was not dictated by soil fertility, rather by moisture gradients, which were a result of soil texture and depth, inclination, physiographic position, and underlying drainage patterns in bedrock (Ramia 1993). Thus, risking simplification, savannas occur at Piñero's highest elevations due to low soil moisture and at Piñero's lowest elevations because of excessive moisture (prolonged saturation), with forests occupying the gradients between. Among forest types, those with the greatest vertical complexity presented the greatest diversity of food types for herbivorous prey. Most of Piñero's forests were seasonally deciduous. A forest that is nearly leafless for five months of the year will present a hardship to obligate arboreal folivores, and few would be expected (August 1983). Although soft fruits were available from both native and introduced trees, hard fruits such as the dry pods of Leguminosae were important food for a variety of terrestrial mammals in Hato Piñero.



Figure 1. Northwest and north-central Venezuela. Shaded areas show location of Hato Piñero study area in relation to locations where intensive Smithsonian research projects were initiated in the 1970s.



Figure 2. Color-coded vegetation map of study area.


Figure 3. Monthly precipitation. Records for 1996-1997 from Hato Piñero. Monthly averages for 34 years in nearby El Baúl from Sistema Nacional de Informacion Hidrologica y Meteorologica, Caracas, Venezuela.



Figure 4. Mean percent of ground surface covered by water in two forest types during rainy season. BSD (Bosque Semi-deciduo) data collected along six foot transects (11,600 m). Maximum inundation was 90% of ground surface shallowly flooded. BSV (Bosque Siempre Verde) data comes from one 300 m transect section at the base of a hill system.

Mean Monthly Water Depths in Flooded BSD



Figure 5. Mean depth of flooding along six transects in semi-deciduous forest. Maximum depths were localized (such seasonal streams feeding into caño or caño spreading beyond its banks) and approximately one meter.



Figure 6. Complete furthest neighbor cluster analysis on all plots on foot transects (59 x 500m²). Variables were tree (>4m tall) species frequencies, with added variables of canopy height, mean DBH, substrate type, and elevation category. Of 101 tree species identified in 70 plots total (11 without structural data) rare trees (occurring in 2.86% or less of the plots) were removed for this analysis, leaving a total of 80 tree species. This dendrogram omits an entire dry savanna/forest type SS/CH, which is populated by woody tree species, but all are under 4m. Vine frequencies were recorded concommitant with tree frequencies but not used in analyses. Understory species were recorded in coverage categories, a variable not compatible with the counts per species made for trees.

Tree Species Accumulation Curve BSDT1: along two transects



Figure 7. Species area curves for low elevation semi-deciduous forest in Hato Piñero. Heavy line presents rate of new species encounters along a relatively homogenous stretch of forest (13 10 x 50 m plots spaced over 1850 m interval along Candelaria transect). Light line presents rate along a transect passing through more variation, both in micro-elevations and in variable proximity to a permanent caño (13 10 x 50 m plots spaced over 2400 m interval along Caujaral Norte transect).



Figure 8. Complete furthest neighbor cluster analysis on all forest plots (70 x 500m²). Variables were tree (>4m tall) species frequencies. Of 101 tree species identified in the 70 plots rare trees (occurring in 4.28% or less of the plots) and common trees (in > 50% of the plots) were removed for this analysis, leaving a total of 65 tree species. Highlighted are plots not occurring on foot transects:10/11 fell within BSD plots on this cluster run without structural variables. These are as follows: BSDG (gallery); BSDQ (quebrada); BSDS (unlike BSDT1 & 2 and BSG, never inundated). The remaining plot (CGS3) fell within the BSF type, reflecting its location at the upper end of a phenology trail abutting the CG transect (CGT plots) which dominated the BSF type. Circles denote three high hill forests (BSC, Fig. 6), that without physiognomic variables consistently clustered with BSD plots.

PLANTS USED AS FOOD (TT, TP, DA, OV, GC) MAST, TUBERS, SOME STEMS



Figure 9. Numbers of species of plants that contribute to the diets of prey in three categories (trees > 4 m in height, vines > 4 m in height, and "understory" being woody or herbaceous species < 4 m in height). Potential prey considered were *Tayassu tajacu*, *Tayassu pecari*, *Dasyprocta agouti*, *Odocoileus virginianus*, and *Geochelone carbonaria*). Species in which mature individuals sometimes do not exceed 4 m in height may be represented in both trees and understory.

PLANTS USED AS FOOD (TT, TP, DA, OV, GC): MAST, TUBERS, SOMESTEMS





Spacing	Number	Relative
Species	of trees	density
Vochysia venezuelana	151	56.55
Protium heptaphyllum	18	6.74
Leguminosae sp.	18	6.74
Ficus maxima	16	5.99
Annona jahnii	13	4.87
Copaifera officianalis	13	4.87
Pterocarpus acapulcense	11	4.12
Ouratea grossourdii	8	3.00
Annona purpurea	5	1.87
Cochlospermun vitifolium	3	1.12
Genipa americana var caruto	3	1.12
Hecatostemon completus	2	0.75
Randia hebecarpa	2	0.75
Astronium graveolens	1	0.37
Jacaranda obtusifolia	1	0.37
Bombacopsis quinata	1	0.37
Curatella americana	1	0.37

Table 1. Tree species inventory of Bosque Siempre-Verde

Species	Number of trees	Relative density
Protium heptaphyllum	128	26.02
Erythroxylum orinocense	123	25.00
Astronium graveolens	71	14.43
Jacaranda obtusifolia	25	5.08
Vitex capitata	25	5.08
Copaifera officianalis	18	3.66
Randia hebecarpa	11	2.24
Genipa americana var caruto	10	2.03
Luehea candida	9	1.83
Tabebuia ochracea	7	1.42
Connarus venezuelanus	7	1.42
Trichilia unifoliata	7	1.42
Soracea sprucei	7	1.42
Ouratea grossourdii	7	1.42
Allophyllus occidentalis	5	1.02
Annona jahnii	3	0.61
Cochlospermun vitifolium	3	0.61
Curatella americana	3	0.61
Byrsonima crassifolia	3	0.61
Bowdichia virgiloides	3	0.61
Pterocarpus acapulcense	3	0.61
Unk	3	0.61
Lonchocarpus fendleri	2	0.41
Roupala montana	2	0.41
Vochysia venezuelana	2	0.41
Tabernaemontana cymosa	1	0.20
Sciadodendron excelsom	1	0.20
Cassia moschata	1	0.20
Capparis sp.	1	0.20
Machaerium aculeatum	1	0.20

 Table 2.
 Tree species inventory of Bosque Seca de Mezcla

Table 3. Tree species invento	ory of Bosque Seca	de Cerros
	Number	Relative
Species	oftrees	density
Emithermalium anina canaa		12.40
Eryinroxyiam or mocense	60	10.49
Tabebula ochracea	47	10.62
Myrcia guianensis	47	7.93
Guellarala alvaricala	41	5.40
Illenea canalaa	32	5.40
Auophynus occiaentans	20	4.38
Annona jannii Teri-leilei everifeliste	20	4.22
Tricnilia unifoliata	20	4.22
Astronium graveolens	23	3.88
Curatella americana	21	3.54
Machaerium aculeatum	20	3.37
Cochlospermun vitifolium	18	3.04
Protium heptaphyllum	17	2.87
Bowdichia virgiloides	16	2.70
Pterocarpus acapulcense	16	2.70
Genipa americana var caruto	14	2.36
Annona purpurea	13	2.19
Jacaranda obtusifolia	11	1.85
Connarus venezuelanus	11	1.85
Coutarea hexandra	11	1.85
Platymiscium diadelphum	9	1.52
Vitex capitata	9	1.52
Copaifera officianalis	8	1.35
Byrsonima crassifolia	7	1.18
Godmania aesculifolia	5	0.84
Bursera tomentosa	4	0.67
Spondias mombin	3	0.51
Soracea sprucei	3	0.51
Randia hebecarpa	3	0.51
Sterculia apetala	3	0.51
Roupala montana	2	0.34
Tabernaemontana cymosa	1	0.17
Sciadodendron excelsom	1	0.17
Casearia sylvestris	1	0.17
Cycropia peltata	1	0.17
Psidium guianensis	1	0.17
Ouratea grossourdii	1	0.17
Lonchocarpus fendleri	1	0.17

Table 4. Tree species	inventory	ofBosque	Seca de Falda
		Number	Relative
Species		of trees	density
Guettardia divaricata		160	22.16
Allophyllus occidentalis		136	18.84
Luehea candida		109	15.10
Erythroxylum orinocense		60	8.31
Myrcia guianensis		46	6.37
Annona purpurea		39	5.40
Astronium graveolens		22	3.05
Pterocarpus acapulcense		17	2.35
Guazuma tomentosa		13	1.80
Platymiscium diadelphum		11	1.52
Cordia hirta		9	1.25
Curatella americana		8	1.11
Trichilia martiana		8	1.11
Acacia glomerosa		8	1.11
Spondias mombin		7	0.97
Bursera tomentosa		7	0.97
Copaifera officianalis		7	0.97
Godmania aesculifolia		6	0.83
Tabebuia ochracea		6	0.83
Genipa americana var car	uto	6	0.83
Swartzia pittieri		5	0.69
Sterculia apetala		5	0.69
Strychnos fendleri		4	0.55
Cycropia peltata		3	0.42
Cupania americana		3	0.42
Annona jahnii		2	0.28
Protium heptaphyllum		2	0.28
Cassia moschata		2	0.28
Tabernaemontana psycho.	trifolia	1	0.14
Sciadodendron excelsom		1	0.14
Acromia aculeata		1	0.14
Hymenaea courbaril		1	0.14
Cochlospermun vitifolium		1	0.14
Trichilia unifoliata		1	0.14
Albizia caribea		1	0.14
Soracea sprucei		1	0.14
Lonchocarpus fendleri		1	0.14
Machaerium sp.		1	0.14
Vitex capitata		1	0.14

Table 5. Species <4m in height of Sabana Seca con Chaparros Alto			
	% Herbaceous	Food	
Species	coverage	species	
Andropogon angustatus	11 to 75		
Trachypogon plumosus	< 50		
Axonus canescens	< 30		
Annona jahnii	< 10	x	
Chromolaena odorata	< 10		
Jacaranda obtusifolia	< 10		
Protium heptaphyllum	< 10		
Copaifera officianalis	< 10	x	
Cochlospermun vitifolium	< 10		
Elephantopus mollis	< 10		
Curatella americana	< 10		
Erythroxylum orinocense	< 10		
Casearia mollis	< 10		
Casearia sylvestris	< 10		
Lasiacis anomala	< 10		
Paspalum sp.	< 10		
Byrsonima crassifolia	< 10		
Peltaea speciosa	< 10		
Clidemia rubra	< 10		
Psidium guianensis	< 10		
Psidium salutare	< 10		
Ouratea grossourdii	< 10		
Bowdichia virgiloides	< 10		
Galactia jussiaeana	< 10		
Machaerium aculeatum	< 10		
Platymiscium diadelphum	< 10		
Securidaca pubescens	< 10		
Roupala montana	< 10		
Guettardia divaricata	< 10	x	
Serjania adjusta	< 10		
Melochia villosa	< 10		
Sterculia apetala	< 10		
Vitex capitata	< 10	x	
Vochysia venezuelana	< 10		
34 species		Index 40	

Table 5 Chassies <4m in beight of Sabana Se

Table 6. Species < 4 in height of Sabana Seca con Chaparros Bajo				
	% Herbace	ous		Food
Species	coverage	e		species
Andropogon angustatus	< 75			
Chromolaena odorata	< 10			
Jacaranda obtusifolia	< 10			
Protium heptaphyllum	< 10			
Copaifera officianalis	< 10			х
Connarus venezuelanus	< 10			
Cyperus meyenianus	< 10			
Paspalum sp.	< 10			
Curatella americana	< 10			
Erythroxylum orinocense	< 10			
Casearia mollis	< 10			
Casearia sylvestris	< 10			
Axonus canescens	< 10			
Cenchrus echinatus	< 10			
Paspalum sp.	< 10			
Sporobolus jacquemontii	< 10			
Cyperus sp.	< 10			
Hyptis suaveolens	< 10			
Byrsonima crassifolia	< 10			
Pavonia cancellata	< 10			
Sida acuta	< 10			
Cecropia peltata	< 10			
Psidium guianensis	< 10			
Psidium salutare	< 10			
Ouratea grossourdii	< 10			
Bowdichia virgiloides	< 10			
Galactia jussiaeana	< 10			
Guettardia divaricata	< 10			x
Randia formosa	< 10			
Serjania adjusta	< 10			
Melochia villosa	< 10			
Vitex capitata	< 10			x
32 species			Index	30

Table 6 Species < 1 in height of Sahana Seca n Chan

Table 7. Tree species inventor	ry of Bosque Semi-	-Deciduo Tipico
	Numher	Relative
Species	of trees	density
	01 4000	
Ptarocarnus acanulcansa	250	18.94
Acacia alemenera	148	11.21
Actuality and a second and	140	7.42
Astronium graveoiens	90	7.42
sizyphus cyclocaraia	97	C.1
Ruprechua tenutifiora	60	5.00
Jaesaipina coriaria	59	4.47
Japparis odoratissima	22	3.94
occoloba caracasana	41	3.11
richina unifoliata	40	3.03
Ispiaosperma cuspa	30	2.73
sempa americana var caruto	26	1.97
spondias mombin	25	1.89
Copernicia tectorum	24	1.82
Ilbizia caribea	23	1.74
fecatostemon completus	22	1.67
łuazuma tomentosa	22	1.67
Joutarea hexandra var hexandra	20	1.52
Ink	20	1.52
onchocarpus fendleri	19	1.44
'ordia collococca	18	1.36
wartzia pittieri	18	1.36
ombacopsis quinata	17	1.29
ravaisia integerrima	15	1.14
richilia trifolia	15	1.14
lupania americana	15	1.14
ecythis ollaria	14	1.06
huettardia divaricata	9	0.68
Yochlospermun vitifolium	8	0.61
'ithecellobium tortum	8	0.61
Capparis sp.	7	0.53
Innona purpurea	6	0.45
Cerrus hexagonus	6	0.45
'ithecellobium dulce	б	0.45
'ithecellobium saman	б	0.45
liscidea cartaginensis	б	0.45
'apindus saponaria	б	0.45
outeria glomerata	б	0.45
lbizia guachapele	5	0.38
andia venezuelensis	5	0.38
lcantocerus tetrogonus	4	0.30
Sapium biglandulosum	4	0.30
labebuia ochracea	3	0.23
Brosimium alicastrum	3	0.23
Luehea candida	3	0.23

 Table 7. Tree species inventory of Bosque Semi-Deciduo Tipico 1

Table 7Continued.		
	Number	Relative
Species	of trees	density
Unk	3	0.23
Ronchefortia spinosa	2	0.15
Ficus maxima	2	0.15
Soracea sprucei	2	0.15
Rubiaceae sp.	2	0.15
Sterculia apetala	2	0.15
Dugetia riberensis	1	0.08
Sciadodendron excelsom	1	0.08
Margaritaria nobilus	1	0.08
Lonchocarpus crucis-rubierae	1	0.08
Machaerium aculeatum	1	0.08
Myrospermom frutescens	1	0.08

Table 6. The species invento	ry or Bosque Sem	I-Deciduo Típico 2	
	DTruch or	D alabian	
de estes	Number	Accelative	
Species	of trees	density	
Zizvphus cvclocardia	27	8.39	
Pterocarpus acapulcense	26	8.07	
Unk	25	7.76	
Capparis odoratissima	21	6.52	
Coutarea hexandra var hexandra	20	6.21	
Pithecellobium tortum	19	5.90	
Acacia glomerosa	18	5.59	
Astronium graveolens	17	5.28	
Caesalpina coriaria	14	4.35	
Trichilia trifolia	13	4.04	
Hecatostemon completus	12	3.73	
Trichilia unifoliata	12	3.73	
Coccoloba caracasana	11	3 42	
Ruprechtia tenuiflora	10	3.11	
Cordia collococca	7	2.17	
Dugetia riberensis	6	1.86	
Cerrus hexagonus	6	1.86	
Acantocerus tetrogonus	5	1.55	
Copernicia tectorum	4	1.33	
Bombacopsis quinata	4	1.24	
Swartzia pittieri	4	1.24	
Pithecellobium dulce	4	1.24	
Lonchocarpus fendleri	4	1.24	
Pithecellobium pistaciaefolium	3	0.93	
Sapindus saponaria	3	0.93	
Guazuma tomentosa	3	0.93	
Unk	3	0.93	
Albizia caribea	2	0.62	
Brosimium alicastrum	2	0.62	
Guapira olfersiana	2	0.62	
Genipa americana var caruto	2	0.62	
Aspidosperma cuspa	1	0.31	
Bignoniaceae sp.	1	0.31	
Sapium biglandulosum	1	0.31	
Lecvthis ollaria	1	0.31	
Pithecellobium saman	1	0.31	
Pseudonamonis umbillifera	1	0.31	
Derris moniliformis	1	0.31	
Machaerium caicarense	1	0.31	
Myrospermom frutescens	1	0.31	
Platymiscium diadelphum	1	0.31	
Allophyllus occidentalis	1	0.31	
Pouteria glomerata	1	0.31	
Unk	1	0.31	

Table 8. Tree species inventory of Bosque Semi-Deciduo Tipico 2

Table 9. Tree species inventory of Bosque Semi-Deciduo Galeria				
Number	Relative			
of trees	density			
69	28.63			
25	10.37			
24	9.96			
17	7.05			
15	6.22			
13	5.39			
12	4.98			
10	4.15			
8	3.32			
7	2.90			
5	2.07			
5	2.07			
5	2.07			
3	1.24			
3	1.24			
3	1.24			
3	1.24			
2	0.83			
2	0.83			
1	0.41			
1	0.41			
1	0.41			
1	0.41			
1	0.41			
1	0.41			
1	0.41			
1	0.41			
1	0.41			
1	0.41			
	Number of trees of trees			

Table 10. Tree species inventory of Bosque Semi-Deciduo Seca			
	Number	Relative	
Species	of trees	density	
Luehea candida	25	15.82	
Astronium graveolens	20	12.66	
Acacia glomerosa	18	11.39	
Guettardia divaricata	16	10.13	
Allophyllus occidentalis	10	6.33	
Sterculia apetala	8	5.06	
Strychnos fendleri	7	4.43	
Hymenaea courbaril	4	2.53	
Pterocarpus acapulcense	4	2.53	
Genipa americana var caruto	4	2.53	
Spondias mombin	3	1.90	
Annona purpurea	3	1.90	
Godmania aesculifolia	3	1.90	
Cassia moschata	3	1.90	
Albizia caribea	3	1.90	
Myrcia guianensis	3	1.90	
Zanthoxyllum caribaeum	3	1.90	
Sapindus saponaria	3	1.90	
Tabernaemontana psychotrifolia	2	1.27	
Tabebuia ochracea	2	1.27	
Ronchefortia spinosa	2	1.27	
Swartzia pittieri	2	1.27	
Curatella americana	2	1.27	
Cycropia peltata	2	1.27	
Coutarea hexandra	2	1.27	
Cordia hirta	1	0.63	
Copaifera officianalis	1	0.63	
Machaerium sp.	1	0.63	
Vochysia venezuelana	1	0.63	

Table 10 Tr fD .: n • a

Table 11. Tree species inventory of Bosque Semi-Deciduo Quebrada			
	Number	Relative	
Species	oftrees	density	
Tetragastris panamensis	6	11.54	
Mangifera indica	4	7.69	
Didymopanax morototoni	4	7.69	
Protium heptaphyllum	4	7.69	
Lygodium venuston	4	7.69	
Annona jahnii	3	5.77	
Tabebuia ochracea	3	5.77	
Inga spuria	3	5.77	
Coutarea hexandra	3	5.77	
Unk	3	5.77	
Guettardia divaricata	2	3.85	
Sterculia apetala	2	3.85	
Vochysia venezuelana	2	3.85	
Spondias mombin	1	1.92	
Ceiba pentandra	1	1.92	
Copaifera officianalis	1	1.92	
Hirtella racemose	1	1.92	
Connarus venezuelanus	1	1.92	
Curatella americana	1	1.92	
Strychnos fendleri	1	1.92	
Genipa americana var caruto	1	1.92	
Vitex capitata	1	1.92	

Table .fD aidua • . **.**... . : -

Table 12. Physiognomic characteristics of forest types along foot transects used for animal observations. Types presented progress from dry fire adapted ridge top forests on the far left to seasonally saturated valleys on the far right. Substrates and elevations are discussed in more detail in the main text.

Variable	SS/C H	BSC	BSM	BSF	BSD S	BSD T	BSD T	BSV
Canopy Height m	3.6	6.6	6.7	10.9	17.5	19.1	18.8	16
Canopy Cover (CC) %	26	43.4	65	60.6	62.5	60.6	74.4	87.5
Mid Story Cover %	3	16.5	7.5	43.4	47.5	52.8	30.5	22.5
1 m Understory %	1	7.2	5	6.9	7.5	38.1	24.3	7.5
DBH Canopy Trees cm	14.2	14.7	17.6	24	28.2	48.2	47.1	27.3
Spacing Canopy Trees m	5.8	6.3	6.6	6.5	8.5	8.8	9.6	4.8
Densiometer (CC) %	12.2	66.4	94.5	98	95	93	98.8	100
Sample Size	5	10	4	8	2	16	27	4

Table 13. Vine species invent	ory of Bosque Sec	a de Cerros
	#of	Relative
Species	vines	density
bbecles	VIIIes	density
Sariania adiusta	13	48.15
Arrahidaea mollisima	6	22.22
Combretum fruticosum	4	14.81
Marsdenia macrophylla	1	3.70
Banisteriopsis muricata	1	3.70
Machaerium humboldtianum	1	3.70
Securidaca pubescens	1	3.70
Table 14. Vine species invent	ory of Bosque Sec	a de Mezcla
	# of	Relative
Species	vines	density
Combretum fruticosum	4	66.67
Arrabidaea mollisima	1	16.67
Serjania adjusta	1	16.67
		1 1 1
Table 15. Vine species invento	ory of Bosque Sec	a de Falda
	# \cf	Pelotine
Species	vines	density
Serjania adjusta	32	43.24
Xylophragma seemannianum	16	21.62
Marsdenia macrophylla	11	14.86
Arrabidaea mollisima	4	5.41
Paullinia leicocarpa	4	5.41
Combretum fruticosum	3	4.05
Tetracera volubilis	2	2.70
Cydista aequinoctialis	1	1.35
Pithecoctenium crucigenum	1	1.35

	# ^F	Peletimo
Species	# OI	donaitu
species	Villes	density
Xylophragma seemannianum	19	65.52
Paullinia leicocarpa	4	13.79
Cydista aequinoctialis	2	6.90
Pithecoctenium crucigenum	1	3.45
Bignoniaceae sp.	1	3.45
Tetracera volubilis	1	3.45
Serjania adjusta	1	3.45
Table 17. Vine species invent	ory of Bosque Sen	ni-Deciduo Tipico 1
	# of	Relative
Species	vines	density
•		
Xylophragma seemannianum	19	26.76
Marsdenia macrophylla	16	22.54
Tetracera volubilis	6	8.45
Callichlamys latifolia	5	7.04
Cydista aequinoctialis	4	5.63
Cydista diversifolia	4	5.63
Entada polystacha	4	5.63
Combretum fruticosum	3	4.23
Mucuna pruriens	3	4.23
Machaerium humboldtianum	2	2.82
Paullinia pinnata	2	2.82
Philodendron acutatum	2	2.82
Paullinia leicocarpa	1	1.41
Table 18. Vine species invent	ory of Bosque Sen	ni-Deciduo Tipico 2
	#of	Relative
Species	vines	density
Marsdenia macrophylla	3	25.00
Tetracera volubilis	3	25.00
Cydista diversifolia	2	16.67
Xylophragma seemannianum	2	16.67
Combretum alternifolium	1	8.33
Machaerium humboldtianum	1	8 3 3

Table 16. Vine species inventory of Bosque Semi-Deciduo Seca

Table 19. Vine species invo	entory of Bosque Sen	ni-Deciduo Galeria
	# of	Relative
Species	vines	density
Tetracera volubilis	13	68.42
Combretum alternifolium	6	31.58
Table 20. Vine species invo	entory of Bosque Sie	mpre-Verde
	Number	Relative
Species	of vines	density
Marsdenia macrophylla	4	100

Table 21. Species <4 r	n in height of Bosque Seca d	e Cerros
	% Herbaceous	Food
Species	coverage	Species
Melinis minutiflora	31 to 40	
Trachypogon plumosus	21 to 30	
Andropogon angustatus	11 to 40	
Hyparrhenia rufa	< 40	
Annona jahnii	< 20	X
Jacaranda obtusifolia	< 20	
Protium heptaphyllum	< 20	
Curatella americana	< 20	
Erythroxylum orinocense	< 20	
Casearia sylvestris	< 20	
Lasiacis anomala	< 20	
Guettardia divaricata	< 20	X
Randia formosa	< 20	
Vitex capitata	< 20	X
Chromolaena odorata	< 10	
Godmania aesculifolia	< 10	
Tabebuia ochracea	< 10	
Bromelia plumieri	< 10	
Cochlospermun vitifolium	< 10	
Pectis elongata	< 10	
Connarus venezuelanus	< 10	
Olvra latifolia	< 10	
Sporobolus iacauemontii	< 10	
Hyntis suaveolens	< 10	
Byrsonima crassifolia	< 10	
Myrcia quianensis	< 10	
Psidium anianansis	< 10	
Psidium salutara	< 10	
Ourataa arossourdii	< 10	
Boudichia virailoidos	< 10	
Calactia inceiacana	< 10	
Gaiacila jassiaeana	< 10	
Roupaia montana Contenne lencendre	< 10	
Coularea nexanara		
Genipa americana var cai	<i>uuo</i> < 10	X
Auopnyuus occidentalis	< 10	
meiocnia viitosa	< 10	
sterculia apetala	< 10	
Lantana camara	< 10	
38 species		Index 80

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Table 22. Species $\leq 4 \text{ m in h}$	eight of Bosque Se	ca de Mezcla	
	06 Harbaaaaya		Food
Secolog	% Herbaceous		Food
species	coverage		species
Lasiacis anomala	11 to 20		
Randia formosa	11 to 20		
Astronium graveolens	< 10		
Jacaranda obtusifolia	< 10		
Protium hentanhvllum	< 10		
Erythroxylum orinocense	< 10		
Andropog on angustatus	< 10		
Genina americana var caruto	< 10		v
Randia hehecarna	< 10		v
Viter capitata	< 10		~ ~
10 species	× 10	Teday	20
To species		Index	50
Table 23. Species $< 4 \text{ m in he}$	eight of Bosque Se	ca de Falda	
	% Herbaceous		Food
Species	coverage		species
Annona purpurea	< 10		x
Lasiacis anomala	< 10		
Olyra latifolia	< 10		
Oplismenus burmanni	< 10		
Dorstenia contraierva	< 10		
Randia formosa	< 10		
6 species		Index	10
Table 24. Species $< 4 \text{ m in he}$	eight of Bosque Se	mi-Deciduo Se	eca
	% Herbaceous		Food
Species	coverage		species
Randia formosa	< 75		
Oplismenus burmanni	< 20		
Calathea propinqua	< 10		x
3 species		Index	10

Table 25. Species $\leq 4 \text{ m m}$	neight of Bosque Se	im-Deciduo Tipico I	
	% Herbaceous	Fo	bd
Species	coverage	spec	ies
Bromelia chrysanta	< 75	X	:
Selaginella horizontalis	< 75		
Panicum laxum	< 40		
Lasiacis anomala	< 30		
Oplismenus burmanni	< 30		
Hyparrhenia rufa	21 to 30		
Thalia geniculata	21 to 30	X	
Acantocerus tetrogonus	< 20		
Scleria pterota	< 20		
Olyra latifolia	< 20		
Bactris guineensis	< 10	X	
Bromelia pinguin	< 10	X	
Pharus latifolia	< 10		
Calathea latifolia	< 10	X	
Maranta arundinacea	< 10	X	
Piper tenue	< 10		
Randia formosa	< 10		
Randia hebecarpa	< 10	x	
Randia venezuelensis	< 10		-
19 species		Index 15	5
			-
Table 26. Species < 4 m in	height of Bosque Se	mi-Deciduo Tipico 2	
	% Herbaceous	Fo	bd
Species	coverage	spec	ies
Bromelia chrysanta	11 to 75	X	
Selaginella horizontalis	11 to 75		
Oplismenus burmanni	< 30		
Lasiacis anomala	11 to 30		
Bromelia pinguin	11 to 20	x	
Acantocerus tetrogonus	11 to 20		
Scleria pterota	11 to 20		
Randia formosa	< 10		
8 species		Index 9:	5
•			

Table 25. Species < 4 m in height of Bosque Semi-Deciduo Tipico 1

Table 27. Species $\leq 4 \text{ m in}$	height of Bosque Se	mi-Deciduo Q	uebrada
• • • • • • • • • • • • • • • • • • •			
	% Herbaceous		Food
Species	coverage		species
Olyra latifolia	11 to 20		
Lasiacis anomala	< 10		
Selaginella horizontalis	< 10		
3 species		Index	0
Table 28. Species < 4 m in	ı height of Bosque Si	empre-Verde	
	% Herbaceous		Food
Species	coverage		species
Tacaranda obtucifolia	< 10		
Jacaranaa ootusijoila	< 10		
Scieria pterota	< 10		
saccioiepsis myoros	< 10		
5 SDECIES		Index	1 0

Table 27 Sr a in haight of Da mi D aidu 4 с,

Table 29. Food tree	es of Bosq	ue de Cerr	os (BSC)			
Food Species		Relative	: Frequency			
Myrcia guianensis			7.93			
Guettardia divaricata			6.91			
Annona jahnii			4.22			
Genipa americana vai	r caruto		2.36			
Annona purpurea			2.19			
Vitex capitata			1.52			
Copaifera officianalis			1.35			
Spondias mombin			0.51			
Randia hebecarpa			0.51			
Number of species	that are food	l producers	9.00			
Percent of all trees t	hat are food	l-producers	27.49			
Percent all species	that are food	1 producers	23.68			
Table 30. Food tree	es of Bosa	ue Seca de	e Mezcla (BSM)		
Food Species		Relative	Frequency			
Vitex capitata			5.08			
Copaifera officianalis			3 66			
Randia hebecarna			2.24			
Genina americana vai	r caruto		2.03			
Annona iahnii	0077020		0.61			
Capparis sp			0.01			
Cassia moschata			0.20			
Number of species i	that are foor	Intoducers	7.00			
Dercent of all trees t	that are food	-producers	14.02			
Demoent all species	that are food	I producers	22 22			
Fercent an species	uiai are 1000	r producers	20.00			
	C D	a 1	T 11 (D	att)		
Table 31. Food tree	es of Bosq	ue Seca de	e Falda (B	SF)		
T 10			P			
Food Species		Relative	: Frequency			
Guettardia divaricata			22.16			
Myrcia guianensis			6.37			
Annona purpurea			5.40			
Guazuma tomentosa			1.80			
Spondias mombin			0.97			
Copaifera officianalis			0.97			
Genipa americana vai	r caruto		0.83			
Cassia moschata			0.28			
Annona jahnii			0.28			
Acromia aculeata			0.14			
Vitex capitata			0.14			
Number of species	that are food	l producers	11.00			
Percent of all trees t	hat are food	l-producers	39.34			
Percent all species	that are food	1 producers	28.21			

Table 32. Food tree	es of Bosq	ue Semi-d	eciduo Se	ca (BSDS)
			-		
Food Species		Relative.	Frequency		
Guettardia divaricata			10.13		
Genipa americana vai	r caruto		2.53		
Spondias mombin			1.90		
Annona purpurea			1.90		
Sapindus saponaria			1.90		
Myrcia guianensis			1.90		
Copaifera officianalis	•		0.63		
Number of species	that are food	producers	7.00		
Percent of all trees t	that are food	-producers	20.89		
Percent all species	that are food	producers	24.14		
Table 33. Food tree	es of Bosqu	ue Semi-d	eciduo Tip	bico 1 (BS	SDT1)
Food Species		Relative	Frequency		
Zizyphus cyclocardia			7.35		
Caesalpina coriaria			4.47		
Capparis odoratissim	a		3.94		
Genipa americana vai	r caruto		1.97		
Spondias mombin			1.89		
Copernicia tectorum			1.82		
Guazuma tomentosa			1.67		
Guettardia divaricata			0.68		
Pithecellobium tortum	1		0.61		
Pithecellobium dulce			0.45		
Pithecellobium saman			0.45		
Annona purpurea			0.45		
Sapindus saponaria			0.45		
Pouteria glomerata			0.45		
Brosimium alicastrum			0.23		
Ficus maxima			0.15		
Number of species	that are food	producers	16.00		
Percent of all trees t	that are food	- -producers	27.05		
Percent all species	that are food	producers	28.57		

Table 34.	Food free	es of Bosq	ue Semi-d	eciduo Tij	5100 2 (B	SDST2)
Food Speci	.es		Relative	Frequency		
Zizyphus cj	yclocardia			8.39		
Capparis c	odoratissim	a		6.52		
Pithecellob	oium tortum			5.90		
Caesalpino	a coriaria			4.35		
Pithecellob	oium dulce			1.24		
Copernicia	ı tectorum			1.24		
Pithecellob	oium pistaci	iaefolium		0.93		
Guazuma t	omentosa			0.93		
Sapindus s	aponaria			0.93		
Genipa am	ericana vai	r caruto		0.62		
Brosimium	alicastrum			0.62		
Pithecellob	oium saman			0.31		
Pouteria glomerata		0.31				
Number of species that are food producers			13.00			
Percent of all trees that are food-producers			32.30			
Percent	all species	that are food	d producers	29.55		
	•		•			
Table 35.	Food tree	es of Bosa	ue Semi-d	eciduo Ga	leria (BS	DG)
1 4010 001						
Food Speci	.es		Relative	Frequency		
Pouteria g	 lomerata			28.63		
Annona iai	hnii			2.07		
Genipa am	ericana vai	r caruto		2.07		
Zizvnhus c	vclocardia			1.24		
Conaifera	officianalis			0.83		
Pithecelloł	ojj iela iano vium ligustr	ium		0.05		
r unecenorum ngusu um Pithacallohium nistaciaafolium		0.41				
Pithecellot	oium tortum			0.41		
Guazuma t	omentosa			0.41		
Randia hel	becarpa			0.41		
Myrcia gui	anensis			0.41		
Number	of species	that are foor	d producers	11.00		
Percent	of all trees t	hat are food	1-producers	37 34		
1 01 00110			- Fro addoord	27.24		

37.93

Percent all species that are food producers

 Table 34. Food trees of Bosque Semi-deciduo Tipico 2 (BSDST2)

Table 36. Food trees of Bosq	ie Semi-deciduo Quebrada (BSDQ)	
Food Species	Relative Frequency	
Mangifera indica	7.69	
Annona jahnii	5.77	
Guettardia divaricata	3.85	
Spondias mombin	1.92	
Copaifera officianalis	1.92	
Genipa americana var carute	1.92	
Vitex capitata	1.92	
Number of species that are	food producers 7.00	
Percent of all trees that are	food-producers 25.00	
Percent all species that are	food producers 31.82	
Table 37. Food trees of Boso	ue Siempre-Verde (BSV)	
Food Species	Relative Frequency	
Ficus maxima	5.99	
Annona jahnii	4.87	
Copaifera officianalis	4.87	
Annona purpurea	1.87	
Genipa americana var carute	1.12	
Randia hebecarpa	0.75	
Number of species that are	food producers 6.00	
Percent of all trees that are	food-producers 19.48	
Percent all species that are	food producers 35.29	

Table 38. Foo	d vines of Bo:	sque Seca de 🤇	Cerros (BSC)			
Food Species			Relative Frequency			
Combretum fr	14.81					
Number of vin	1.00					
Percent of all	14.81					
Percent of all v	16.67					
Table 39. Foo	d vines of Bo	sque Seca de 1	víezcia (BSM)			
Food Species			Relative Frequ	lency		
Combretum fr	uticosum			66.67		
Number of vin	1.00					
Percent of all v	66.67					
Percent of all vine species that are food producers				33.33		
Table 40. Food	l vines of Bos	que Seca de F	alda (BSF)			
Food Species			Relative Frequency			
Combretum fri	uticosum			4.05		
Number of vin	1.00					
Percent of all v	4.05					
Percent of all	Percent of all vine species that are food producers					
Table 41. Foo	d vines of Bo:	sque Semi-deo	ciduo Tipico 1	(BSDT1)		
Food Species			Relative Frequ	lency		
Entada polyst	acha			5.63		
Combretum fr	uticosum			4.23		
Philodendron	acutatum		2.82			
Number of vin	3.00					
Percent of all	12.68					
Percent of all	23.07					

Table 42. Fruiting phenology (and foliage phenology for selected species). Large X representes mature fruits, particularly those																	
available to terrestrial mammals. Large X also represents period of active growth of foliage in representatives from																	
Marantaceae Araceae Combretaceae and Entada (Leguminosae) Small x represents potential year-round use																	
of tubers of Marantaceae, stems of Combretaceae and Araceae, roots of <i>Entada</i> and fleshy basal leaves of Bromeliaceae										ae.							
COMMON NAME	SCIENTIFIC NAME	AUTHOR	FAMILY	FORM	D	J	F	М	Α	м	J	J	Α	s	0	N	
Mango	Mangifera indica	L.	Anacardiaceae	Tree					х	X	x					\square	
Јођо	Spondias mombin	L.	Anacardiaceae	Tree							Χ	Χ	Χ	Х			
Manirito	Annona jahnii	Safford	Annonaceae	Tree								Χ	Χ	Х			
Manirote	Annona purpurea	Moc. & Sesse	Annonaceae	Tree									Χ	Х	Χ	\square	
Picaton	Philodendron species		Araceae	Vine	x	x	x	х	x	x	x	X	х	х	х	x	
Corozo	Acromia aculeata	(Jacq.) Lood. Mart.	Arecaceae	Tree			Χ	Χ	Χ	Χ	Χ	Χ	Χ	Χ	Χ	X	
Piritu	Bactris guineensis	(L.) E. Moore	Arecaceae	Tree					Х	Х	Х	Х	Х	Х	Χ		
Palma Llanera	Copernicia tectorum	(H.B.K.) Mart.	Arecaceae	Tree							Х	Χ	Χ	Χ		\square	
Maya	Bromelia chrysanta	Jacq.	Bromeliaceae	Understory	X	Χ	x	x	x	x	x	x	x	х	х	X	
Chiguichigue	Bromelia pinguin	L.	Bromeliaceae	Understory	x	x	х	x	х	х	x	x	x	х	Х	x	
Guamacho	Pereskia guamacho	Weber.	Cactaceae	Tree					X	X	x						
Merecure	Lycania pyrifolia	Griseb.	Chrysobalanaceae	Tree							Χ	Χ				\square	
Chupa Chupa	Combretum fruticosum	(Loefl.) Stuntz.	Combretaceae	Vine	x	x	x	x	x	x	x	x	x	x	x	x	
Tapocho de Monte	Calathea latifolia	(Link.) Kl.	Marantaceae	Understory	x	x	x	x	x	x	x	Χ	Χ	Χ	Χ	X	
Tapocho de Monte	Calathea propinqua	(P.&E.) Koem	Marantaceae	Understory	x	x	x	x	x	x	x	Х	Х	Х	Х	Х	
Lairen	Maranta arundinacea	L.	Marantaceae	Understory	x	x	x	x	x	x	x	Х	Χ	Х	Χ	X	
Platanico	Thalia geniculata	L.	Marantaceae	Understory							Χ	Χ	Χ	Х	Χ	X	
Guayabito	Myrcia guianensis	(Aubl.) D.C.	Myrtaceae	Tree										Х			
Caruto	Genipa americana var caruto	(H.B.K.) Schum	Rubiaceae	Tree					Х	Χ	Χ						
Espinito, Cabrito	Guettardia divaricata	(H.G.B.) Standl.	Rubiaceae	Tree								Χ	Χ	Х			
Cruceto	Randia hebecarpa	Griseb.	Rubiaceae	Shrub	Χ	Χ										X	
Guacimo	Guazuma tomentosa	Kunth.	Sterculiaceae	Tree		Χ	Χ	Х	Χ	Χ							
Guarataro	Vitex capitata	Vahl.	Verbenaceae	Tree							Χ						
Dividive	Caesalpina coriaria	(Jacq. Willd.)	Leguminosae	Tree		X	Х	Х									
Canafistolo burrero	Cassia grandis	L.	Leguminosae	Tree	х	Х										х	
Canafistolo	Cassia moschata	H.B.K.	Leguminosae	Tree	x	Х	Х	Х	Х	х	х	Х	х	х			
Aceite	Copaifera officianalis	L.	Leguminosae	Tree		X	Х	Х	Х	X							
Caujate	Entada polystacha	D.C.	Leguminosae	Vine	x	x	х	х	x	x	х	Х	Х	х	Х	х	
Carocaro	Enterolobium cyclocarpum	(Jacq.) Griseb	Leguminosae	Tree	х	X	х	х	х								
Saman	Pithecellobium saman	(Jacq.) Benth.	Leguminosae	Tree	х	Х	Х	х									

Table 43. Areal estimates of habitat types in Hato Piñero. SS/CH = dry savanna with chaparros. BS = dry forest. BS/AP = dry forest/crops. M = mangos. BSD = semi-deciduous forest. BSV = evergreen forest. PS = dry pasture. SI = flooding savanna. "Core" refers to areas in which hunting does not occur. "Poached" refers to areas where it does. Open water estimate presented, but is an underestimate.

Category	Core ha	Poached ha	Total ha		
SS/CH includes	3,355.5	3,355.5	6,711		
poached					
SS/CH all core	2,937	0	2,937		
SS/CH Subtotal	6,292.5	3,355.5	9,648 st		
BS includes poached	1,426.7	652.3	2,079		
BS all core	2,907	0	2,907		
BS Subtotal	4,333.7	652.3	4,986 st		
BS/AP	238	238	476 st		
M (Valle Hondo)	0	7.0	7 st		
BSD includes	17,409.32	3,617.68	21,027		
poached					
BSD all core	407	0	407		
BSD Subtotal	17,816.32	3,617.68	21,434 st		
BSV includes	0	11 Valle	11		
poaching		Hondo			
BSV all core	37	0	37		
BSV Subtotal	37	11	48 st		
PS includes poaching	42.9	100.1	143		
PS all core	1,663.0	0	1,663		
PS Subtotal	1,705.9	100.1	1,806 st		
SI includes poaching	21,542.4	1,314.6	22,857		
SI all core	1,842	0	1,842		
SI Subtotal	23,384.4	1,314.6	24,699 st		
Other side of Pao	Outside of	Study Area	16,743 st		
	Primary				
Conspicuous open			123 st		
water					
Hato Piñero ST			79,970		
Forest			26,951		
Open			26,505		
SS/CH			9,648		
Outside of study			16,743		
area					
Inside study area			63,227		

CHAPTER 3 DISTRIBUTION, ABUNDANCE, AND BIOMASS OF POTENTIAL JAGUAR AND PUMA PREY

Introduction

This chapter provides the foundation for discussions in subsequent chapters, as well as context for the spatial characteristics of cat attacks on livestock. The prey base study revolved around the following questions, which this chapter begins to address.

- Is the natural prey base in the study area sufficient to support jaguar and puma without a subsidy from domestic livestock? This can be addressed through the standing crop biomass and annual gross productivity of important prey.
- 2) Is natural prey patchily distributed? What areas are most productive?
- 3) How do natural prey densities, distributions and/or vulnerability vary by season (in response to water availability/inundation and/or plant phenology)?
- 4) Will jaguar and puma hunt opportunistically, taking prey in proportion to rate of encounter, or are they selective (e.g selecting larger prey over smaller prey)?
- 5) How do the spatial and temporal patterns of primary productivity influence prey distributions?
- 6) How does prey distribution influence jaguar and puma use of space?
- 7) How are 5 and 6 related to the interactions between cats and cattle?
8) If the frequency of cattle depredation has an inverse relationship with availability and vulnerability of natural prey, is there a converse direct relationship with availability and vulnerability of livestock?

This chapter will address questions 2 and 3 in full and questions 5, 7, and 8 in part. The task of setting forth patterns of abundance, and biomass of the prey base was sufficiently broad and lengthy that it required this chapter of its own. This sets the stage for subsequent chapters that, with botanical and faunal background condensed, will be able to examine biomass estimates and an array of questions in considerably greater detail and freedom.

Methods

Linear Foot Transects

Reconnaissance using vehicles and ultra-light aircraft, and review of a preliminary vegetation map, facilitated the design of a system of 26 foot transects. The number of lines and kilometers sampled were distributed as follows: dry hill forests [4, 9.8 km]; semi-deciduous forest not adjacent to permanent water [3, 5.5]; semi-deciduous forest near permanent caño or prestamo [4, 7.51]; interspersions of semi-deciduous forest and savanna crossed perpendicularly [2, 4.5]; semi-deciduous forest edge, parallel to pasture [1, 2]; small flooding savannas and managed pastures near forest [5, 5.65]; large flooding savanna, close to forest [2, 4]; large open flooding savanna away from forest [2, 4.7]; higher elevation, non-flooding pastures [3, 3.55]. This design took in a cross-section of habitat types, and facilitated tests of proximity to water, habitat interspersion indices, and distance to cover. Transects actually employed each month depended upon water levels. Restricted accessibility and laborious walking through water with tall

emergent vegetation during the rainy season, and destruction of markers by livestock caused the savanna sample to be less complete than the forest sample.

The narrow footpaths cleared in forest with machetes were marked at 50 m intervals. Cattle ate both plastic and metal tags in some pastures and savannas, forcing us to resort to 1.8 m metal stakes topped with orange spray paint at 100 m intervals. Sign, feces, and sightings of prey and predators were recorded along a systematic calendar of morning and dusk walks. A subset of forested transects was originally walked at night (beginning at 2200 hours) using adjustable beam Koehler Wheat lamps. Though interesting, these walks were discontinued, as the exertion did not justify their low productivity. Distance estimates, group number and dimensions, behavior, time, and location were recorded for all visual observations. These data on terrestrial and arboreal mammals, cracids, and terrestrial tortoises were used for habitat specific density comparisons and coarser grained absolute densities via the models in DISTANCE (Buckland et al. 1993). Analyses used perpendicular distances to centers of clusters. Subjective degree of inundation by percentage and mean water depth was recorded every time a transect was walked in the rainy season.

Vehicle Transects

One driver and two observers proceeded in a truck driven at 20 km/hr beginning at 0600, 1800, and 2200 hours. During the night the two observers used spotlights (200,000 and 400,000 cp) and headlamps. Two routes (high and low) were sampled twice each (dry and wet season), while another route (large open savannas in the south) was sampled once. All routes were approximately 16 km in length. Species, time, group size, behavior, location and habitat type were recorded for each observation. Availability of habitats was recorded for the high and low routes. The low route was extremely

heterogenous: small pastures and savannas surrounded by forest, strips and large blocks of forest, permanent prestamos and caño, and low hills. Much of the low route flooded during the wet season, some of the savannas retained water long after the rains ceased, and surface water was available throughout the dry season, albeit, more widely dispersed as the season progressed. The high route started out in similarly heterogenous mixed forest and savanna types, but within 4 km entered the massif of El Baúl. In the higher hills, short dry forests and savannas on rocky soils with poor water retention and fertility dominated. Pockets and strips of taller forests occurred along hills bases and valleys, often in a dendritic pattern. The overall availability of surface water was lower on the high route. The third route began in interdigitated savanna and forest, then skirted the tongues of semi-deciduous forest that extended into the large savannas, and ended in an open treeless expanse. Though these savannas flood completely, during the dry season the only surface water available is at windmill pumps and prestamos.

Capybara and Caiman Counts

Several full-days of observation of capybara (*Hydrochaeris hydrochaeris*), caiman (*Caiman crocodilus*), and turtles (*Podocnemis voglii*) at Lagunas Alta, Cerritos, and Escorzonera during the 1996 dry season made it clear that capybara activity patterns varied among sites. At times, capybara make heavy use of forest and shrub cover. Each group has its own activity pattern. Consequently the timing of counts needs to be groupspecific and repeated counts often necessary to obtain confidence that entire groups have been observed. The late dry season is optimal, as visibility and capybara concentrations are at maximum. As water bodies gradually dry out, small groups of capybara merge into larger groups in some areas, sometimes traveling several kilometers to do so.

During the first capybara census (April 2-23, 1997) every area on the ranch that possibly contained capybara was visited (on foot or by boat), some up to 6-10 times. With the more productive hours and occupied sites identified, a second census (April 13-20, 1998) was more efficient. With the help of Diego Giraldo (Universidad Simon Bolivar) capybara were classified as: male or female adults (>40 kg); juveniles (20-30 kg); infants (5-15 kg, born preceding October-November); newborns (2 kg); or adults gender undetermined. Caution was necessary to avoid excessive estimates by double counting more mobile groups in semi-forested areas. Where poaching was taking place late night visits were required. Caiman were sometimes counted during the same visits. Age specific counts were used to generate biomass estimates.

In 1985, Allan Woodward and Dennis David, both competent crocodilian specialists, assessed Piñero's entire caiman population. In 1986, Lee Fitzgerald, also a competent crocodilian specialist, conducted another ranch-wide survey. With their information available, I limited my night-counts to a sample of the same areas that Woodward, David, and Fitzgerald had sampled, using my counts as a calibration factor, if necessary, for the counts made 10 years previous. In 1996 and 1997, we calibrated our eyes to the size classes used by the Venezuelan government agency PROFAUNA (Ayarzagüena 1983; Thorbjarnarson, 1991a; Thorbjarnarson & Velasco 1998; Velasco & Ayarzagüena 1995) by estimating animal sizes at night, then capturing the animals with nooses and measuring and releasing. Subsequently we made night counts at Caño de la Canoa, Tapa de Los Patos, Rio Pao, Caño Caujaral, Lagunita Escorzonera, Caño de la Iguana, Lagunas Alta & Cerritos, and Laguna Grande. Additional counts were made at Caño Manglarito during our capybara censuses and by Juhani Ojasti's wildlife management class. With the exception of those counts made during the April capybara census, most caiman counts were made in the month of March. On three occasions I conducted sighting fraction experiments, capturing caiman, then releasing them with small cyalume lights attached to their head, counting visible lights every 15 minutes for several hours. The ratio of average number of lights visible to the known number of lights provided an estimate of sighting fraction. This manipulation provided an opportunity to record weights in conjunction with the snout-vent lengths used to determine size classes. Later, when it became apparent that a caiman's head is the only body part that retains its original size and shape after predation by jaguar, it became necessary to capture a few more animals to calibrate skull length with size class with weight. Size class distributions were based on a sample of 5,998 animals. Size class-weight relationships were based on project captures and data in (Ayarzagüena 1983) and (Thorbjarnarson 1991a). Biomass was estimated as the product of: 1) numbers in size classes; and 2) average weight per size class.

Capture-Mark-Release-Recapture: Tortoises, Turtles, Anacondas

Morrocoy tortoises (*Geochelone carbonaria*) were frequently encountered along forested transects during moist months. Between April 20 and June 14 of 1997, we also captured, marked, and released tortoises in a 42.5 ha square plot in forest adjacent to a transect. Cleared and flagged trails divided the completely forested plot into 35 approximately square blocks. Block interiors were searched between 0730 and 1000 hours. Each tortoise captured was given an individual numerical marking via notched marginal scutes, allowing a record of its capture history. Additional morrocoy measurements and observations were recorded by Tibisay Escalona in 1996, and our crew in 1996 and 1997. Average weights derived from 87 captures were combined with

population estimates generated using DISTANCE (Buckland et al. 1993) density estimates and Schnabel's multiple capture-recapture model (Seber 1982) for biomass estimates.

We conducted mark-recapture exercises with galapago turtles (*Podocnemis voglii*) in prestamos in two pastures, Lagunita Escorzonera, and a section of Caño Caujaral. We used haul seines in the prestamos, chicken wire funnel traps in the caño, and funnel traps and short nylon hoop traps in Escorzonera. The marginal scutes of Escorzonera galapagos were notched to identify their order of capture. White epoxy enamel marks painted on the carapace also provided identification. Three days of basking counts were made at both Laguna Alta and Escorzonera. Three days of head counts in the water were made at Escorzonera. After Escorzonera, with abundant measurements in hand, prestamo and caño galapagos were simply marked with a small hole drilled through a rear marginal, and subsequent holes added for each recapture. The freshwater turtle capturerecapture efforts all took place between mid-April and early May. The lowest water levels of the year and separation of first and second samples by no more than 6 days guaranteed that the populations were closed. Average weights derived from 181 measured turtles were combined with Chapman's adjusted Lincoln-Petersen Estimator (Seber 1982) for biomass estimates.

Incidental to work on mata mata (*Chelus fimbriatus*) reproduction, we caught, marked, and released 36 of these large turtles (up to 13 kg) during October and November 1996 (high water) in Caño Caujaral. Most successful for mata mata was a long stick with a shark hook attached, basically a thin gaff used when mata mata were breathing near the surface. This did not cause a single injury. Large mesh sinkerless flag

gill nets also worked, but caught an equal proportion of mata mata and large freshwater stingrays (Potamotrygonidae).

Anacondas (*Eunectes murinus*) up to 50 kg were also captured, measured, and released in 1996 (Rio Pao and Caño Caujaral). In 1997, small samples were marked in Rio Pao and Caño de la Iguana.

Additional Brief Assessments

In February 1996, ten prestamos were haul seined and mass and species composition of fish and turtles recorded. Hoop nets employed in the Pao River and trammel nets employed with Caño Caujaral provided some familiarity with the fish fauna. Iguanas (*Iguana iguana*) were counted, by boat, along Caño Caujaral, Caño de la Iguana, and Rio Pao in 1997. During 1997 and 1998, 90+ trap nights with large nationals (98 cm long x 52 cm tall x 40 cm wide 50% baited with fruit, 50% with dog food and sardines), 120 trap nights with mid-sized tomahawks (61-66 cm x 17-25 cm x 17 cm baited with dog food and sardines), and 369+ trap nights with Shermans (23 cm x 9 cm x 8cm baited with oat mixes and queso llanero) provided some additional insights on terrestrial vertebrates. A standardized short form was used for opportunistic observations while driving or during other field activities, providing important additional information on group sizes and habitat affinities.

Camera Traps

Animal tracks were abundant in moist soft substrates during the rainy season, but only large hooved animals left good tracks in the forest during the dry season. Camera traps were used in several areas during the dry season, to complement the visual observations recorded on walking transects. TrailTimer infrared sensing camera trap systems were combined with inexpensive (<\$100) Canon, Kodak, and Vivitar cameras loaded with 400 ASA Fujichrome film. During the 1997 dry season, exploratory work took place along water holes in drying Caño Caujaral/Roseta. During the 1998 dry season, up to 12 units were employed along retired foot transects. For two weeks, ten cameras were divided between two transects (low elevation semi-deciduous forest vs dry hill forests). During that time, the remaining free cameras were employed along drying creek beds, a jaguar kill, and prestamos. During the remainder of the dry season all units were employed along a foot transect paralleling Caño Caujaral through semi-deciduous forest. As the next dry season (1998-1999) began, 12 to 14 units were employed along the same three transects, and also along a narrow forested stream valley in steep hills. In January 1999, all units still functional were deployed opportunistically along known animal travel routes near drying caños and prestamos and baited (plantains, bananas, mangos, guavas, fish, dog food, raw beef, oat-banana-peanut butter mixes, and salt) for two weeks.

Results

Distribution of Animals According to Encounter Rates

Vehicle transects

With the caveat that transects along dirt roads result in a bias towards edgepreferring species, and miss details that foot travel in irregular topography can detect, vehicle transects provided useful sketches of general patterns. During the dry season, jaguar prey biomass was highest along the well-watered low route consisting of interspersed forest, savannas, and low hills. Capybara, white-tailed deer (*Odocoileus virginianus*), and collared peccary (*Tayassu tajacu*) were more numerous on this low route than along the route dominated by hills, rocky soils, dry forest types, dry savanna, and less abundant surface water (Table 44, Fig.11). However, rabbits (*Sylvilagus floridanus*) were more abundant on the high route and the *Sylvilagus* detected on the low route were using the edges of a small hill. Crab-eating foxes (*Cerdocyon thous*) were only slightly less common on the high route than the low.

Observations in the large, seasonally flooded savanna during the dry season were dominated by deer. Capybara were scarce there because there were no large ponds on the route (Fig. 11). The deer were detected near the savanna/forest ecotone. During the heat of the day they were in shade, not exposed savanna. Crab-eating foxes were common in the savanna.

These general distributional patterns continued during the rainy season, but animals became more dispersed as surface water and green forage became more widely available. Vehicle transect data indicated no massive exodus from low areas in response to the shallow flooding. Instead, animals appeared to "spread out" within large annual use areas, making use of more dispersed resources, fewer surface water constraints, and the phenology of favored plant foods. Interesting side notes are that ocelots (*Leopardus pardalis*) were using savanna (though not common, this occurred along foot transects as well) and tayra (*Eira barbara*) used dry grassy hillsides on the high route during the rainy season. The latter was presumed to be associated with nearby strips of semi-deciduous forest in valley bottoms.

Foot Transects and Camera Trapping

The primary intent of transects was abundance estimates of select prey species, and thereby, availability. However, contrasts in animal distributions within and among transects illustrated the patterns of prey distributions across the landscape.

Contrasts in encounter rates over a variety of habitats are presented in Fig. 12. Diversity (and biomass) was high on La Candelaria transect (21 sp.). In this wide tongue of semi-deciduous forest, connected to larger blocks, strongly-forest dependent species such as tapir (*Tapirus terrestris*) occurred, but the nearby edge resulted in high numbers of white-tailed deer. Deer numbers were lower on Caujaral Norte (20 sp.), but a large group of white-lipped peccary (*Tayassu pecari*) appeared to offset the drop in cervid abundance, particularly considering that the bars exhibited are independent of group size. Although this white-lipped herd used the area most heavily in the dry season, animals and sign were detected during the rainy season, albeit in more scattered locations, and with clear evidence of use "outside" the sampled area. Collared peccaries were less frequent in Caujaral Norte than La Candelaria, and when group size is considered, even more so than Fig. 12 suggests. Jaguar and tapir sign frequencies were highest in Caujaral Norte, and ocelots (*Leopardus pardalis*) abundant, particularly near the caño. Howler monkeys (Alouatta seniculus) and yellow-knobbed currasow (Crax daubentoni) were also more common in Caujaral Norte. In vegetation-based cluster analyses, many forest plots from Candelaria and Caujaral Norte fell within the same clusters. Composition of forest plots near the stream bed of Caño Caujaral Norte did differ from La Candelaria. The Caujaral Norte transect was 100% forested, while La Candelaria was 86%. The remaining 14% of La Candelaria was small pockets of savanna, locally called calcetas. Mean distance to nearest edge recorded at 100 m intervals was 1448 m (n=27) for Caujaral Norte and 247 m (n=22) for La Candelaria.

Of the nine transects presented in Fig. 12, collared peccaries occurred on seven, white-lipped peccaries on one. The size of the contiguous caño-side forest in Caujaral

Norte (see above interspersion index), its connection to a long riparian strand extending north of Piñero, the proximity to permanent water (means: 68 m Caujaral Norte: 512 m La Candelaria: 653 m Bosque de Los Cerritos; 279 m Lado de Cerro Guaical; 522 m Encima de Cerro Guaical), as well as forest composition in damper areas all may have played a factor in determining the areas where white-lipped peccaries concentrated.

Collared peccaries used forests in the hills (Bosque de Los Cerritos, Lado de Cerro Guaical, Encima de Cerro Guaical, and Bosques de Las Penitas, Fig. 12). Whitetailed deer, *Dasypus novemcinctus*, *Geochelone carbonaria*, and other taxa also used hill forests.

Puma sign occurred on four transects in Fig.12, jaguar sign on three. Caujaral Norte and La Candelaria forests (jaguar and puma presence recorded) were 100% relatively high stature (mean canopy height and overstory tree DBH 19 m 47 cm and 18 m and 39 cm, respectively) bosque semi-deciduo (BSD). El Bosque de Los Cerritos (only puma recorded) crossed a number of forest types as it ascended and descended a hill. While the first 350 m of bosque siempre verde (BSV) had a canopy height of 16 m and overstory tree DBH of 27 cm, the bosque seca types (BS) had canopy heights of 12, 7, and 4.5 m, and the well-represented sabana seca con chaparros (SS/CH), canopy heights under 4 m. On El Lado de Cerro Guaical (only puma recorded), also a mix of types (81% BS 9.5% BSD 9.5% SS/CH), mean canopy height was 10 m, mean overstory tree DBH 20 cm. Las Penitas (jaguar presence recorded) was a mix of short dry hill forest (BSC and BSF), high dry pasture, pockets of tall semi-deciduous forest (BSDS), and sections of sabana seca con chaparros (SS/CH). Mean canopy heights and mean overstory tree DBH measurements were as follows: BSC 4.37 m 6.8 cm; BSDS 17.5 m 28.2cm; BSDS 13 m 21 cm; SS/CH 4.4 m 14.75 cm. While a jaguar was seen on the dry, mostly open Las Penitas transect (Fig. 12), it was probably not focusing on SS/CH or dry pastures, it may have been interested in the hill-base pockets of BSD or hill flank BS forests where collared peccaries and rabbits occurred (camera trapping and foot transect data), but it probably was enroute to a valley filled with moist seasonally flooded forest with permanent water where it was frequently radio-located.

Diversity declined as elevations increased (Bosque de Los Cerritos, Lado de Cerro Guaical, Encima de Cerro Guaical, Bosques and Pastos de Las Penitas Fig.12). Collared peccaries did use hill sides covered by bosque seca types but rarely occurred in sabana seca con chaparro types (Fig. 13). On a 2750 m transect that crossed a hill (Fig. 13, Bosque de Los Cerritos), all species of interest clustered in the BS types and were rare in SS/CH. *Cebus olivaceous* sometimes used hill side forests, specifically, richer BS mixes. Both cebids clustered at lower elevations closer to permanent water. White-tailed deer used both BSD and BS but appeared to avoid ridge-tops (Figs. 12, 13). Puma were recorded on this hill trail. Jaguar were not. The transect Encima de Cerro Guaical (Fig. 2) had pockets of BSD in short hill-top valleys. This sort of inter-digitation of habitats facilitated a wide distribution of animals.

Chacalacas (*Ortalis ruficauda*) exhibited a slightly broader ecological amplitude than yellow-knobbed curassows, better tolerating drier forest types, open areas, and distance from water (Figs. 12, 13,14). Nine-banded armadillos (*Dasypus novemcinctus*) used both BSD and BS (Figs. 12, 13). *Dasyprocta agouti* used both BSD and BS but seemed to prefer lower elevations (Figs. 12, 13). *Agouti paca* was rare on the ranch. The few sightings that occurred (both along riparian zones) did not fall within foot transect or

camera trapping sampling efforts. *Cerdocyon thous* was very common in Piñero. It occurred in all forest types except SS/CH but was clearly a creature of edge, occurring commonly along savannas (Figs. 12, 13, 14). *Procyon cancrivorous* appeared uncommon in comparison, and used low elevation BSD and pasture edges. *Leopardus pardalis* occurred in wet and dry forests, and also made use of savanna and pasture edges (Figs. 12, 13, 14); logical given the high seasonal densities of rodents such as *Zygodontomys brevicauda* in those habitats.

Myrmecophaga tridactyla and *Tamandua tetradactyla* occurred in both BS and BSD, but *Myrmecophaga* made more use of short stature dry forests on hills than the more arboreal Tamandua (Fig. 12). *Geochelone carbonaria* used both BSD and BS types (Figs. 12, 13). *Eira barbara* preferred BSD and proximity to water (Fig. 12, but made forays into more open habitats (Figs, 12, 14). *T. tajacu* frequently occurred along the edges of savanna (Figs. 12, 14). Crossings were not often seen, but clearly occurred (Fig. 15). Capybara were counted directly because the transect system was not designed to estimate their abundance. They were common in Potrero Los Venados (Fig. 12) a small savanna dotted with prestamos and close to forest: a habitat matrix. They also occurred in the forests near the water bodies Tapa Escorzonera and Laguna Cerritos (Figs. 12, 13). The phenomenon of capybara in forest near water was a common one: project observers posted at water holes in the dry season noticed that some herds spent most of the day in forest cover (preyed upon by jaguar in same area). Capybara also occurred in more open savannas such as Mata de Guafa 2 (Fig. 14).

Overall diversity was lower in savannas than forests. The three pasture transects (Los Venados, Los Cerritos, Claro Cerrillos) in Fig. 12 represent a gradient from: 1) low

elevation savannas dotted with prestamos and adjacent to BSD nearby; to 2) higher elevation pastures with scarcer surface water, poorer soils, adjacent to BS. White-tailed deer were very common on the Los Venados transect (mean distance to BSD 116 m, mean distance to permanent water 147 m). Densities were lower on the Los Cerritos pasture transect, where high dry soils were ameliorated by proximity to a lake and water tanks (mean distance to water 650 m) and annual applications of fertilizer, and proximity (mean 86 m) to BS. Prey availability on the Claro Cerrillo transect (Fig. 12) was clearly low. Though mean distance to ecotone was only 19 m, that species-poor narrow-strip of forest lining a seasonal rivulet was primarily productive in the rainy season. The fruits available then (*Annona purpurea, Annona jahnii, Lycania pyrifolia*, Table 42) were presumably related to the concentrations of collared peccaries (groups as large as 42) in the area that time of year. During the dry season, all animals were scarce in this area. Mean distance to water was 800m and soils were poor.

Similar patterns of prey distribution in savannas are presented in Fig. 14. These are all low elevation savannas, with the gradients being indices of interspersion and access to water. Mean distance to ecotone, proceeding from Juncal Saman Gacho (rear) to Guanabano Abierto (front) were: 84, 30, 87, 305, 352, and 765 m respectively. Mean distance to permanent water in the same sequence was 570, 341, 486, 303, 269, and 1772 m respectively. White-tailed deer abundance was limited by distance to cover and water during the dry season. Prey diversity and abundance in wide-open and poorly watered savannas was very low. Conversely, prey were abundant in small (frequently not over 1 km or less in any direction) savannas surrounded by strips and blocks of semi-deciduous

forest. Caiman and turtles in the prestamos dotting such savannas added to overall prey biomass.

The Los Venados transect (Fig. 12) was an example of such a situation. Deer densities were high, there were good numbers of capybara, caiman, and freshwater turtles, and collared peccary were using the forest edge. Radio-locations of cats in the forests adjacent to these small savannas attest to their importance to felids (Daniel Scognamillo, Ines Maxit, Laura Farrell pers.comm.). Worthy of mention is that *Guazuma tomentosa*, the most important mid-dry season food for peccaries, though a tree of semi-deciduous forest, prospers at the forests' edge.

Figure 15 exhibits felid and prey distributions along a 2650 m transect crossing sabana arbolada and BSD alternatively. The majority of animals, and hence, prey diversity clustered in and around the forest. Deer and chacalacas used sabana arbolada more than the other species, though anteaters also crossed it. Deer observations also clustered around the permanent water source. Jaguar tracks were observed at the transect's beginning and end. This area was part of a male jaguar's circuit, and tracks were often seen on nearby dirt roads, sometimes for several continuous km.

Camera trapping data from deep forest and the caño bisecting it (Fig. 16) demonstrated a species composition very different from those of hills (Figs. 12, 13). Yellow-knobbed curassow were common, chacalaca absent. White-lipped peccary were abundant, collared peccary relatively scarce. Deer were far scarcer than in more heterogenous areas. Ocelots were common. Never common, tapir were present. Although sample sizes were small for large cats, in these habitats, the number of jaguar images was twice that of puma images. The frequency of crab-eating fox images was

surprisingly high given all other data demonstrating the species proclivity for edge (Fig. 16). Nearly every fox photographed was on the dry caño bed. Annuals establish themselves rapidly as waters recede and opportunities for scavenging are high where aquatic forms are being stranded. The drying caño bed was clearly a travel corridor for ocelots and white-lipped peccaries. It may have constituted a rich seasonal edge for the foxes.

Giant anteaters were not infrequent in deep forest (Figs. 12, 16), thus they occurred in nearly every terrestrial habitat in Piñero. Wading birds and other large birds were common in and near the caño. Pooled camera trapping images from drying caños (other than Caujaral) and prestamos (in or adjacent to forest) during the dry season (n=90) were 40% wading birds, 7% crab-eating raccoons, 5% jaguars, 3% crab-eating foxes, and 2% pumas. Of all images taken in hills (n=30), 40% were crab-eating foxes, 20% giant anteaters, 13% rabbits, 13% collared peccaries, 10% ocelots, and 3% chacalacas. Wading birds were common in Piñero, but neglected by most of my methodology. Frequencies from camera trapping (Fig. 16 and preceding image data in text) are the only quantification I have. Suffice to say, rolls of film in camera traps placed to view the water's edge ran the risk of being filled with wading bird images. Seasonal Changes in Distributions, Densities, and Group Sizes of Prey

Use areas of the amphibious capybaras retracted during the dry season, and expanded during the wet. Small groups of capybara aggregated during the extreme end of the dry season, coalescing into larger groups in excess of 100 animals. Freshwater turtles were very concentrated (maximum estimated at 1,466/ha) in the dry season. Marked turtles were observed 5 km from their dry season ponds during the rainy season. The highest caiman densities I recorded were 609, 690, 653, and 958 per hectare during

the dry season. The rainy season's shallow flooding facilitated dispersal and by July and August, caiman were encountered on foot transects that were dry land at other times of the year. There also was overland movement of caiman in the dry season. As the quality of smaller water bodies diminishes, some caiman move to more permanent habitats. The shallower and hotter the water the more easily the caiman are prompted to move. Some caiman embedded themselves in rubbish in forests along drying caños, waiting for the change in weather. Swimming a haul seine through a prestamo in the rainy season was illustrative. In the dry season each haul yielded kilos of fish, turtles, and young caiman. In late June it yielded nothing, while fish swam in an adjacent road bed. Distributions of amphibious and aquatic prey were very strongly influenced by season.

Changes in seasonal ranges were less striking in ungulates. White-lipped peccaries frequented mud-wallows during the dry season. Despite the species reputation for long-distance movements, group locations were fairly predictable in the late dry season. Heavy infestations of ticks in their intensive use areas near mud wallows suggested that the mud was either a barrier or a relief for tick bites. All indications (cameras, transects, opportunistic observations) were that the white-lipped peccaries used a larger area during the wet season than the dry. Pooled observations suggest that their dry season home range was a subset of their wet season range.

Seasonal shifts in white-tailed deer and collared peccary ranges were less obvious. Observations of deer during the dry season frequently revolved around water (prestamos and water tanks). Yet, deer were in the same general areas during both seasons. Group size did not differ between seasons (Table 45). Smaller group sizes recorded on transects than in opportunistic observations could be due to bias for larger groups in opportunistic

observations, but the lower proportion of juveniles observed on transects suggest poorer detection was the cause. Even in open habitats, the foot traveler created more of a disturbance than the vehicle rider, (a mild wake of disturbance through savanna grasses) and in many cases, the observer's height was lower and thus more obstructed. The proportions of juveniles were slightly higher during the rainy season, concurring with the observations of Brokx (1972) that white-tailed deer breed year round, with a pulse of parturition in the late rainy season. The proportion of juveniles was also similar to that found by Brokx (1972). Widespread surface water in the wet season resulted in shifts, but not large movements. As Brokx (1972) put it "the interspersion of habitats in many areas was such that the seasons merely shifted emphasis from one part of the home range to another".

Mean collared peccary group sizes recorded on transects were significantly larger (p<.05, T =1.74, 42 degree of freedom) in the dry season (6.77) than wet (4.93). Robinson and Eisenberg (1985) had observed the same phenomena on their grid system in Hato Masaguaral (Table 46). Mean group sizes recorded in opportunistic observations were consistently larger than observations made on transects , and dry and wet group sizes roughly the same (Table 46). Mean group sizes recorded were larger on the few occasions when peccaries crossed open areas on transects (Table 46). Proportion of young observed on transects was less than the proportions recorded in opportunistic observations. The differences between opportunistic observations and transect observations, and between observations in the open versus in forest imply detection factors. First-hand knowledge of rainy season under storygrowth obtained from cleaning transects causes me to discount the statistically significant difference in group sizes

between dry and wet as an artifact of better visibility in the dry season. Reproduction of collared peccary appeared to be year-round, and though Castellanos (1982) identified a parturition pulse in the transition between the late dry and early wet season, I could not attest to its validity (Table 46).

Without telemetry data or repeated observations of marked collared peccaries throughout the year, a definitive statement on how the seasons affected home range is impossible. Since different collared peccary groups occupied very different sorts of areas within the single study area, a tight generalization might be difficult even with better data. Table 47 is a list of seven areas in which, between foot transects, phenology trails, and opportunistic observations, we recorded collared peccary in both wet and dry seasons. The habitats that these different groups occupied ranged from very lowelevations subject to considerable flooding to low ridges that never inundated and the hill sides and valleys between. Collared peccary presence was noted in forests inundated up to 70-90% with an average depth of 10 cm. Seasonal home-ranges of collared peccary in Hato Piñero presumably echo those in Hato Flores-Moradas (adjacent to south boundary of Hato Masaguaral), where Castellanos (1982) found that the mean wet season home range was three times the mean dry season range (Fig. 17). Within that average there was considerable variation. Some seasonal ranges were roughly equal in size, but with different foci. The distribution of water over the landscape during the rainy season would seem to facilitate dispersal. However, rising water can also present an inconvenience as areas elevated above widespread water contract. Foot travel on transects provided a firsthand view of how limited the peccary hoof-marked pockets of forested land became in lower plains. In some cases, patchy plant distributions and moisture-facilitated increases

in primary production could require less searching than in the dry season. Although it can be presumed that most collared peccary groups were less confined by availability of water or wallows after the arrival of the rains, the heterogeneity present in Piñero precluded a blanket generalization.

Abundance and Biomass

Counts revealed capybara to be less abundant than their highly visible nature (in comparison to peccary) and proclivity for semi-open to open habitats had suggested (water is an open habitat even when lined with forest). Capybara sometimes spend considerable time in forest cover. Despite that, our familiarity with the study area, activity patterns, and repetitious counts, yielded a confident estimate of 547 animals for the entire study area (Table 48). Some examples of mean, median, max and min dry season group sizes are 15, 15, 40, 1 (n=27) in Los Venados/Juncal, 10, 10, 23,1 (n=15) in Escorzonera/Guaical, and 31, 16, 144, 1 (n=34) in Los Patos/Puente Benjamin. Taking population structure into account and assigning weight estimates resulted in a biomass estimate of 20,315 kg for the 63,227 ha study area.

April counts measure minimum biomass. Adults lose weight during the late dry season due to reduced forage quality. Mortality is highest during the dry season. And although some reproduction can occur year-round, with capybara there is a very clear birth pulse between September and December, with the peak in October and November. All those factors point towards maximum biomass at the end of the rainy season. Several factors soften the contrast between the maximum and the minimum. Newborn weigh approximately 1.5 kg, not a huge increment of increase. During the dry season, those same first-year animals are growing, as are the animals approaching their second year (maturity), even if adults can lose as much as 5% of their weight (Ojasti 1973). Taking these overlapping factors into account results in a maximum of 22,654 kg in November. The increase is due to five months (June through November) when high forage quality and availability as well as the addition of new (albeit small) animals allow weight gains.

Caiman densities varied a great deal. The two larger lakes set amidst hills appeared oligotrophic. Laguna Grande densities ranged between .875 and 1.61/ha. Laguna Alta densities ranged between 37 and 44/ha. Surface area and total volume of smaller water bodies were very dynamic. The drying of very small ponds and shallow caños and severe shrinking of permanent pools resulted in very high densities (e.g. 609-958/ha). Caiman habitats are in a constant flux. Along caños, stretches dry out completely forcing caiman to walk to the next pool. Sampling in the deeper more productive pools or sections of any caño can generate a misleading extrapolation for the entire water body. Walking many kilometers along or in drying caños helped generate realistic estimates. Prestamos and caños with abundant shelter, such as short emergent aquatic vegetation or woody debris became havens for the year's young caiman. Many productive deeper pools with numerous large animals and with scant hiding cover saw a marked reduction in the proportion of the same class of young animals between the beginning and end of the dry season. Situations where caiman biomass became very concentrated, arose when the numerous animals inhabiting a long caño or wide savanna during the wet season were drawn into a single pool as the dry season progressed.

A caiman biomass estimate generated from dry season counts fails to address seasonal variation in biomass. Reduced stress during the wet season and the October-November birth pulse might result in peak biomass in November. Unfortunately caiman dispersal during the wet season is so extreme that numerical evaluations are impractical.

The caiman biomass estimate of 167,827 kg in the 63,227 ha study area, based on four years of counts, an estimate of 15,408 animals for the study area, size class proportions based on 5,998 observations, and 407 ha of late dry season water surface (Table 49) will have to suffice.

Two groups of white-lipped peccary used Piñero. The larger group (approximately 107 animals) frequented the forest surrounding the northern section of Caño Caujaral (BSD with a high percentage of briefly deciduous species). Two transects ran though this area and I deployed camera traps on and off of transects (Figs.12, 16). In the dry season, the peccaries made heavy use of mud wallows as pools sequentially dried out. The group sometimes traveled along the dry caño bed, but more frequently wove in and out using trails that were easily recognizable due to the volume of traffic and tracks. Some pockets of forest in some (not all) of this area were cool and green overhead during the dry season: a perception given validity by daytime *Geochelone carbonaria* activity when the tortoises were embedded in cover elsewhere. The local name of the core area, "La Roseta" referred to how the caño, with a single canal downstream, branched out into numerous active and retired stream beds (ramales) in the north. These areas were low, and hence subject to considerable inundation. Small hills penetrating this deep green strip where it bisected the massif of El Baul presumably relieved the peccaries during the wettest months, and would be expected to impart dietary variety. The group was less confined during the rainy season, though the full limits of its movements an unknown. Despite the Candelaria transect's three years of existence, T. pecari sign was observed on it for the first time during botanical sampling in late 1999, testimony to the importance of long-term studies and risks of short-term evaluations. Because faunal sampling on the

transect had been retired, this one-time event is not shown in Fig.12. Nor does the observation detract from conclusions drawn from Fig. 12. The presence of white-lippeds was palpable in Caujaral Norte/Rosetta. The forest was full of trails. The creek bed was modified (Figs. 12, 16).

The smaller group of white-lipped peccaries, approximately 60 animals, used the northeastern corner of the ranch. Observations of animals and sign ran from the BSD laced rim of oligotrophic Laguna Grande through a large block of semi-decidous forest between the lake and Rio Pao. This area also was subject to inundation but was sprinkled with a few low hills. It also had an old river bed, Caño Rosario, that though technically dry much of the year, maintained green vegetation longer than the surrounding forest, and was lined with a disproportionate amount of saman trees (*Pithecellobium saman*). This group used mudwallows in Caño Matajei a tributary of Rio Pao, but avoided the river, perhaps due to the heavy traffic of poachers. Although, I was personally less familiar with this group, it was studied by Barreto et al. (1997) and Hernandez et al. (1995).

Good group counts of white-lipped peccaries are difficult to obtain. In flight there is chaos. Even without flight there is a good deal of coming and going, usually in fairly dense cover with narrow openings. Group structure has rarely been reported in the literature (Barreto & Hernandez 1988; Bodmer et al. 1997a; Fragoso 1998; Fragoso 1999; Hernandez et al. 1995; Kiltie & Terborgh 1983; Mayer & Wetzel 1987; Sowls 1997). Pooling averages of four methods of estimates of population structure in Piñero yielded 71% adults and 29% juveniles. Kiltie and Terborgh (1983) reported that in 60 observations in the Peruvian Amazon the proportion of peccary youngsters was usually

less than 20%. Assigning weight to two size classes resulted in a biomass estimate of 5,005 kg for the 63,227 ha study area (Table 50).

The most common freshwater turtle in the study area, the galapago (Podocnemis *voglii*) is an impressively adaptable small-bodied generalist. it occupied a variety of habitats (prestamos, lakes, caños, and rivers). The larger bodied and more specialized terecay (*Podocnemis unifilis*) had a more restricted distribution. Basking counts along the Rio Pao were 7.5% P. unifilis : 92.5% P. voglii. The composition of captures in the deepest remnant pool in Caño Caujaral at the end of the dry season were 27% P. unifilis : 73% *P. voglii*. During high water, the caño was connected to the rivers because all the lower elevations on the ranch were flooded. During the dry season it simply ended in a section of semi-deciduous forest locally referred to as Rabo de Agua (tail of the water). The *P. unifilis* in Rio Pao were residents and reproduction was occurring. Those in Caño Caujaral were smaller individuals that had been stranded as the high water receded. The high proportions in the pool sampled were a reflection of the species' preference for deeper water. The terecay were forced into the pool, while presumably a number of P. *voglii* remained in shallower sections of the caño and some may have simply embedded in mud to wait out the dry season. Though a few introduced P. unifilis were also seen in Laguna Alta, the species could be considered rare in Piñero. P. voglii nests between October and February. The greatest frequency of recently predated *P. voglii* nests was during late December and January

Mata mata turtles (*Chelus fimbriatus*) were quite common in Caño Caujaral. In less than 200 m of Caño Caujaral three of 38 captures in relatively high water between October 27 and November 30, 1996 were recaptures. Individuals were sometimes found

wandering forest in the late dry season, presumably looking for the nearest pool with water. In December of 1999 I found 5 shells of 5 adult *C. fimbriatius* in a circle of 4-5 meters in forest just beyond the bank in the northern part of Caño Caujaral. The remains were old, and no sign of the presumed predator present. Mean weight of 36 mata mata was 6.894 kg (n=36). Maximum was 13.5 kg. Females captured October 27 and 31 contained eggs. Clutch sizes of the brittle spherical eggs obtained by induced oviposition were 13 and 8. Mean diameter and mass of 5 eggs were 37.9 mm and 33.5 gm. Since all females were palpated, indications were that the nesting season was largely over by November. Mata mata were presumably in the rivers, but we had no indication that they were in the prestamos. *Kinosternon scorpiodes* was encountered several times on transects, at savanna edge during the rainy season.

In some water bodies (e.g. Lagunita Escorzonera and Caño Manglarito) *P. voglii* reaches impressive concentrations. The modified Lincoln-Petersen estimator developed by (Chapman 1951) and the variance calculations for it from (Seber 1982), as discussed in (Lancia et al. 1994) yielded an estimate of 1,466 galapago/ha (95% confidence interval (CI) of 450-2,482) from a total of 188 captures in Escorzonera. When 5/188 turtles are recaptures and the center of the lagunita is speckled with bobbing turtle heads, it is clear that numbers are high.

Table 51 presents results of late dry season capture-mark-recaptures in two typical prestamos and a deep pool in Caño Caujaral. Ramo (1982) estimated 377.8 galapago/ha (95% CI 296.2-482.9, n=526) in a caño in Hato El Frio in Estado Apure. The variety and number of ephemeral and permanent water bodies in our study area was staggering. The limitations of extrapolating from a sample of three typical water bodies is recognized.

Taking into account possible bias, in which the areas were chosen due to visible turtles, and hence higher chances for capture success, and knowing that some ponds and stream stretches are less productive, a conservative biomass estimate can still be generated. Using the average of the lower limit of the three confidence intervals in Table 51, multiplying by dry season water area 407 ha and mean weight of *P. voglii* (1.247 kg n=181) results in a study area biomass estimate of 56,674 kg for the 63,227 ha study area.

The estimate for caiman biomass was 167,827 kg (Table 49), putting the biomass ratio of the relatively small freshwater turtles to the much larger and more visible caiman at .338. Since caiman are so vastly more visible, and individuals larger, this at first seems counter-intuitive. Consider the following. The ratio of galapago/caiman biomass in well-studied Escorzonera was .519. The estimate of 56,674 kg does not factor in the biomass of mata mata and terecay, both much larger than galapago (terecay are roughly twice the size). Given the uncertainty that the small number of water bodies sampled imposes, the estimate of 56,674 kg is conservative. The biomass of freshwater turtles may be higher.

In contrast to Hato El Cedral in Apure (Muñoz & Rivas 1994), anacondas (*Eunectes murinus*) were neither common nor widespread. Piñero possesses much less year-round water than the lower areas of Apure (Llanos Bajos). Mean weight of 17 anacondas captured in Piñero was 17.2 kg. A Lincoln Petersen estimator run on 11 captured in the shallow mud flats of Caño La Iguana indicated 6.7 anaconda/ha, but the conditions were extreme drought and the real catchment area uncertain. La Iguana was a stream running though savanna with a relatively low, even shrubby at times, riparian. The largest specimen, 4.85 m long and 50 kg, was from Caño Caujaral, where, for reasons unknown, anaconda were very rare. Anacondas were relatively common in Rio

Pao, where during the dry season, they could be located, often in mating balls in riverside holes in the steep clay banks. This was a setting where a capture-recapture effort could have been fruitful. However, water management authorities purged excess water from an upstream reservoir during the time set aside for the exercise, eliminating opportunities for easy captures. Anacondas were observed in one other habitat (a permanent pool in low elevation caño). Although common along the banks of Rio Pao, and concentrated in the nearly dry Caño la Iguana, anacondas were not abundant at Piñero.

Maximum counts of iguana (*Iguana iguana*) were 16/3.8 km along Caño Caujaral, 17/3.8 km along Rio Pao, and 31/km at Caño la Iguana, where dry conditions forced concentrations. As speculation: 16 iguanas per 3.8 km of stream side forest (both sides) = 4.21 iguanas/linear km of stream side forest (both sides); rounded up for undetected to 5/km; estimated mean weights for males 1.53 kg and for females 1.14 kg (Dugan 1982), with 1:1 sex ratio, resulting in an average iguana = 1.33 kg; summing total stream lengths using ARCVIEW, Mata de Guafa, La Iguana, Rio Pao, Caño Caujaral, and Caño la Canoa = 100.7 kg; yields a total of 669.6 kg of iguana for the study area. Though lacking any measure of confidence, this figure is some measure of the magnitude of iguana biomass, an item neither readily accessible, nor important to large cats.

DISTANCE Density Estimates, Density Validations, Distribution Validations

The input data from transect lines were assigned to the following habitat categories: A) BSD near Caño; B) Standard BSD not near Caño; C) Hill Forests-BS mixes; D) High dry pastures-PS; E) Small flooding savanna near edge and water-SI; and F) Wide open savanna, near and away from edge and permanent water-SI. Sabana Seca con Chaparro (SS/CH) sections with few to no animal observations were omitted from

input, and from abundance estimations. Two transects with forested and open stretches were sectioned according to habitat types. Total input was from up to 28 lines. Data from each individual line were pooled over time. Analyses started with "all forest pooled" and "all savanna pooled", and were then stratified by habitat as far as sample size allowed. Every analysis started with half-normal, hazard rate, and uniform models and no truncation. Preliminary results were reviewed and models that fit poorly were eliminated. After the preliminary analyses most data sets were truncated (elimination of the animal observations collected at the furthest distances from the transect where detection patterns were inconsistent). Truncation usually eliminated less then 5% of the total number of observations and rarely exceeded 10% (Buckland et al. 1993).

Deer were less common in forest (strata A, B, C, all forest pooled) than expected. A half-normal model (Buckland et al. 1993) using observed group size 1.0513 from the 39 observations on 14 lines (after discarding 9.3% of total observations), with data truncated at 100 m resulted in a density estimate of .01/ha, with a 95% confidence interval of .005-.023/ha (Table 52 – converted into individuals/km²). Although fond of forest edge, and making use of fruit production in forests, deer were not common in forest interior (see contrast between Candelaria and Caujaral Norte transects in Fig. 12).

Deer densities were very high in stratum E; small savannas with abundant edge and permanent water. Data quality were such that truncation was not needed (no improvement). A hazard rate model (Buckland et al. 1993) using observed group size of 1.592 from103 observations along 6 lines and a strip width of 350 m< resulted in a density estimate of .147/ha and a 95% confidence interval of .083-.261/ha. The number of observations was smaller and conformation of data poorer in strata F (wide-open

savannas). Truncating at 230 m, eliminating 5.9% of the observations, a hazard rate model using observed group size of 1.437 from 16 observations on 4 lines resulted in a density estimate of .108/ha and a 95% confidence interval of .025-.457/ha (Table 52). Deer densities were lower on high, dry pastures (strata D), where observed group size was 1.172. Truncating at 190 m, discarding 3.3% of the observations, a half-normal model used the remaining 29 observations to generate a density estimate of .015/ha with a confidence interval of .004-.065/ha (Table 52). These density estimates validate distribution patterns suggested in Figures 12 and 14.

Collared peccary densities were generated using strata A, B, and C pooled. The total number of observations was 48. Stratification would have generated more variation in estimates, and the distribution patterns of collared peccary (Figs. 12, 13, 15) justified the pooling. A uniform model (Buckland et al. 1993), using observed group sizes of 5.583 on 14 lines with no data truncation applied (no improvement) resulted in a density estimate of .113/ha and a confidence interval of .075- .17/ha. Collared peccary were encountered in open areas of transects (near savanna edge) three times. Because their use of open areas was brief, no attempt was made to generate collared peccary densities in open strata (Table 52).

Agouti densities were pooled among all forests (strata A, B, C) due to similar sampling constraints and distribution. A uniform model using 14 observations of observed group size of 1.143 and no data truncation resulted in a density estimate of .006/ha and a confidence interval of .003-.012/ha (Table 52). More specifically, Agouti preferred hill bases and flanks, not ridges. Eliminating three high hill lines (strata A, B,

edited C) did not reduce the sample and generated a density estimate of .007/ha and a confidence interval of .004-.015/ha (Table 52).

Geochelone distributions were similar to agouti: they occurred in both BSD and BS, but shunned higher ridges. A hazard rate model truncated at 6 m using 26 observations in all forest pooled (strata A, B, and C) yielded a density estimate of .95/ha and a confidence interval of .474-1.903/ha (Table 52). Tortoise size, camouflage, relative immobility, and lack of alarm vocalization meant that observations far from the transect were rare and inconsistent. Tortoise detection functions were unique, with a steep drop in observation frequencies a short distance from the line. Of 30 total visual observations 53% were encountered directly on the transect (distance = 0), and 27% within 3 m. This translates to 80% percent of all tortoises observed within 3 m of the transect, only ten percent between 4-6 m, and an odd ten percent between 10-30 m. When adequate observations to generate reasonable density estimates can be collected within 3 m of the lines, the implication is that the animal is very common.

A hazard rate model using data from strata A, B, and edited C (no ridges) truncated at 6 m resulted in a density estimate of .992/ha and confidence interval of .456-2.158 from 22 observations. Focusing solely on BSD (strata A and B, all hill forests excluded) a hazard rate model, truncated at 6 m, generated a density estimate of 1.076/ha and a confidence interval of .471-2.456/ha using 20 observations (Table 52).

Tortoises were captured and marked in a 42.5 ha grid between April 20 and June 14, 1997. During the transition from dry to wet season tortoises leave dry season refugia (root wads, detritus piles, and inherited burrows). This period of easy observations lasts approximately 6 weeks before rapidly growing under story reduces ground-level visibility. Schnabel's multiple capture estimator for closed populations (Seber 1982) used on data from 25 morrocoy captures and 4 recaptures yielded a 95% confidence interval of 1.093 –2.166/ha, similar to the DISTANCE estimates (Table 53). The grid was located in low elevation BSD with a stratum B foot transect forming one boundary. Moskovits (1988), working on Isla Maraca in Brazil just south of Venezuela's Estado Bolivar, used a Lincoln Petersen estimator to generate a density estimate for adult *Geochelone carbonaria* of 1.049/ha with a confidence interval of .688-2.063/ha. Using the same methods she obtained a density estimate of .2/ha for adults of sympatric *G. denticulata*, and a confidence interval of .0965-1.12/ha. Estimates from Piñero foot transects, the Piñero grid, and Isla Maraca are all in rough agreement.

Cebid densities were relatively low at Piñero (Tables 52, 53). *Cebus olivaceous* densities in all forest pooled were .053/ha with a confidence interval of .028-.097/ha (half-normal, no truncation, 14 lines, mean observed group size 6.3 from 20 observations). Eliminating high ridges meant eliminating 4 observations as *Cebus* sometimes used BS mixes at relatively high elevations (density =.053/ha, CI = .025-.112/ha, 11 lines, no truncation, mean group size 6.5, 16 observations). Further stratification required no reduction in observation number. In low elevation BSD (strata A & B) densities were .061/ha and the confidence interval .03-.123 (Tables 52, 52).

Alouatta seniculus was less widespread and even less common than *Cebus* (Table 52). On occasion *Cebus* were seen bounding up dry exposed SS/CH in hills, crossing pastures, and frequenting caño sides in the late dry season. *Cebus* used hill-side BS mixes. *Alouatta* did not. On two occasions, both at low elevations, a small groups of *Alouatta* were observed amidst a larger group of *Cebus*, with the *Alouatta* higher and

more stationary. *Alouatta* densities for all forest pooled were .023/ha (CI .008-.064,half normal model, truncation at 40 m, 14 lines, 14 observations, mean group size 3.43). Densities in strata A & B alone were .024/ha (CI .008-.078/ha, uniform model, 10 lines, 12 observations, mean group size 3.5).

Two foot transects were located in a 2 km² grid used for *Cebus* behavior studies (Miller 1992). Concerned about the contrast between Hato Masaguaral and Hato Piñero *Cebus* estimates [Table 52 and (Eisenberg et al. 1979)], I asked Dr. Lynne and Steve Miller for density estimates for their study area. Their two estimates follow. Steve's assumed average of 25 individuals seen every other day in the 2 km 2 grid (25 x .5 / 2 km²) yielded an estimate of 6.25/km² (Table 54) (Steve Miller pers.com.). Lynne obtained a troop home range estimate (based on one radio-collared female) of 1500 ha. Her estimate was the result of the following logic: 1) seven troops used her grid at times; 2) their ranges might overlap only partially; 3) there are other groups which cruised through the area infrequently on which data are not collected; 4) assuming that 1 & 2cancelled each other; 5) resulted in seven groups per 1500 ha, and with modal group size of 20, an estimate of 140 Cebus/1500 ha = .093/ha or ~ 9 /km² (Lynne Miller pers.comm.). Although the logic in these calculations differ, and may even seem circuitous, they come from field workers familiar with their site, and are both fairly close to the density estimates generated by DISTANCE. Applying Lynne's more careful group size estimate of 20 to Steve's simpler calculations results in a density estimate of 5/km² (Table 54). The differences in *Cebus* and *Alouatta* densities between Hato Masaguaral and Hato Piñero were valid (Lynne Miller pers.comm).

Tortoises reveal themselves by their unwary slow movement, capuchins by their animated activity. The validation the grids provided for their DISTANCE density estimates may not apply equally to furtive mid-sized mammals such as *Sylvilagus*.

Cracids are ideal for distance sampling. Their elevation, activity, and vocalizations result in samples sufficient for detailed stratification. *Crax daubentoni* was most abundant in low elevation BSD (Table 52). It used forest edge and tree islands in savanna but was scarce in those situations (Table 52). *Ortalis ruficauda* was less common in BSD than *C. daubentoni*, but more common in hills. Density of *Crax* in low elevation BSD (38.5/km²) density of *Ortalis* in hill forest (38.5/km²) and conversely, density of *Crax* in hill forest (7/km²) density of *Ortalis* in BSD (10/km²). The generalist *Ortalis* penetrated savannas and pastures more successfully (Table 52), attaining high densities along the edge of small well-watered savannas (strata E).

All remaining densities presented in Table 52 were generated with dangerously small sample sizes. *Myrmecophaga tridactyla* densities in all forest pooled were .0039/ha with a CI of .002-.010/ha (uniform model, 7 observations, no truncation). That estimate was refined by removing high hills from the samples without losing observations, resulting in an estimate of .005/ha and CI of .002-.013/ha (uniform model, 7 observations, no truncation). Only two observations were available for all open habitats pooled (Table 52). Though not an abundant species in forest or savanna, our methods probably did not adequately measure the abundance of *Myrmecophaga* in open habitats. Despite the small sample in forests, Piñero densities compare favorably with the data from Hato Masaguaral (Table 52). Samples were scarcely larger for *Tamandua tetradactyla*. Density for all forests pooled was .003/ha with CI of .001-.009/ha (uniform

model, 8 observations). *Tamandua* is an animal of lower elevations, and the density for strata A & B was .005/ha with CI of .001-.018/ha (high variation) generated with a uniform model and 6 observations.

The number of *Eira barbara* observations was low, and the distance distribution problematic. The animals were moving away from the line. A uniform model generated a density estimate of .003/ha with CI of .001-.009/ha with mean group size of 1.4 from 5 observations.

The crab-eating fox *Cerdocyon thous*, was common in Piñero but represented poorly in foot transect data. There were only three observations in the all forest-pooled strata (Table 52). Sample size was seven for all open habitats pooled and variation very high (Table 52). The same seven observations used for strata E and D still resulted in high variation. More reasonable variation was obtained from 4 (!) observations in stratum E. A uniform model generated a density estimate of .003/ha and a CI of .001-.009/ha. *Cerdocyon* works habitat edges. Transects were designed to sample blocks of representative habitats, not meander along fence rows and road sides. Foot transects did not adequately evaluate *Cerdocyon* abundance. Another example of the limitation of foot transects are 78 white-lipped peccary sign records (tracks, trails, feces) on 16,650 m of the Roseta transect without a single sighting. Multiple methods are critical.

A uniform model using six observations of *Sylvilagus floridanus* in all forestpooled generated a density estimate of .008/ha and a CI of .004-.017/ha. *Sciurus granatensis* was not encountered in hill forests. A uniform model confined to strata A & B generated a density estimate of .009/ha and a CI of .004-.020 from nine observations.

Sorted Encounter Rates

On the average, Cerdocyon thous was the third most frequently encountered species during vehicle transects (Table 55). Along roads it is more abundant than peccaries, agoutis, and tortoises, a reversal from the relationships depicted in Table 52. Sylvilagus floridanus also appears more abundant along roads than in habitat interiors (Table 55). Abundance does not translate directly to biomass, and *Cerdocyon* drops in importance when ranking is the product of numbers and mean weight (Table 56). However, even when compared with deer and capybara, which weigh 8 times as much, along roads, *Cerdocyon* consistently ranks among the top four contributors of mammalian biomass. In the same ranking, *Sylvilagus*, drops (Table 56). Collared peccary biomass is underestimated from the road, its relationship to road edge being the opposite of Cerdocyon. The sum of encounter rate/body weight products along vehicle transects in the hills was an order of magnitude lower than along the two low elevation routes (Table 56). Although significant prev was missed on road counts, the difference must be assumed significant. Body weight estimates came from (Eisenberg et al. 1979; Linares 1998), and data from animals live-trapped during this study.

Sorted (ranked) encounter rates from foot transects in forest and open habitats can be useful indicators of relative abundance (Table 57). Foot transect encounter rates multiplied by mean body weight/species provide another biomass index (Table 58). Numerically abundant animals (e.g. *Dasypus novemcinctus* ranked third in forest, Table 57) drop in overall importance when body weight is figured in (*Dasypus novemcinctus*, ranked sixth in forest, Table 58). Uncommon but large bodied species may rise in importance. *Tapirus terrestris* ranks sixth in forest sign frequency alone (Table 57) and third when bodyweight is factored in (Table 58). *Panthera onca* goes from 13th to 7th

when bodied weight is multiplied by sign frequency (Table 58). Though these indices have utility, the caveat is that tapir left better sign than pumas, and jaguars better sign than agouti. Body weight had a relationship with track depth (even if not linear). Hooves left a sharper impression than soft paws. Peccary and deer, though common, also left excellent sign year-round. *Dasypus*, though probably common, left an abundance of sign in burrows and miniature excavations disproportionate to its actual abundance. Sign is useful, but best compared within species across habitats than among species. Deer, capybara, and peccaries emerge as major contributors to total mammalian biomass (Tables 56, 58).

Among-site ranking of camera trap image frequencies (rather than absolute numbers of images/site) provides additional indices (Table 59). This highlights the abundance of *Crax daubentoni* in forest interior; the frequency of *Tayassu pecari* in Caujaral Norte/La Roseta; the relative abundance of *Panthera onca* in the same area (and a possible preference for watered sites); the abundance of wading birds along drying caños; the preference of *Odocoileus* for forest with edge nearby (La Candelaria); and abreviated diversity in the hills, where *Cerdocyon thous* and *Sylvilagus floridanus* emerge as more common elements among a relatively depauperate community.

Standing Crop Biomass Estimates From Distance Density Estimates

The components used for biomass estimates were 1) densities (Table 52); 2) area of habitat strata and poached areas within strata (Table 12); 3) animal population structure (Tables 45, 46); 4) mean body weights (Eisenberg et al. 1979; Linares 1998); and 5) effects of hunting on densities (Karanth et al. 1999; Polisar et al. 1998). A number of stratum specific densities were generated but habitat map polygons were not totally equivalent to strata. SI (Table 12) was equivalent to strata E and F, indeed the same
polygon could contain areas of both, though deer densities differed between the two. Judgement calls were necessary, and they tended to be conservative.

Deer densities for forest and dry pasture/pasto seco came from Table 52. Sabana inundable SI was represented by far more strata F than E, though densities were higher in E (Table 52). I believe that the density of 10.8 deer/km² was too high for the interior of large savannas. The density of 8.3/km² used for SI in Table 60 represented the bottom end of the strata 95% confidence interval for stratum E, was well within the stratum F confidence interval, and fell in the middle of the range of 4-12.5/km² that Brokx (1972) found on protected ranches.

Collared peccary densities in Piñero agreed well with those from Hato Masaguaral (Table 52). Still, because peccary habitat varies in quality, the low end of the confidence interval, 7.5/km² (Tables 52, 60) was used. For *Dasyprocta* I used the high end of the confidence interval for all forest pooled, as the transects may have tended towards an underestimate (Tables 52, 60). For *Sylvilagus* I used the density estimate for BSD and, knowing it was a bit more common in BS, the high end of the confidence interval for that habitat (Tables 52, 60). Encounter rates for armadillo sign on forested foot transects were .35 that of collared peccary. Applying that proportion to density estimates yields approximately 4 armadillos/km² (Table 60). The *Myrmecophaga* and *Geochelone* densities for all forest pooled (Strata A, B, C, Tables 52, 60) were accepted without modification. In both cases this is a conservative estimate: *Geochelone* because it attains higher densities in specific strata, and *Myrmecophaga* because the animals using savannas have not been included (Table 60). Population structure for deer was reduced to .765 adults:.235 juveniles (Table 45) using 40 kg for mean weight of adults (Brokx 1972; Eisenberg et al. 1979) and half that for juveniles. Population structure for collared peccary was reduced to .77 adults:.23 juveniles (Table 46) using 23 kg for adults (Eisenberg et al. 1979) and half that for juveniles. Population structure was not available for remaining taxa. Body weights used were as follows:*Dasyprocta* 3.8 kg; *Sylvilagus* .8 kg; *Dasypus* 3.8 kg; *Myrmecophaga* 27 kg; *Geochelone* 4.32 kg; *Tapirus* 200 kg (Eisenberg et al. 1979; Linares 1998) and (Polisar unpublished data). Habitat areas subject to hunting and free from it had been evaluated with ESRI's ARCVIEW 3.1 (Table 12). Though guided by some knowledge, the designation of poached areas was somewhat arbitrary, as was the level by which densities were reduced (poached densities = unpoached x .3). Karanth et al. (1999) found prey biomass in a hunted site to be 74% lower than in an un-hunted area. Pooled *Mazama americana* and *Dasyprocta punctata* densities in a heavily hunted area in Guatemala were 3/10 of those in an adjacent national park (Polisar et al. 1998).

When transect data are viewed in light of all taxa recorded, prey densities were far from equitably distributed across the landscape (Figure 18). The extreme high of sign/sighting encounter rates was in La Roseta in the late dry season, where a large group of white-lipped peccary concentrated and jaguars, anteaters, deer, and tapir visited shrinking water holes. The extreme low was in El Guanabano Concreto, a line crossing tree-less savanna in the southern sector of the study area. Semi-deciduous forest and areas characterized by heterogeneity, including small savannas ringed with forest, had high encounter rates. Rancho de Sol, another fairly wide-open southern savanna also had low encounter rates. Merecure and Claro Cerillos, the type of high dry pasture (PS) where puma attacks on calves typically occurred, had low prey encounter rates. All data suggest that prey diversity and biomass were relatively low in the maternity pastures where puma attacks on calves sometimes reached unacceptable levels (Tables 52, 56, Figs. 11, 12, 18).

Discussion

Prey diversity and abundance varied greatly across the landscape at Piñero (Figs. 11-16 and 18). Forest sampling was adequate to explain some of this variation in terms of food available to herbivores (Tables 9, 10). It is safe to assume, that in savannas, access to primary productivity dictated grazer/browser distributions in similar ways. However, sampling in open areas was inadequate to elucidate the details. Prey distributions were patchy, and more so during the dry season than the wet. Contents of patches varied. While La Roseta and Caujaral Norte (Figs. 12, 18) were rich with whitelipped peccary during the dry season, Los Venados (Figs. 12, 18) was rich in capybara, caiman, and deer. Capybara and caiman were poorly evaluated via foot transects. Their distribution was very patchy and if factored into Figure 18, would elevate the relative importance of some savannas (Los Venados, Juncal Saman Gacho, Mata de Guafa 1 & 2) and some forests (Caujaral Sur). The extremely patchy, but considerable biomass of amphibious mammals and reptiles was a critical factor in overall prey distribution (Tables 48, 49). A nearly identical home range, used successively by two adult male jaguars, encompassed both La Roseta/Caujaral Norte and Los Venados/Juncal Saman Gacho; all pockets of productivity with contrasting prey types.

Prey data revealed areas of greater abundance, which cat traffic generally confirmed. Big blocks of semi-deciduous forest were very important. With diverse plant foods, they supported a diverse prey base (Figs. 9, 10). August (1983) stated that in Hato Masaguaral, mammalian diversity was related to habitat complexity (Figs. 12, 13, 15, 18, Table 12) and commented on the probable correlation between habitat complexity and diversity of food resources (Figs. 9, 10). Although high-stature low-elevation semi-deciduous forests in Piñero produced important prey for jaguar, their seasonal leaf fall meant they were poor in obligate arboreal folivores (August 1983).

The juxtaposition of contrasting productive habitats, which also produced productive edge, seemed the key in defining desirable jaguar home ranges. In this way, the jaguar may be similar to the tiger, whose prey is most abundant where "grasslands and forests form a mosaic and the interdigitation of many different vegetation types supports a rich ungulate community" (Sunquist et al. 1999a). The ungulate community of the llanos is hardly equal to that of South East Asia. It is neither cervid nor bovid rich. Larger caviomorph rodents fill some niches occupied by cervids and bovids in the Old World Tropics (Eisenberg & McKay 1974). Nonetheless, the patterns of prey production across landscapes bear similarities.

The most striking changes in seasonal distributions were among the aquatic/amphibious caiman and capybara. Both attained high local densities during the dry season, reducing search time for predators. Yet, is unclear how that affected vulnerability to predators. A single caiman in several cm of water in the middle of forest during the rainy season may be as vulnerable as one amidst 200 companions within meters of deep water during the dry season. Large capybara groups aggregated from smaller groups during the late dry season would seem less vulnerable than isolated small groups during the rainy season. Nonetheless, the capybara's need for proximity to water is a constraint that does increase site fidelity (even during the considerable time spent in brush or forest near water). The numerous capybara groups that do not converge into mass aggregations may be more vulnerable during the dry season.

Inferences can be made about contrasts between dry and wet season ranges in white-tailed deer and collared peccary ranges. The impression of expanding ranges during the rainy season as surface water becomes widely available was legitimate, but not universally applicable. Both ungulates maintained year-round residence in areas that remained roughly constant between seasons. There was no sign of seasonal migration. Piñero possessed such variety within one study area that during wet months peccary ranges in uplands might expand while in the lowlands they might contract. Without implying any correlation between seasonal responses of small carnivores and large herbivores, it is helpful to recall that Sunquist et al. (1989) found wet season ranges were smaller than dry season ranges for crab-eating foxes, ocelots, and hog-nosed skunks in Hato Masaguaral. In southern Florida, white-tailed deer home ranges in Big Cypress National Preserve (BCNP) and Everglades National Park (ENP) changed little between the wet and dry seasons. Female home ranges were slightly smaller during the wet season. Male home ranges were slightly larger (Labisky et al. 1995). The latter was correlated with the rut. Rainfall patterns in BCNP/ENP are pulsed in a manner very similar to Los Llanos, with comparable dynamics of shallow flooding and drought (Sargent 1992). However, the Everglades region is lower in elevation than the Llanos. Abutting the sea, its hydrology differs, and moisture effects are often felt more keenly than drought. Elevations in the ENP are between 0 and 2 m above sea level (Dalrymple & Bass 1996). Elevations in Piñero are between 65 and 396 m above sea level.

Primate densities in Piñero appear to be far lower than those in Hato Masaguaral, with nearly an order of magnitude difference (Table 52). There are several possible and potentially complementary explanations for this difference. One may be an artifact of scale. The study area at Hato Masaguaral was approximately 3,000 ha (Troth 1979). The study area at Hato Piñero was 63,227 ha, larger by a factor of 21. By good fortune, the boundaries of the Masaguaral study area appear to have contained some highly productive habitats. The area of one habitat type, BSD, alone at Piñero was 21,434 ha, seven times larger than the entire Masaguaral study area. This larger sampling frame may have allowed inclusion of more areas of marginal habitat. Beyond scale, there appear to be some real differences between the forests. Hato Masaguaral's semideciduous forests contain far higher proportions of *Ficus* sp. and *Copernicia tectorum* (Robinson 1986; and see Chapter 2). Both are used by *Cebus*, with inter-specific fruiting asynchrony among Masaguaral *Ficus* providing food much of the year (Robinson 1986). This abundance of *Ficus* would also benefit *Alouatta* in Masaguaral. Although expanding during our tenure, the Piñero population of *Alouatta* was recovering from a Yellow Fever epidemic (Theresa Pope pers.comm). Differences in *Cebus* densities between two adjacent states in Los Llanos and the probable lifestyle differences between collared peccary in lowlands and uplands within Piñero urges caution when making generalizations about a species from one study area (Kiltie & Terborgh 1983).

Dry deciduous forests (BS) in hills supported less faunal diversity than lower elevation forests (Figs. 12, 18) but were still quite productive for some prey (Figs. 12, 13, Table 52). The driest forest type, the drought resistant and fire-adapted Sabana Seca Con Chaparros (SS/CH) occurred in the highest elevations of Piñero, but also owing to aspect,

soils, and drainage, often occurred at intermediate locations. Food resources were scarce in this type (Figs. 9, 10), habitat complexity was low (Table 12) and the prey base negligible (Figs. 11, 13). Schaller (1983) considered a very similar habitat covering hills in his study area in the Pantanal to be "barren". He excluded it from density calculations. Independently arriving at the same conclusion, in this study the area covered by SS/CH was excluded from calculations of ecological density and biomass. Small mammal diversity and trapping success is low in such *Trachypogon* savannas (Utrera et al. 2000).

In Piñero, attacks by puma on livestock outnumbered those by jaguar. These attacks generally involved young calves and occurred in high dry pastures (PS) relatively poor in prey. There was coincidence in this. Adult cows can forage in water, but need a dry place to rest. Calves cannot forage in water, and for appreciable survivorship, should be moved out of flooded areas. Hato Piñero did not manage cattle as loosely as ranches described from the Pantanal (Crawshaw In Press; Quigley & Crawshaw 1992; Schaller & Crawshaw 1980). In some areas in the Pantanal cattle, were nearly feral. Concentrations of weakened livestock in forest patches in a matrix of flooded savanna almost invited jaguar attacks. The motivation for Piñero's maternity pastures being located in high dry pastures was to increase calf survivorship, not to avoid attacks by jaguars in the lowlands. Yet, by all appearances that responsible shifting of cows to upland pastures introduced the possibility of tender calves to pumas residing there.

Paradoxically, the areas richest in prey, due to flooding, could not harbor the pulse of calf production and rearing in the wet season, but drier, more prey-poor areas could. Why were pumas more implicated than jaguars in these calf losses? Were there jaguars in the same areas? If so, why weren't they more involved in attacks on calves?

The answer may lie in some subtleties of resource partitioning among the two cats.

Collared peccaries occurred in all the areas where white-lipped peccaries occurred, but not the reverse (Figure 12). Is it possible that a similar, yet far more subtle relationship exists between jaguar and puma? On foot transects puma sign occurred in wider variety of habitats than jaguar sign (Fig. 12) including drier sites (Figs. 12, 13). In the moistest area, where white-lipped peccaries and tapir frequented, jaguar sign was more common then puma (Figs. 12, 16, Table 59), although the number of puma in the entire study area was estimated as twice that of jaguars. Caution must be applied: puma occurred on transects running through partially flooded forests, and jaguars were seen in hills. Clearly pumas occurred everywhere jaguars did and vice versa. However, the data suggest that, in Piñero, puma may be more at home in a wider variety of habitats, including drier types, than the jaguar. Perhaps puma occur in the drier habitats with greater frequency and jaguars the opposite.

To debate whether *Puma concolor* can handle a wider variety of habitats than *Panthera onca* overlooks that the former occupies a range running from the Yukon and British Columbia to Tierra del Fuego, including relatively xeric areas in the United States (Logan et al. 1996; Weyhausen 1996) and semi-arid scrub in La Pampas de Argentina where "bare rock hills...provided good cover for pumas" (Branch et al. 1996). Despite the puma's greater tolerance, the patterns of overlap and separation between jaguars and pumas vary greatly among areas. In Jalisco, Mexico, the areas used by the two species completely overlapped (Nuñez et al. In Press-a). Jaguars and pumas in Jalisco did avoid direct contact (Nuñez et al. In Press-a). This "separation by physical distance" (Nuñez et al. In Press-a) would seem a prudent strategy in Piñero, where the weight ratio of jaguars

to pumas was 1.65 (n=2 & 4) for females, and 1.72 (n=2 & 2) for males (Sunquist et al. 1999b). In examining jaguar and puma food habits in the Brazilian Pantanal, Crawshaw and Quigley (In Press) admitted to a bias towards jaguar as their study focused on "the lower, more remote areas of the ranch where jaguars were more common". (Emmons 1987; 1991) observed that in the Peruvian Amazon jaguars used river and lake margins more than puma. In moister parts of Venezuela, specifically in the states of Amazonas and Bolivar (moist tropical evergreen forest), jaguars, not puma, were most frequently implicated as cattle killers (Juan La Vieri pers.comm.).

Interviews (focusing on cattle depredation) with 37 ranch owners in Los Llanos Altos resulted in the following trends. Mean size of ranches experiencing jaguar attacks was 12,230 ha. Mean size of ranches without jaguar attacks was 2,719 ha. Puma attacks on livestock were independent of ranch size. Jaguar attacks on livestock were positively correlated with the amount of forest on ranches. Puma attacks were not correlated with proportion of forest cover. The area of ranches subject to seasonal inundation was 29.6% of those ranches that experienced solely jaguar depredation and 8.4% of ranches that experienced solely puma depredation. Ranches with depredation by jaguar, but not puma had an average of 15 km of caño. Ranches without jaguar depredation has an average of 4.6 km of caño. Ranches with depredation solely by puma had an average of 0.3 km of caño. In ranches with depredation solely by jaguar, an average of 13% of the pastures had no forest. In ranches with depredation solely by puma, 52% of pastures were without forest (Gonzalez-Fernandez In Press).

In Piñero, jaguars may have established first rights to the most productive areas, even if pumas furtively coexist in, or adjacent to, the same areas. That is speculation,

nothing more. Like collared peccaries, some pumas occupied low lying areas, others occupied higher areas. What is clear is that the location of maternity pastures introduces calves to specific areas that are poor in terms of natural prey. The ranges of the puma in those areas are large enough to harbor pockets of natural productivity, which the maternity pastures are not. To a cat accustomed to risking attacks on 23 kg peccary, a 50 kg calf must seem as large as it is vulnerable, and hence, highly profitable. For some puma, the equation that they use fails to factor in an exasperated rancher's response. If losses accumulate, the cat ends up dead.



Fig. 11. Animal observations along three 16 km vehicle transects. Each transect presented represents one day of sampling at 0600, 1800, and 2200 hours. Routes described in methods. Habitat proportions of the low and high routes are presented in Table 44. Codes are as follows: LP (*Leopardus pardalis*); PR (*Procyon cancrivorous*); EB (*Eira barbara*); TT (*Tayassu tajacu*); AP (*Agouti paca*); DA (*Dasyprocta agouti*); SF (*Sylvilagus floridanus*); GC (*Geochelone carbonaria*); CT (*Cerdocyon thous*); OV (*Odocoileus virginianus*); HH (*Hydrochaeris hydrochaeris*).

Fig. 12. Nine separate foot transects in contrasting habitats. Encounter rates presented are animal sign (tracks, feces) recorded in standardized protocol pooled with animal encounters (both independent of group size) per km walked. Rear lines (La Candelaria and Caujaral Norte) are semi-deciduous forest. Progressing forward from rear, Los Cerritos and Cerro Guaical (lado and encima = side and top) are forests of hill flanks and ridges. Las Penitas is a mixture of dry pastures, dry hill forests and strips of semi-deciduous forest. Los Venados, Pastos de Los Cerritos, and Claro Cerrillos progress from moist savanna to dry pastures respectively. Codes are as follows: CC (*Caiman crocodilus*); HY (*Herpailurus yagouarundi*); TI (Tinamidae); AS (*Alouatta seniculus*); SG (*Sciurus granatensis*); CO (*Cebus olivaceous*); PR (*Procyon cancrivorus*); HH (*Hydrochaeris hydrochaeris*); SF (*Sylvilagus floridanus*); PO (*Panthera onca*); PC (*Puma concolor*); TA (*Tapirus terrestris*); DA (*Dasyprocta agouti*); OM (*Tamandua tetradactyla*); MT (*Myrmecophaga tridactyla*); CT (*Cerdocyon thous*); EB (*Eira barbara*); TP (*Tayassu pecari*); LP (*Leopardis pardalis*); GC (*Geochelone carbonaria*); DN (*Dasypus novemcinctus*); OR (*Ortalis ruficauda*); CD (*Crax daubentoni*); TT (*Tayassu tajacu*); OV (*Odocoileus virginianus*).



Fig. 13. Animal observations in 50 m intervals along a foot transect that began in valley then ascended and descended a hill. Animal codes as Fig. 11 & 12. Forest codes as follows: BSV = Bosque Siempre Verde (dominated by *Vochysia venezuelana*); BS = Bosque Seca (forests on dry gravel soils, sometimes fairly diverse though short stature, 3 sub-types here pooled for simplicity); SS/CH = Sabana Seca con Chaparros (a very thin and short stature forest, with no trees exceeding 4 m in height, on dry rocky substrates/thin soils). SS/CH Alta on high exposed ridges. SS/CH Bajo on lower elevations. Portions of BSV shallowly flooded from June through January.





Fig. 14. Six foot transects in savannas. Encounter rates presented consist of animal sign (tracks and feces) recorded in standardized protocol pooled with animal encounters (both independent of group size) per km walked. Lines in the rear (Los Juncales) are savannas embedded in habitat matrices and have abundant edge. Middle lines (Mata de Guafa 1 & 2) are in simpler areas, but also have abundant edge. Both front lines lay in a large open savanna. El Guanabano con molino y orilla de bosque is close to a windmill water pump and forest edge, while El Guanabano abierto crosses the nearly tree-less savanna. Codes as in Fig.11, and Fig 12.



Fig. 15. Animal observations in 50 m intervals along a foot transect crossing several different habitats on level terrain. Forests were slightly higher than savanna (difference less than 0.8 m). When savannas were completely flooded, patches of non-flooded (albeit damp) terrain remained in parts of forest. In the dry season large areas of savanna sometimes burned. Forest did not. NV refers to sign data (tracks and feces) recorded in a standardized fashion. V refers to encounters with animals, group size considered. Codes as in Fig.s 11 & 12.



FREQUENCY OF ANIMAL OBSERVATIONS ALONG A LINE OF INTERSPERSED SAVANNA AND SEMI-DECIDUOUS FOREST: NUNGERAL/RABO DE AGUA

Fig. 16. Species frequency distribution based on 292 camera-trapping images in a humid area. All images collected in dry season. Front row of bars represent images collected along the Caño Caujaral Norte foot transect and a trail leading to the pools and wallows upstream from the transect (La Roseta). Rear row of bars represent images collected in forest directly adjacent to the caño, and along the edge of its shrinking intermittent pools. Frequencies represent a species occurring in an image and do not consider group size. Every single jaguar or tapir record represents an individual, while single cracid records could be individuals or small groups. Single records of white-lipped peccaries usually represent the presence of a large group. Codes as in Fig. 11 & 12. Data collected by field observers walking the Caujaral Norte transect are presented in Figure 12. This heavily forested area is connected to forests outside Piñero via the caño, and differs from other parts of the study area in this degree of connectivity, and retention of moisture during the dry season.





Figure 17. Contrasts in seasonal home-ranges: examples from three female radiocollared peccary *Tayassu tajacu* in Hato Flores Moradas, Estado Guarico (elevation 60-75 masl, roughly equivalent to Monte de Los Caballos in Hato Piñero). Top figure based on 280 locations. Bottom two figures based on 390 locations. Castellanos (1982) recorded average dry season home ranges of 35.33 ha and wet season home ranges of 99.82 ha. Despite that average, his figures indicate considerable variation, presumably due to the individual patterns of drought, inundation, and localized food production in each collared peccary group's area. Due to Piñero's greater topographic relief and heterogeneity, there is probably similar variation among groups.

Figure 18. Comparative encounter rates (observations/km) among 26 linear transects. Sign (which does not directly measure group size) and visual observations independent of group size are pooled. All taxa recorded are included in the figure. This includes preferred prey, less important prey, and some taxa that could not be considered prey.



Table 44. Percentage proportions of habitat types along two 16 kmvehicle transects.

Rough Habitat Classification	Low Route	High Route
Arbustos (regeneration)	1.6	0
Bosque Semi-Deciduo	59.1	18
Sabana Inundable	33.2	3
Sabana Arbolada Inundable	.9	1.6
Pastos Inundables	2.4	0
Bosque Seca	2.8	14.9
Pastos Altos	0	12
Sabana Seca con Chaparros	0	50.5

Table 45. Group sizes and crude population structure of *Odocoileus virginianus*. All entries are from Hato Piñero study area except the Brokx (1972) observations from Estado Apure. The juvenile class is rough for all entries, translating to animals less than 12 months old, usually less than 10 months, hence including young fawns as well as considerably more mature animals. The Brokx (1972) figures for juveniles listed do not include an arbitrary adjustment factor of 1.5 (for young fawns assumed not seen) that he later applied to his data. The differences between opportunistic observations, open transects, and forested transects suggest decreased detection along forested transects.

	Mean	Range	Sample	Percent	Adult	Adult	Percent
	Group	Group		Adults	Percent	Percent	Juveniles
	Size	Size			Males	Females	
Opp. Obs. Wet	2.089	1-5	94	74	28	72	26
Opp. Obs. Dry	2.096	1-7	415	79	30	70	21
All Transects	1.408	1-5	138	82.6	32.3	67.7	17.39
Wet							
All Transects	1.408	1-4	131	91.23	37.6	62.4	8.77
Dry							
Total Transects	1.408	1-5	269	86.5	34.9	65.1	13.5
Forest	1.079	1-2	41	na	na	na	na
Open	1.487	1-5	229	na	na	na	na
Brokx 1972	na	na	165	79	31	69	17-21

Table 46. Group sizes and crude population structure of *Tayassu tajacu* in Hato Piñero and Hato Masagural (Robinson and Eisenberg 1985). Barreto and Hernández (1988) worked in a large block of semi-decidous forest in northeast of Hato Piñero (Caño Matajei).

Source	Mean Group Size	Range Group Size	SD	Sample (# obs.)	Percent Adults	Adult Percent Male	Adult Percent Female	Percent Subadult	Percent Juvenile	Percent SA & J
All Transects All Seasons	5.73	1-16	3.75	51	92.07	47.06	52.94	1.83	6.10	7.93
All Transects Wet Season	4.93 *	1-16	3.46	29	93.40	33.33	66.67	1.89	4.72	6.60
All Transects Dry Season	6.77 *	1-15	3.93	22	89.66	54.54	45.45	1.72	8.62	10.34
Forest Transects All Seasons	5.42	1-16	3.56	48						
Open Transects All Seasons	10.67	8-15	3.79	3						
Opportunistic Observations Wet Season	8.64	1-42	9.26	22	78.57			3.57	17.86	21.43
Opportunistic Observations Dry Season	8.67	1-40	7.66	55	77			8.85	14.15	23.00
Robinson & Eisenberg 1985 Total	6.5	1-48		66						
Robinson & Eisenberg 1985 Wet Season	5.3 *			15						
Robinson & Eisenberg 1985 Dry	10.2 *			33						
Barreto & Hernández 1988 Wet Season	10.6									
Barreto & Hernández 1988 Dry Season	4.4									
Barreto & Hernández 1988 Total		1-35		6						

Table 47. Sites along an elevational cross-section of Hato Piñero in which groups of *Tayassu tajacu* were observed during both dry and wet seasons. Observations were recorded on foot transects, on phenology trails, and in conjunction with other tasks and travel. In Nüngeral/Monte de los Caballos and La Candelaria/Monos Norte, presence was recorded even when 70-90% of the forest floor was flooded at an average depth of 10 cm. Most of the observations along the Claro Cerrillos Potrero/Quebrada were during the rainy season, suggesting that the group was more confined during the dry season, expanding their range during the rainy season, in part due to moisture, in part due to patterns of fruit production in the forest.

Site	Elevation & Vegetation	Dry	Wet
Nüngeral/Monte de los Caballos	Low, BSDT1, SI	X	Х
La Candelaria/Monos Norte	Low, BSDT1, SI	Х	Х
Caño Caujaral Sur	Low, BSDT1, BSDT2, BSDG	X	X
Escorzonera, Cerro Guaical	Low. Medium, High, all types BSD, all types BS, SS/CH	Х	Х
Orilla de Laguna Grande Sur y Este	Low, Medium, High, BSDS, all types BS, SS/CH	Х	Х
Cerritos Bosque	Low, Medium, High, BSV, all types BS, SS/CH	Х	Х
Claro Cerrillos Potrero/Quebrada	Medium, High, BSDQ, BS, SS/CH, PS	Х	X

Table 48. *Hydrochaeris hydrochaeris* biomass for study area. Estimates based on counts made April 1998, supported by counts made April 1997. Biomass is minimum at that time. Maximum of 22,654 kg was calculated to occur in November, taking into account: 1) adult weight losses during the dry season (December-April); 2) adult weight gains during the rainy season (May through November); 3) the birth pulse between September and December and its peak in November; and 4) subsequent growth and mortality of juvenile animals (partly ameliorates adult weight loss during the dry season).

Place Name	Class Unk	Adult	Adult Male	Adult Female	Sub adult	Crias (Sep- Dec)	Crias Recien Nacidos	Totals
Caño Manglarito	20	7	8		14	8	8	65
Via al Manglarito		13			12			25
Caño Caujaral		19	2					21
Potreros Los Venados/Juncal Saman Gacho		34	8	10	14	16	1	83
Escorzonera		3	3	1	6	6		19
Tapa Guaical			4	7	8			19
Puente Benjamin/ Los Patos/Los Caribes	50	75	3	6	6	25		165
Laguna Los Cerritos		24	6	1	4	5		40
Laguna Alta			1					1
Caño la Iguana	15	2	1			2		20
Caño Mata de Guafa/ Caño Canoa			2	3	4	6		15
Laguna Grande		21	7	6	11		7	52
97 Estimate Rio Pao	22							22
Sums	107	198	45	34	79	68	16	547
Average weight per age/sex class at time of count (kg)	38.2	46.75	46.75	46.75	30	13	1.5	
Mass per class (kg)	4087	9256	2104	1589	2370	884	24	20315

Table 49. *Caiman crocodilus* biomass estimate for study area in Hato Piñero (llanos altos boscosos Estado Cojedes, Venezuela). Based on counts by three teams over four years (unpublished data from Woodward and David in 1985, Fitzgerald in 1986, and Polisar in 1996 and 1997). All years with no recent harvest history. Sighting fraction most commonly 0.9, but also ranging from 0.678 - 0.927 based on direct personal experience (unpublished data from Polisar 1996 and 1997) and water depth.

Size Class Categories	Percent in each size class (n=5998)	Snout-vent length (cm) dimensions/ size class	Mean weight (gm) in each size class (n=364 +)	Ranch biomass (gm) based on total of 15,408 caiman
Class I	16.8889	<20	100	260,225
Class II	31.5605	20-59.9	1482	7,206,736
Class III	27.8426	60-89.9	10024	43,002,837
Class IV	23.7079	90	32127	117,357,143
	Sum 100%			167,826,942 Sum
		Total Dry Season	Biomass Estimate	167,826.9 kg

Table 50. *Tayassu pecari* biomass estimates for primary study area in Hato Piñero (llanos altos boscosos, Estado Cojedes, Venezuela). There are two groups that use the study area. The larger one (approximately 107 animals) frequents the forest surrounding the northern section of Caño Caujaral, using a wider area during the rainy season. The smaller group (approximately 60 animals) frequents the forested area between the northeastern shore of Laguna Grande, the old bed of Caño Rosario, and Caño Matajei, where it was studied by Hernández and Barreto (1988). The below derives a very rough estimate of population structure to estimate biomass of these 167 animals. "Young" column pools juveniles and newborns.

	1	1	
Observation Sites	Methods	% adults	% young
Forest near Caño Matajei (H & B 1988)	Short foot transects	56.7	43.3
Roseta (extreme N. Cãno Caujaral)	Opportunistic observations	73	27
	41 camera trapping photos		
Roseta, much of N. Cãno Caujaral	from seven sites	86	14
Caujaral Norte foot transect	Long foot transect	67	33
Average of above four*		71	29
Rough weight estimates		35	17.5
Rough biomass estimate for study area (kg)	5,005 kg	4,165	840

Table 51. Freshwater turtle population estimates from three <u>representative</u> habitat types in Hato Piñero and one in Caño Mucuritas, Hato El Frío, Estado Apure. Piñero estimates used a modified Lincoln-Peterson index (Chapman 1952, Seber 1982). Apure estimates used a Schnabel's estimator because sampling occurred over three years (Ramo 1982). Assumptions of population closure were presumably violated. Piñero sampling took place during very short-intervals in late dry season. Average of low end of three Piñero confidence intervals (111.67) used for study area biomass estimates: 1) because there are habitats poorer than the ones sampled; 2) to err on the conservative side.

Place name	Sample	Population estimate	95% confidence interval
Saman Gacho	21	319/ha	100-537
Los Venados	18	213/ha	63-363
Pozo de Caujaral	87	254/ha	172-336
Caño Mucuritas	526	378/ha	296-483

Table 52. DISTANCE density estimates across strata. Figure in each box is individuals/km² estimate based on observations made from foot transects. Strata are as follows:

- A = bosque semi-deciduo near caño, 3 lines;
- B = bosque semi-deciduo not near caño, 7 lines;
- C = hill forests, 4 lines; edited C = only hill base, 1 line;
- **D** = high dry pastures, 5 lines;
- **E** = small pastures, low elevation, near forest and water, 6 lines;

F = wide open savanna, 2 away from edge and permanent water, 2 closer to edge and water.

Species codes as previously listed. Last two columns to right are estimates from Hato Masaguaral, Estado Guarico, made by Eisenberg et al. (1979). E = ecological density; C = crude density.

- * = calculated, but author views as underestimate.
- Second figure in some boxes is 95 % confidence interval.
- In bold font are numbers likely to be used for Piñero estimates.

	A, B, & C	A, B Edited C	A, B	C	D,E,F	D	E, D	Е	F	H.M. West E/C	H.M. East E/C
OV	1.0 .5-2.3	.9 .3-2.8			7.8	1.5 .4-6.5		14.7 8.3 -26	10.8 2.5-46	3/2.5	4/2
TT	11.3 7.5 -17										12/8.5
DA	.6 .3-1.2	.7 .4-1.5								>3/ >1.5	80/ 40
GC	95	99	108								
СО	5.3	5.3	6.1							0/0	44/19
AS	2.3		2.4							151/ 41	50/ <20
CD	7.1	39.1	38.5	7		.5	.6	.7			
OR	18		10	38.5		.6	8.8	18.6			
MT	.39	.5			.009 *					.18/ .12	.18/ .12
ОМ	.3		.5							3/2	3/2
EB			.3							??	2/1
СТ	.1 *	.1*			.9* .1- 6.7		1.2 * .2- 8.7	.3 * .19		4/2.5	4/2.5
SF	.8 .4-1.7									10/5	35/11
SG			.9* .4- 2.0							50/ 26.5	40/17. 2

Geochelone carbonaria	Low End 95% CI	High End 95% CI	Density estimate
Capture- mark- recaptures in 42.5 ha grid Schnabel's estimator	1.093	2.166	See confidence interval at left
DISTANCE All forest 14 transects truncation 6 m	.474	1.903	.95
DISTANCE Excluding higher hill transects 11 transects	.456	2.158	.992
DISTANCE Only low elevation BSD 10 transects truncation 6 m	.471	2.456	1.076

Table 53. Comparisons among approaches: tortoise density estimates (#/hectare).

Cebus olivaceous	Low End 95% CI	High End 95% CI	DISTANCE Density Estimate	Density Estimate Miller Methods
DISTANCE	2.8	9.7	5.3	
All forest				
14 transects				
DISTANCE	2.5	11.2	5.3	
Excluding				
high hills				
11 transects				
DISTANCE	3.0	12.3	6.1	
Only low				
elevation BSD				
10 transects				
Dr. Steve Miller				5
Grid in BSD				
Dr. Lynne Miller				9
Grid in BSD				

Table 54. Comparisons among approaches: capuchin densities (#/km²).

Table 55. Ranked vehicle transect encounter rates. Some species, most notably *Cerdocyon thous* make heavy use of ecotones, and correspondingly, frequent the dirt roads of Piñero, to the point that off-road counts actually underestimate the abundance. This is in contrast to the norm: many animals are missed in counts made from vehicles, particularly in irregular topography and dense cover. While collared peccary are very under-represented in these counts, and white-lipped peccaries totally missed, crab-eating foxes and cottontails are potentially under-represented on foot transects. All routes 16 km. Rates were means of dawn, dusk, and night runs. Low and High route data from both wet and dry season. Wide Savanna data collected only during dry season (no vehicular access during wet season).

Wide	Wide	Heterogenous	Heterogenous	High Hilly	High Hilly	Three Route	Three Route
Savanna	Savanna	Low	Low	Route	Route	Mean	Mean
Rank	Rate	Rank	Rate	Rank	Rate	Rank	Rate
OV	89	HH	78	OV	6	OV	38.5
CT	8	OV	20.5	HH	6	HH	29.3
HH	4	CT	13	SF	5	CT	8
LP	1	TT	6	CT	3	SF	2.17
		LP	2	EB	1.5	TT	2
		SF	1.5	LP	.5	LP	1.17
		EB	1	GC	.5	EB	.83
		PR	1			PR	.33
		DA	0.5			DA	.17
						GC	.17
Table 56. Ranked products of vehicle transect encounter rates and mean weight of species. Some species, most notably *Cerdocyon thous* make heavy use of ecotones, and correspondingly, frequent the dirt roads of Piñero, to the point that off-road counts actually underestimate the abundance. This is in contrast to the norm: many animals are missed in counts made from vehicles, particularly in irregular topography and dense cover. While collared peccary are very under-represented in these counts, and white-lipped peccaries totally missed, crab-eating foxes and cottontails are potentially under-represented on foot transects. All routes 16 km. Rates were means of dawn, dusk, and night runs. Low and High route data from both wet and dry season. Wide Savanna data collected only during dry season (no vehicular access during wet season).

Wide	Wide	Heterogenous	Heterogenous	High Hilly	High Hilly	Three Route	Three Route
Savanna	Savanna	Low	Low	Route	Route	Mean	Mean
Rank	Rate x KG	Rank	Rate x KG	Rank	Rate x KG	Rank	Rate x KG
OV	3560	HH	2964	OV	240	OV	1540
HH	152	OV	820	HH	228	HH	1113.4
CT	40	TT	138	CT	15	TT	46
LP	12	CT	65	LP	6	CT	40
		LP	24	EB	6	LP	14
		PR	4.7	SF	4	EB	3.32
		EB	4	GC	2.2	SF	1.74
		DA	1.9			PR	1.55
		SF	1.2			GC	.73
						DA	.65
SUM	3764	SUM	4022.8	SUM	501.2		

Table 57. Ranked foot transect encounter rates. Codes as previously, with addition of CF = Chelus fimbriatus and BC = Big Cat. Forest pool = 763650m. Open pool = 305500m. Because meters walked within each pool is constant, the rates are expressed as actual number of encounters. Some species are more prone to detection by sign than by visuals and vice versa. Also, large heavy-bodied animals, particularly those with hooves, typically leave more sign.

Forest Sign	Forest Sign	Forest Visual	Forest Visual	Open Sign	Open Sign	Open Visual	Open Visual
Rank	Rate	Rank	Rate	Rank	Rate	Rank	Rate
TT	686	OR	341	OV	177	OV	228
OV	668	TT	260	CT	33	OR	90
DN	244	CD	165	HH	20	HH	85
TP	188	CO	106	OR	16	TT	32
OR	86	TP	106	PR	11	CD	15
TA	69	OV	61	CD	6	CT	8
DA	57	AS	49	EB	6	MT	3
CD	54	HH	49	TT	5	GC	2
LP	40	GC	30	LP	5	CC	1
CT	38	DA	16	CC	2	OM	1
GC	36	SG	10	DN	2		
EB	29	EB	10	AS	1		
PO	29	OM	8	BC	1		
MT	27	MT	6	MT	1		
PC	22	DN	5	PO	1		
AS	21	SF	5				
HH	17	CT	4				
PR	10	LP	1				
SF	5	PO	1				
СО	4	PC	1				
HY	3	CC	1				
BC	2						
DM	2						
CS	2						
OM	2						
SG	1						
CF	1						

Table 58. Ranked products of foot transect encounter rates and mean body weight. Codes as previously, with addition of CF = Chelus fimbriatus and BC = Big Cat. Values are not in same scale across columns (sign frequency>visual frequency for some species and opposite in others), but provide a vertical scale within columns.

Forest Sign	Forest Sign	Forest Visual	Forest Visual	Open Sign	Open Sign	Open Visual	Open Visual
Rank	Value	Rank	Value	Rank	Value	Rank	Value
OV	26720	TT	5980	OV	7080	OV	9120
TT	15778	TP	3710	HH	760	HH	3230
TA	13800	OV	2440	CT	165	TT	736
TP	6580	HH	1862	TT	115	MT	81
PO	2030	CD	412.5	PO	70	OR	67.5
DN	927.2	CO	275.6	LP	60	CT	40
PC	902	OR	255.75	BC	55.5	CD	37.5
MT	729	AS	210.7	PR	51.7	CC	10
HH	646	MT	162	MT	27	GC	8.6
LP	480	GC	129	EB	24	OM	4
DA	216.6	PO	70	CC	20		
CT	190	DA	60.8	CD	15		
GC	154.8	PC	41	OR	12		
CD	135	EB	40	DN	7.6		
EB	116	OM	32	AS	4.3		
BC	111	CT	20				
AS	90.3	DN	19				
OR	64.5	LP	12				
PR	47	CC	10				
HY	12	SF	4				
CO	10.4	SG	2.5				
OM	8						
CF	6.9						
SF	4						
DM	3						
CS	2.4						
SG	.25						

Table 59. Species ranked on basis of relative frequencies in camera trapping images. Numbers are presence independent of group size. Smaller bodied animals are presumed proportionally less vulnerable to camera trapping. Individual camera trapping sites have been pooled into crude habitat types. Sampling was not even among these types. The richest types also tended to be the most heavily sampled. Though that is indicative, the smaller overall numbers in the poorer types need the explicit qualification that sampling in them was less intense. Contrasts in the rank order of species among the sites are then more important than absolute numbers. Codes as previously, with addition of WB (wading bird) and OB (other bird). Top five species in bold, other revealing ranks also in bold.

Codes	Orilla de Caujaral Y Roseta	Codes	Sendero Caujaral Norte y Camino Roseta	Codes	Otras Cuerpos de agua a lado de BSD	Codes	Una lengua de BSD en la Candelaria	Codes	Cerros Y Valles Altos
CD	69	ТР	26	WB	36	OV	18	СТ	12
ТР	39	CD	24	OV	13	LP	4	MT	6
LP	28	LP	13	CD	8	ТА	3	SF	4
СТ	25	OV	11	TT	7	CD	2	LP	4
WB	12	PO	8	PR	6	SF	2	CD	3
OV	5	WB	5	РО	5	СТ	1		
PR	3	PC	4	LP	4	PC	1		
OB	2	СТ	3	СТ	3				
CO	2	OB	2	MT	2				
TT	1	TT	2	PC	2				
TA	1	TA	2	CO	2				
PO	1	MT	2						
PC	1	DM	1						

Table 60. Standing crop biomass estimates from DISTANCE density estimates. Species total in right colomn. DN estimate based on ranked encounter rates and comparison to Hato Masaguaral (Eisenberg 1979). MT estimate neglects individuals in savanna and thus is conservative.

Species	Crude strata	Density (km2)	Unpoached (km2)	Poached (km2)	Total #	Biomass
ov	all forest	1.0	221.87	42.88	234.73	
OV	pasto seco	1.5	17.59	1.00	26.84	
VO	sabana inundable	8.3	238.80	13.15	1,973.28	
OV totals					2,234.85	78,890.15
TT	all forest	7.5	221.87	42.88	1,760.50	35,835.08
DA	all forest	1.2	221.87	42.88	282.00	1,072.00
SF	bsd	0.8	178.16	36.17	151.21	
SF	bs	1.7	43.33	6.52	77.32	
SF totals					228.53	182.82
DN	bs	4.0	43.33	6.52	181.14	
DN	bsd	4.0	178.16	36.17	756.04	
DN totais					937.19	3,561.30
MT	all forest	0.4	221.87	42.88	103.25	2,787.25
GC	all forest	95.0	221.87	42.88	22,300.00	96,336.00

CHAPTER 4 JAGUAR, PUMA, THEIR PREY BASE AND CATTLE RANCHING:ECOLOGICAL PERSPECTIVES OF A MANAGEMENT ISSUE

Introduction

Jaguar and puma depredation on livestock may be influenced by: 1) innate and learned behavior; 2) health and status of individual cats; 3) division of space and resources among jaguar and puma; 4) cattle husbandry practices; and 5) abundance and distribution of natural prey.

Predators select prey based on a cost-benefit analysis of search time, handling costs, and energy gained in the context of prey abundance (Emlen 1966; MacArthur & Pianka 1966). In productive environments, whether homogenous or heterogenous, predators can be expected to be more selective than in unpredictable environments (Emlen 1966; MacArthur & Pianka 1966). The value of a patch, in terms of available prey, is usually reduced by predators, stimulating them to search for subsequent patches (Charnov 1976). This predicts roaming among patches in all instances except those where patch values are resilient. These general postulates have to be able to absorb the variation introduced by learned behaviors and individual preferences. Among five intensively monitored female mountain lions (*Puma concolor*) in Alberta, two never killed bighorn sheep (*Ovis canadensis*), one killed one sheep, one killed five, and one killed seventeen, in one year killing 8.7% of an early–winter herd, including 26.1% of its lambs (Ross et al. 1997). All five cats were healthy, had alternative prey available, and made varying use of those alternatives. The learned ability to handle bighorn sheep,

normally more difficult to take than mule deer (*Odocoileus hemionus*) reduced handling costs for one puma. Risk of injury is a component of potential handling costs (Sunquist & Sunquist 1989). It can be altered by individual hunting skills developed over time, and also passed down lineages. Preference for certain natural or domestic prey may be transmitted from mother to young (Hoogesteijn & Mondolfi 1993; Mondolfi & Hoogesteijn 1986; Quigley & Crawshaw 1992).

Interactions among predators may influence choice of prey. Seidensticker (1976) commented on the potential effects of social dominance. In areas shared with tigers the behaviorally flexible social subordinate leopard appeared to allow the dominant tiger first choice of both habitats and prey (Eisenberg & Lockhart 1972; Seidensticker 1976). Spatial avoidance of a larger predator is likely to influence diet. Leopards (*Panthera pardus*) emphasize smaller prey than tigers (*Panthera tigris*) (Karanth & Sunquist 1995), but Karanth and Sunquist (2000) found no evidence of spatial exclusion of leopards by tigers. The specific nature of inter-predator interactions presumably varies not only among carnivore guilds but also among similar guilds in different study areas. Inter-regional replication of the multiple variables that influence behavior is unlikely.

Analyses of resource partitioning and competitive exclusion require caution. Niche overlap and segregation involves multiple facets of a species' activities, all of which must be measured at an appropriate scale (Goodyear 1992). Overlap in diet may 3333. Environments fluctuate; seasonally, annually, with patterns, even erratically. It follows that levels of interspecific competition fluctuate. Degrees of niche overlap vary over time and space. Recently sympatric species may show more overlap than those with

a long-term history of coevolution (Goodyear 1992). In the context of Pleistocene megafauna extinctions

(12,000 ybp) including carnivores such as the American lion, *Panthera atrox*, and the saber toothed tiger, Smilodon fatalis, (Morgan & Seymour 1997), the post-Pleistocene (8-10,000 ybp) recovery of the puma in North America (Culver et al. 2000), and the even more recent (beginning about 500 years ago) community modifications set in motion by the arrival of europeans, the present version of jaguar and puma coexistence is recent and perhaps still in flux. The community history of predator, prey, and plant interactions likely varies a great deal within the area in which the two cats' distributions overlap. Despite discernible patterns in diet and habitat selection between the two large cats there is striking variance in body size and diet selection among different areas (Aranda 1994; Aranda & Sánchez-Cordero 1996; Branch et al. 1996; Carrillo & Saenz In Press; Carrillo et al. 1994; Crawshaw In Press; Crawshaw & Quigley 1991; Crawshaw and Quigley In Press; Dalrymple & Bass 1996; Emmons 1987; 1989; 1991; Farrell 1999; Gonzalez-Fernandez In Press; Hoogesteijn & Mondolfi 1993; Hoogesteijn & Mondolfi 1996; Hornocker 1970; Iriarte et al. 1990; Logan et al. 1996; Maehr 1997a; Maehr 1997b; Murphy 1998; Nuñez et al. In Press-a; Nuñez et al. In Press-b; Quigley & Crawshaw 1992; Rabinowitz 1986; Rabinowitz & Nottingham 1986; Ross et al. 1997; Scognamillo et al. In Press; Shaw 1977; Sunquist et al. 1999b; Taber et al. 1997; Weyhausen 1996). Cattle ranchers are scarcely concerned with the relationships between fossil or archaeological records and present jaguar-puma-cattle interactions. The concerns are immediate. What is the dynamic between these cats and cattle today? How can the cattle losses that lead to cat control be reduced?

Cattle management offers some possibilities. In some areas cattle have been so lightly managed that they resemble wild prey (Hoogesteijn et al. 1993; Hoogesteijn & Mondolfi 1993; Mondolfi & Hoogesteijn 1986; Quigley & Crawshaw 1992; Schaller & Crawshaw 1980). Indiscriminant shooting can result in disabled incipient "problem cats" (Rabinowitz 1986). Hoogesteijn et al. (1993) suggested that losses could be reduced by: 1) excluding cattle from forest; 2) maintaining adequate distance between calving areas and forests; 3) moving calves out of problem areas and replacing them with bulls; and 4) maintaining adequate populations of wild prey.

Shaw (1977) hypothesized that the number of cattle taken by puma in Arizona was inversely proportional to the size of the deer herd. Hoogesteijn et al. (1993) and Mondolfi & Hoogesteijn (1986) hypothesized a similar relationship for jaguar and puma in Venezuela, where the cats exploit a more diverse prey base. These recent speculations were pre-dated by the observation by Roosevelt (1914) that ranches in Brazil that possessed abundant native prey experienced fewer jaguar problems. Eighty years later these ideas still needed more testing with data.

In 1996, we initiated field work on a team project designed to examine all the factors that could contribute to cat-cattle conflicts: 1) ecology and behavior of jaguar and puma; 2) abundance and distribution of natural prey; and 3) cattle management practices. This paper addresses these issues, with the emphasis on prey base. Subsequent papers will describe the role of felid behavior in more detail. The following questions are addressed in this paper. Can the natural prey base in the study area support the cats or do they need a subsidy from domestic livestock? What are the dominant components of

jaguar and puma diet? How does prey selected relate to prey available? What scenarios are leading to cat/cattle conflicts? How can those conflicts be reduced?

Study Area

Hato Piñero is a working 80,000 ha cattle ranch/wildlife preserve located between 8 40' and 9 00 N and 68 00 and 68 18 W in the southeast corner of estado Cojedes in north-central Venezuela (Eisenberg & Polisar 1999; Miller 1992). The northern boundary of Piñero lies among hills that rise to 396 m above sea level (Farrell 1999). The western boundary is formed by the Cojedes and Portuguesa rivers, the southern and eastern boundaries by the Chirgua and Pao rivers (Fig.1). Smaller streams (caños) run through this basin. The lowest elevations are approximately 65 m above sea level in the open savannas in the southern part of the ranch. The landscape can be characterized as a complex mosaic of interdigitated forests and open areas with vegetation types based on interactions of elevation, substrates, and hydrology. The ratio of open to forested areas is roughly 50:50 depending upon interpretation (Fig.2). Our 63,227 ha study area contained seasonally flooded lowland savanna (39.1%), seasonally flooded semi-deciduous forest (33.9%), dry hillside savannas with chaparral (15.3%), dry hillside semi-deciduous forest (7.9%), pastures in highlands that never flooded (2.9%), every every every forest (.07%) and mango groves (.01%), with remainder developed (Table 43, Fig.2).

The climate is strongly seasonal, with the majority of the 1468.8 mm of precipitation falling during the wet season between the beginning of May and the end of November. The dry season, from December 1 though April is hotter. Relatively impermeable soils causes surface water to accumulate starting in June and peaking in July and August (Fig. 4). The flooding is relatively shallow (Fig.5), with greatest depths occurring in low savannas in the south. Forests typically retain pockets of dry land (Fig.4). The savannas in the south flood completely.

The majority of Piñero's 14,000 head of cattle are *Bos indicus* cebú races (nelore, brahma, guzerat, gir). Approximately 420 horses, mules, and burros fulfill working and breeding needs. A herd of approximately 150 water buffalo are maintained in the southern savannas. Many cattle are moved from lowland pastures to higher areas during the wet season. Cows can forage in water. Calves cannot. Artificial insemination results in a pulse of calving from between July and September. The maternity pastures where this takes place are high, well-drained areas.

Methods

Animal abundance, distributions and population structure were assessed using vehicle transects, linear foot transects, point counts, night counts, camera trapping, capture-mark-recapture methods, and opportunistic observations [(Buckland et al. 1993; Lancia et al. 1994; Seber 1982) see Chapter 3]. Patterns of forest vegetation were assessed using phenology trails and 35,000 m² of quantitative sampling in a vertical profile of Piñero (see Chapter 2). Parameters describing physiognomy were recorded at 100 m intervals along the 26 foot transects used for animal observations (Table 12, see Chapter 2). Forest types were classified using cluster analyses (Figs. 6 and 8, see Chapter 2). Forest composition was tabulated for different types, and number of species and percent of individuals in trees, vines, and under story plants that were used by primary prey presented in Figures 9 and 10 (Chapter 2).

Resident jaguar and puma minimum annual killing requirements were estimated by calibrating body weights to tiger weights (Scognamillo et al. In Press; Sunquist 1981;

Sunquist et al. 1999b). Standing crop biomass was estimated using group counts, night counts, transect-based density estimates, capture-mark-recaptures, population structures recorded during the preceding, and body weights obtained in single or repeated captures or in appropriate literature from studies completed nearby (Ayarzagüena 1983; Brokx 1972; Eisenberg et al. 1979; Linares 1998; Ojasti 1973). Livestock biomass was estimated using figures provided by Ferdinando Corrales (Manager of Hatos Piñero, Paraima, Sembra, and an associated slaughterhouse). Gross productivity was figured using our standing crop biomass and population structure estimates, combined with values for demographic parameters (average number of litters per year/average number of young per litter/stage specific survival rates) and growth rates that were either local or realistic as possible (Bodmer et al. 1997a; Brokx 1972; Eisenberg et al. 1979; Hayne 1984; Hellgren et al. 1995; Kleiman et al. 1979; Ojasti 1973; Ojeda & Keith 1982; Smythe 1978; Sowls 1997; Teer 1984). Jaguar and puma food habits were estimated from scats with known source and from kills encountered opportunistically and/or associated with intensive radio-tracking (Farrell 1999; Scognamillo et al. In Press; Sunquist et al. 1999b). Age/stage of observed kills was determined using indices provided in (Dimmick & Pelton 1994; Ojasti 1973) for white-tailed deer, collared peccary, and capybara, and through calibrations of head-length (all that is left afterward) to snout-vent-length and weight calibrations obtained from spectacled caiman in Piñero.

Results

Annual minimum killing requirements for resident jaguars and pumas were estimated at 11,366 kg and 12,849 kg respectively, 24,215 kg combined (Figure 19). Standing crop biomass of all major food species (excluding livestock) was 374,489 kg, of

which 149,988 (40%) was mammalian and 224,501 (60%) was reptilian. Minimum killing requirements for both cats combined represented 6.465% of the standing crop: 3.035% for jaguar, 3.43% for puma (Table 61). Including tapir, terrestrial tortoises, and iguanas, items not represented in the diet, standing crop was 474,494 kg (Table 61).

The standing crop of cattle was around 4,656,000 kg of which 160,000 to 384,000 kg were in the size class most vulnerable to large cats (Table 62). Buffalo constituted around 123,750 kg, and horse, mules, and burros pooled 118,300 kg (Tables 62, 63). Biomass estimates, for the entire 63,227 ha study area, are presented as kg/km² in Table 64. Percentages of the kg/km² pooled along taxonomic groups and the domestic (introduced)-wild (recent native) dichotomy are presented in Table 65. Piñero biomass estimates including and excluding domestic livestock are compared to other sites in the New and Old World in Table 66. Annual gross productivity of major and mammalian prey is presented in Table 67. Cat killing needs represented 33% of gross annual productivity (Figure 19, Table 67).

Scat contents (Figure 20) are a more bias free indication of diet than kills (Figure 22). Numerical occurrence of items appearing in scats (Figure 20) can cause smaller prey items to appear to be more important to a predator's survival than their actual caloric contribution justifies. Small rodents and marsupials will sustain a cat for a far shorter time than will large ungulates or rodents (Figure 20). With the exception of turtles, smaller prey did not appear in the kill sample (Figure 21). Both cats focused on large-bodied prey, with puma taking more medium-sized and smaller prey than jaguar (Figure 20). Jaguar took more peccary than did puma (Figs. 20 and 21). Both cats took white-tailed deer in a proportion less than relative abundance, although puma used deer slightly

more than did jaguar (Figs. 20, 21, Tables 61, 67). Both cats used capybara in far greater proportions than relative abundance (Figs. 20, 21, Tables 61, 67). Given the very low relative abundance of white-lipped peccaries (Tables 61, 67), the jaguar's use of them (Figs. 20, 21) suggests preference. Puma took many more calves than did jaguars (Figs. 20, 21).

The small sample of caiman killed by jaguar included large and small animals (Fig. 22). Puma kill adult/subadult/juvenile ratios were A 2/SA 1; A 8/SA 2/J 1; A 1 for deer, capybara, and collared peccary respectively. Jaguar kill adult/subadult/juvenile ratios were OLDER THAN J 2/J 1; A 4/SA 1; A 1 for capybara, collared peccary and white-lipped peccary respectively. These data are inadequate to demonstrate any preference for specific age classes, but suffice to demonstrate that adults are being taken. Very young animals are probably underrepresented as those kills are less conspicuous and consumption may be more complete. Average adult weights for deer, capybara, collared peccary, and white-lipped peccary are 40, 46, 75, 23, and 35 kg, respectively. Large male deer may weigh slightly over 50 kg, as may large capybara (Brokx 1972; Ojasti 1973). The largest caiman kill recorded was around 50 kg. The largest caiman weighed was 75 kg. The largest anaconda weighed was 50 kg. In general, 50 kg is large prey in this region.

Discussion

In Nepal, the Serengeti, and the Amazon, large predators need to kill approximately 8-10% of the standing crop biomass of prey (Emmons 1987; Schaller 1972; Sunquist 1981). In Hato Piñero that proportion would require a minimum of 242,150 kg to 302,687 kg. With wild mammals and reptiles combined there was a minimum of 374,489 kg (Table 61), enough to support 1.24-1.55 as many cats as were present. If potential dietary components apparently being bypassed were factored in, such as red-footed tortoises (Table 61) the margin by which the estimated minimum is exceeded becomes wider. This suggests that, in context of the entire study area, a subsidy from domestic livestock was not necessary to sustain the resident cats. The biomass ratios indicate that wild mammals could provide approximately 49.5-62% of the annual requirements, predicting some use of reptiles, which does occur (Figs. 20, 21, 22, Table 61). It is fitting to assess the proportion that mammals contribute before the reptiles. Many caiman and turtles are inaccessible to cats, safe in the depths of their aquatic environments.

The estimated annual needs of the cats constituted 33% of gross productivity (Table 66). Robinson and Redford (1991) and Robinson and Bodmer (1999) suggested a maximum human harvest of 20% of production for long-lived species, and 40% for short-lived species. Last reproduction occurred at over ten years of age for long-lived species and between five and ten years of age years in short-lived species. Using longevity in the wild, white-tailed deer would be categorized as short to medium lived species, with emphasis on short. Few deer live over ten years. Life expectancy in the wild is frequently less than 3 years (Brokx 1972; Winston 1991). There were no capybara over five years in age in a harvested population in Apure, Venezuela (Lord & Lord 1988), and Robinson and Redford (1986) estimate age at last reproductive potential of capybara. Using last age of reproduction estimates of 13 years for collared and white-lipped peccaries, Robinson and Redford (1991) classify them as long-lived species. Hellgren et

al. (1995) found fecundity rates in collared peccaries over seven years of age were less than animals between 3-7 years of age, but roughly equal to animals 2-3 years of age and greater than animals between 1-2 years of age. Some wild females in Texas and Arizona did exceed ten years in age (Hellgren et al. 1995; Sowls 1997). Though classified as a long-lived species, Robinson and Redford (1991) commented on the high productivity of peccaries and Robinson and Bodmer (1999) consider a harvest <40% of production sustainable for both species. The high production rates of peccaries and capybara make them resilient to over harvesting (Bodmer et al. 1997b). The addition of caiman and freshwater turtle production would elevate the total prey production estimate considerably. Production estimates support the assertion that, when the entire study area is considered, resident cats did not require a livestock subsidy.

An efficient predator will accept all potential prey encountered when food is scarce or unpredictable, and exercise greater selectivity when food is common and adequate productive patches known (Emlen 1966; MacArthur & Pianka 1966; Sunquist & Sunquist 1989). Thus, diet breadth, in the context of diversity of potential prey, reflects relative scarcity or abundance of prey. Jaguar scat analyses from the Peruvian Amazon yielded 40 prey taxa (n=25) (Emmons 1987). Rabinowitz and Nottingham (1986) recovered 17 taxa from 228 scats, with some questions regarding methods of scat identification and thus, sample size. Analyses from the Chaco of Paraguay yielded 23 taxa (n=106) (Taber et al. 1997). Based on 44 scats, jaguar diets at Piñero appear to include approximately 10 taxa (Figure 20). Fifty jaguar scats from the dry forests of Jalisco, Mexico, yielded seven prey species (Nuñez et al. In Press-b). Comparing diet breadth among these studies has several confounding factors. First, is the different levels

of prey diversity among the study areas and local idiosyncrasies of prey availability. Second, is differences in sample sizes among studies. Nuñez et al. (In Press-b) estimated 35-50 scats as the minimum to adequately document diet. Anderson (1983) suggested a sample of 90-100 scats was necessary to calculate food habits of pumas within 10% of actual use patterns. Emmons (1987) obtained diverse taxa with only 25 scats. The number at which the universal asymptote is obtained is not known. It is likely to vary among sites. Broad inference is all that is possible. The diet of jaguars in Piñero appears to be more specialized than the diet in the Peruvian and Belizean rainforest sites (Emmons 1987; Rabinowitz & Nottingham 1986).

Foraging theory predicts that items will be added to the diet only when the energy gained outweighs the costs invested (Emlen 1966; MacArthur & Pianka 1966). In Belize, 54% of jaguar scats contained armadillos (Rabinowitz & Nottingham 1986). In Piñero, armadillos outnumber capybara (Tables 48 and 60). The search time required to obtain armadillos (relatively dispersed in forest habitats) probably equals or exceeds the search time for capybara (relatively concentrated in somewhat predictable habitats, rarely >500 m from water (Ojasti 1973)). The handling costs to capture armadillo may equal handling costs for capybara. Capybara weigh ten times as much as armadillos, which in Piñero, are practically ignored (Figs. 20, 21). If cat movements were random or even systematic armadillos might be encountered more frequently than capybara.

In the Peruvian Amazon, terrestrial tortoises were tied with collared peccary as the numerically most frequent items in the diet (Emmons 1987; 1989). In Piñero, where terrestrial tortoises are an order of magnitude more abundant than the larger mammalian prey (Table 60) they are virtually ignored. Though dispersed in forest, they must be

encountered. The large cats in Piñero have adequate natural prey to make choices, another indication that the natural prey base is adequate.

The prey base is adequate when the entire Piñero basin is considered, but it is far from uniformly distributed (Figs. 12, 14, 18). Piñero has low alpha-diversity in comparison to rain forests, but its high horizontal beta-diversity results in patches in which prey production is high. Cats move through and between those patches. Some semi-deciduous forests have seasonal concentrations of white-lipped peccaries. Others have resident groups of collared peccaries. Prey abundance is high in lowland forestsavanna mixes and in well-watered small savannas surrounded by forest. The latter contain capybara, caiman, turtles, and deer. Collared peccaries often use the adjacent forest edge. The areas that have low prey abundance are the large open savannas in the far south of the study area, and the high dry pastures, set in hills, that are used for calving (Figs. 12,14, 18). Pumas residing in the vicinity of these maternity pastures do have pockets of productivity within their ranges, but the immediate vicinity of the pastures has low native prey abundance and diversity (Figs. 12, 18). In managing the calving season successfully by moving cattle to higher ground, ranching operations may coincidentally reduce some potential problems with jaguars while increasing the potential for problems with pumas. Patches that were poor become rich, their wealth in calves.

The ratio of abundance of capybara to deer was approximately .25, of capybara to collared peccary approximately .33. In jaguar scats the ratio of capybara to collared peccary approximately .74. In kills, the ratio was approximately 1.2. In puma scats the ratio of capybara to collared peccary was approximately .57. In kills, the ratio was approximately 15. Deer, which were far more abundant than capybara, were used less by

puma and far less by jaguar. In relation to abundance, they were used surprisingly little . Why were capybara such a preferred prey? The profit margin must be high. Capybara are as large as deer, and larger then peccary, yet appear to have less flight capabilities and defenses.

In Piñero, jaguars make rounds, following a rough circuit, as they check on productive patches. The marginal value that Charnov (1976) predicted occurs because prey in patches become wary and/or flee in the presence of a predator, particularly after a herd member has fallen victim (Brown et al. 1999). Capybara have a behavioral constraint that imposes relatively tight site fidelity. They rarely occur more than 500 m from water (Ojasti 1973). Activity centers are rarely more than 300 m from water (Herrera & MacDonald 1989). As a consequence, home ranges are very small. At 6-16 ha in Apure (Herrera & MacDonald 1989), capybara ranges would be approximately 20% of the area of collared peccary home ranges in Guarico (Castellanos 1982). Densities are exceptionally high locally (and exceptionally low away from water). Amphibious like the caiman, they spend far more time in terrestrial habitats, including forest. The patch they occupy may be slow to lose its value. Since the capybara need to reconvene at water, restoration of the value of the patch they occupy may be more rapid. A cat might decide to visit more frequently, or even stay a while.

Handling costs of prey procurement include the physical hazards of capture. Adult caiman, when struggling presumably represent a risk to dentition, as the head snaps from side to side. Collared peccary canines approach those of a jaguar in size, and are sharper. Both peccaries rely on groups for vigilance, and for defense. Presumably the most desirable white-lipped peccary is the one who has allowed itself to become isolated

from its herd. Deer are fast. Though presumably less formidable than peccaries in a herd, their hooves and antlers provide some defense. Capybara incisors, if they connected with soft tissue, could cut deeply. Young calves weigh 30-50 kg, as much as all the large natural prey, more than some. Although cows do rally to the defense of their calves, the short-term cost of a calf is likely to seem low to a predator.

A maternity pasture, in which cows and calves are fenced becomes a patch whose value may never become marginal. Theory would predict no travel from such a patch. And for the unfortunate cats that successfully do the short math, that is what happens. Although the majority of cats do not make a habit of preying on such situations, some do. It pays them sweetly, high profits with low costs, until the end.

In Piñero, the frequency of cattle depredation was inversely related to availability and vulnerability of natural prey and directly related to availability and vulnerability of livestock. There was some coincidence in this. Young calves were not often pastured in the prey-rich well-watered small forest-lined savannas at low elevations. Cattle were virtually absent from some of the most prey rich areas in high-stature semi-deciduous forest due to a lack of suitable forage in those areas.

Aranda (1996), Crawshaw (1995), Crawshaw and Quigley (In Press), and Emmons (1987) reported that jaguar showed a preference for peccaries in the tropical rainforests of Manu, the subtropical rainforests of Iguazu, the transitional subtropical moist-dry forests of Campeche, and the sub-tropical seasonally flooding habitat mosaic of the Pantanal. Converting data of Nuñez (In Press-b) from the deciduous dry forests of Jalisco, Mexico, into proportions, jaguar took 2.6 times as many white-tailed deer than collared peccary. The relative abundance of deer to peccary was 1.714, and the

proportion of average individual biomass of deer to peccary 1.74. The product of both yielded the crude propoportion of deer biomass relative to peccary, which was 2.98 (my calculations). Jaguar did take slightly more collared peccary than did puma (Nuñez et al. In Press-b). More information of details of the prey distribution within the study area would be needed to fully understand preference patterns of the Jalisco cats. In the Paraguayan Chaco, jaguar took an order of magnitude more *Mazama* than peccaries (Taber et al. 1997) a pattern fitting Aranda's predictions for puma from Campeche (Aranda & Sánchez-Cordero 1996). Aranda and Sánchez-Cordero (1996) viewed puma as having a bias towards deer, jaguar a bias towards peccary. Inferences from the Chaco study are limited in two ways. We have no details on the ecology of the two cats in the area. We have little indication of relative abundance of prey items. In subtropical moist forest in Belize, fairly small prey dominated jaguar diets. Armadillos, pacas, and tamandua anteaters were the most frequent items (Rabinowitz & Nottingham 1986). Apparently the frequency of these prey in the cats diets approximated that indicated by indices of prey abundance (Rabinowitz & Nottingham 1986). The source of the 228 scats was hopefully clear. Positive scat identification requires sign nearby or bile acid or DNA analyses (Farrell 1999; Taber et al. 1997). Tamandua are an unexpected prey if larger prey is available. If the data are accurate, the area had been over hunted. Thus, its high density of jaguars is puzzling. At Hato Piñero, jaguar showed a preference for peccary, but a greater preference for capybara. The assessment of dietary overlap across the range of jaguar and puma sympatry is still incomplete. Outliers seem to come from xeric regions. Without adequate measures of prey abundance, preferences cannot be ascertained.

Jaguars have been reported using large reptiles in the Peruvian Amazon (Emmons 1987; 1989), coastal Costa Rica (Carrillo & Saenz In Press; Carrillo et al. 1994) and in seasonally flooded habitat mosaics such as the llanos [Hoogesteijn, 1993 #82; this study]. When large reptiles are a profitable option, jaguars readily exploit them. Puma also take large reptiles [Dalrymple, 1996 #86; this study] but reports are less frequent, a factor possibly confounded by subtle habitat preferences. Jaguars attain their greatest size in seasonally flooded habitat mosaics (Hoogesteijn & Mondolfi 1996).

Studies ranging from Canada into Central America suggest that the puma, though exceptionally flexible, is a cervid specialist (Aranda & Sánchez-Cordero 1996; Dalrymple & Bass 1996; Hornocker 1970; Iriarte et al. 1990; Kunkel et al. 1999; Logan et al. 1996; Maehr 1997a; Murphy 1998; Nuñez et al. In Press-b). When alternatives are abundant or particularly vulnerable, and when cervids are locally scarce, puma will make increasing use of alternatives, such as feral hogs (*Sus scrofa*) (Maehr 1997a) or bighorn sheep (*Ovis canadensis*) [Weyhausen, 1996 #108; Ross, 1997 #112; Eric Rominger pers.comm.]. In the Pantanal, 68.4% of puma kills were capybara (Crawshaw & Quigley In Press). Without adequate context of capybara abundance in relation to other prey, no statement can be made about the level of preference. At Hato Piñero puma preferred capybara over deer. Deer numbers were four-fold those of capybara, yet capybara were far more common in the diet (Figs. 21, 22).

Like the leopard (Sunquist & Sunquist 1989), the puma covers a broad geographical range encompassing diverse habitats and subsequently, diverse prey. In northern Idaho and southern British Colombia, efforts to recover woodland caribou (*Rangifer tarandus*) have been limited by puma switching to these expensive imported

provisions (Eric Rominger pers.comm.). In Alberta, puma males can weigh 75 kg or greater, and can take moose (Ross & Jalkotzy 1996). By comparison, in Belize, male jaguars averaged 57.2 kg, n=6 (Rabinowitz & Nottingham 1986). The average mule deer and elk consumed by Idaho pumas were 63.6 and 175 kg, respectively (Hornocker 1970). In Argentina, pumas eat vizcachas (Lagostomus maximus), other rodents, armadillos (Chaetophractus villosus and Zaedyus pichiy), and hogs (Sus scrofa) (Branch et al. 1996). In Chile, the emphasis of puma diet switches between european hares (*Lepus capensis*) and guanacos (*Lama guanico*) depending on availability (Iriarte et al. 1990). Puma are largest at the northern and southern extremes of their distribution (Iriarte et al. 1990). Recent evidence suggests that North American puma are descendents from a founder event involving a small pool originating in South America (Culver et al. 2000). In the last 10,000-12,000 years this pool reoccupied North America, only to be eliminated by humans in most of the eastern and central United States during the last 450 years. It is possible that the species is still expanding in the north. Both jaguar and puma are adaptable, the puma more so. Their coexistence has taken place in a dynamic theater of vegetation and faunal transitions through time, in fact many different theaters. Some theaters may yet be dynamic today.

Tables 64 and 65 are revealing. The biomass of the native artiodactyls (cervidae 125 kg/km² and tayassuidae 64.59 kg/km²) is roughly equal to that of the introduced perissodactyls (equidae 187 kg/km²). As a result, the domestic mammalian biomass (introduced bovidae and equidae) is roughly equal to the total artiodactyl biomass (bovidae, cervidae, tayassuidae), both being around 97% (Table 65). Roughly 3% of the mammalian biomass is large native prey (Table 65). The mammalian biomass of the

llanos is high, approaching the richest sites of Africa and Asia, and exceeding many productive sites of the Old World Tropics (Table 66). This biomass is in humanfacilitated ecological replacements of the grazers that went extinct in the Pleistocene (Table 66). Approximately 10,000-11,000 years ago the remaining ancient South American ungulates (Toxodontia, Litopterna, and Glyptodonts) and roughly half of the Pliocene's northern immigrants (Proscidea, Perissiodactyla, and Artiodactla) went extinct (Cartelle 1999; MacFadden & Shockey 1997; Martin 1967; Webb 1978). Bovidae never occurred in South America. Although capybara are grazers, they are small relative to the recent mega-grazers. At present, there are 21 species of ungulates in tropical America. Most are at least partially dependent upon forest. In proportion to continent areas, by African standards, there would be 55 ungulates in South America (Ojasti 1983). The savannas of South America were, in some respects, empty when the Spanish arrived, carrying Old World grazers. Feral on the landscape, the Bovids and Equids multiplied. Managed (immunizations, predator control, forage improvements), their biomass climbed even higher.

Before the extinctions, the New World tropics had large herbivores, and an associated assemblage of large predators. In the Pleistocene, there were lions (*Panthera atrox*), jaguars (*Panthera onca*), pumas (*Puma concolor*) and sabertooth cats (*Smilodon fatalis*) in Florida (Morgan & Seymour 1997). The community of a large sabertooth cat (*Homotherium serum*), a smaller lighter sabertooth cat (*Smilodon gracilis*) and a cheetah-like cat (*Miracinoyx inexpectatus*) approximately mirrored the size class distribution of the present community of lion, leopard, and cheetah in Africa (Morgan & Seymour 1997). In the Pleistocene, jaguars were more common in Florida than puma. The point is

this: the communities of large mammals in South America are recent. Individual members may be ancient, some more then others, but the communities are very recent. The native herbivore biomass in the llanos is miniscule compared to Africa. With large grazers reintroduced, the biomass surpasses famous grazing grounds in Africa (Table 66). The vast majority of that biomass is in cattle. The current system cries out for an additional larger felid. Introductions (re-introductions) of *Panthera leo* to eat adult cows are quite unlikely. Yet, it is amazing that there are not more problems between jaguar and puma and cattle. The perspective that the fossils have provided does little to assuage the concerns of ranchers. At present, some puma and jaguar make decisions based on sound logic, but fail to factor in lethal consequences. Cattle ranchers lose when cats take livestock. Ultimately, the cats lose too. Humans introduced bovids into the receptive environment of the New World tropics. In doing so, we created this dilemma, and it thus rests upon us to help the cats make wise decisions. The following chapter discusses management options.

	jaguar	average wt.	puma	average wt.	
male	2.5	87.5	5	51	
female	4	52	7	31.5	
subadults	2		3		
cubs	3		5		
total	11.5	70	20	41	

Tigers of Chitawan	females:	142.75kg	males:	over 200kg	
Estimated prey killed p	ber year:	2950kg		3400kg	
subadult requirements	= female	cub require	ements =	1/4 female	
Sunquist 1981					

Intake ratios in proportion to Chitawan tigers

based on weight ratios with adjustments for metabolism

Jaguar	Puma
0.4	0.256
Estimated annual minim	um prey killing requirement: 24,215kg

Figure 19. Estimated annual prey requirements for resident cats.

Figure 20. Relative frequency that prey items occurred in jaguar and puma scats. Natural prey body size increases towards left axis. Livestock and unclassified natural prey to right. Codes are as follows: OV *Odocoileus virginianus*; HH *Hydrochaeris hydrochaeris*; TP *Tayassu pecari*; MT *Myrmecophaga tridactyla*; CC *Caiman crocodilus*; TT *Tayassu tajacu*; PR *Procyon cancrivorus*; DN *Dasypus novemcinctus*; DA *Dasyprocta agouti*; SF *Sylvilagus floridanus*.



Figure 21. Relative frequency of prey items in jaguar and puma kills. Body size of natural prey increases toward left axis. Domestic livestock to right. Codes are as in Fig. 20.



Figure 22. Size of spectacled caiman preyed upon by jaguar and/or puma. Codes are J for jaguar and U for large cat-species unclear. Class II caiman are immature. Class III caiman could be mature females or immature males. Class IV shown was a mature male.



СМ

Table 61. Summary of the standing crop biomass of natural prey in Hato Piñero study area. Items in italics did not reliably appear in jaguar and puma diets. Biomass of livestock is summarized in Tables 62 and 63.

Item	Total kg in study area
Mammals	
Capybara	20,315-22,654
White-lipped peccary	5,005
Collared peccary	35,835
White-tailed deer	78,890
Agouti	1,072
Nine-banded armadillo	3,561
Cottontail rabbit	183
Giant anteater	2,788
Subtotal mammal	149,988
Tapir	3,000
Total mammal	152,988
Reptiles	
Spectacled caiman	167,827
Freshwater turtles	56,674
Subtotal reptile	224,501
Red-footed tortoise	96,336
Iguana	669
Total reptile	321,506
Sum mammal and reptiles	
with records of use	374,489
If cats harvest .08 of standing crop	
expect minimum standing crop =	302,687
If cats harvest .10 of standing crop	
expect minimum standing crop =	242,150
Total of all above taxa (available	
whether selected or not)	474,494

Table 62. Patterns of biomass among livestock at Hato Piñero. Table depicts sex and age specific numbers, weights, and biomass of cattle (*Bos indicus* and *Bos taurus*). Estimated cattle total is 14,000. The majority of artificial insemination occurs between October and February. The peak of parturition is during July, August, and September. The stages most vulnerable to attacks by large cats are both italicized and in bold. Most attacks involve young calves (69% between 1-30 days of age). In addition to cattle there are: buffalo (*Bubalus bubalis*) 123,750 kg (150 x 825 kg); horses and mules 106,750 kg (203 working, 102 for breeding, total of 305 x 350 kg); young horses and mules 11,100 kg (111 x 100 kg); and burros 450 kg (3 x 150 kg). Total biomass estimate for horses, mules, burros is 118,300 kg, of which 11,100 might be colts, the most vulnerable age. In cattle, the becerro stage is lasts 9 months, mauto y mauta lasts 14 months, hence overall numbers of the older local category may be higher despite mortality. All estimates are crude.

Sex/Age Class	Crude	Crude Weight	Biomass/Class	Biomass/Class	Biomass/Class
	Numbers	(kg)	Jul-Sep	Oct-Dec	Jan-Mar
Toros	200	750	150,000	150,000	150,000
Vacas	7,000	420	2,940,000	2,940,000	2,940,000
Becerros 0-3	3,200	50	160,000		
months					
Becerros 3-6	3,200	120		384,000	
months					
Becerros 6-9	3,200	180			576,000
months					
Mautos y Mautas					
10-24 months	3,600	275	990,000	990,000	990,000
Total biomass			minimum		maximum
Max and min			4,240,000	4,464,000	4,656,000
Biomass of class					
Most vulnerable			minimum	maximum	
to big cats			160,000	384,000	

Table 63. Summary of standing crop biomass of livestock at Hato Piñero. Young calves are a subset of the cattle total.

Type of livestock	Kg
Cattle	4,656,000
Buffalo	123,750
Horses, mules, burros	118,300
Young calves between July and September	160,000
Total livestock: bovid and equid	4,898,050

Item	kg/632.3 km ²	kg/km²
Native mammals		
Capybara	22,654	35.83
Agouti	1,072	1.69
White-lipped peccary	5,005	7.91
Collared peccary	35,835	56.67
White-tailed deer	78,890	124.77
Cottontail rabbit	183	0.29
Nine-banded armadillo	3,561	5.63
Giant anteater	2,788	4.40
Native subtotal	149,988	237.21
Tapir (est. 15 x 200 kg)	3,000	4.74
Total native	152,988	241.95
Domestic "introduced"		
mammals		
Cattle	4,656,000	7363.59
Buffalo	123,750	195.71
Horses, mules, burros	118,300	187.09
Domestic subtotal	4,898,050	7746.40
Total mammalian	5,051,038	7988.36
Reptiles		
Iguana	669	1.06
Caiman	167,827	264.95
Freshwater turtles	56,674	89.63
Terrestrial tortoises	96,336	152.36
Total reptilian	321,506	508.47
mammals and reptiles		8496.83

Table 64. Conversions of biomass estimates for entire 63,227 ha study area into kg/km² estimates.
Table 65. Percentage of total crude mammalian biomass expressed in kg/km² represented by select groups.

Group	Pooled Group	Percent of Total Mammalian Biomass
Bovidae (introduced)		
Cervidae (native)		
Tayassuidae (native)	Artiodactyla	97%
Equidae (introduced)		
Tapiridae (native)	Perissodactyla	2.4%
Agoutidae (native)		
Hydrochaeridae (native)	Rodentia	.5%
Myrmecophagidae	Xenarthra	.12%
Bovidae (introduced)		
Equidae (introduced)	Domestic (introduced)	97%
Native mammalian prey		3%

Sites	Comments	kg/km ²
New World		
Hato Piñero, Llanos, Venezuela	Not comprehensive, larger mammals Including livestock	7,988
Hato Piñero, Llanos, Venezuela	Not comprehensive, larger mammals Excluding livestock	242
Missouri River Breaks,	Not comprehensive, larger mammals	2,243
Central Plains, Montana	Including livestock	
Missouri River Breaks,	Not comprehensive, larger mammals	45
	Excluding livestock	
Hato Masaguaral, Llanos, Venezuela	All nonvolant mammals	8,315
	Including livestock	
Barro Colorado Island, Panama	All nonvolant mammals	2,115
Guatopo, Coastal Range, Venezuela	All nonvolant mammals	1,001
Urucu, Brazilian Terra Firma Amazon	All nonvolant mammals	891
Acurizal, Pantanal, Brazil	Most nonvolant mammals	380

Table 66. Mammalian biomass in New and Old World study areas.

Old World

Wilpattu, Sri Lanka	Ungulates only	766
Kanha, India	Primarily ungulates	1708
Nagarahole, India	Wild & domestic ungulates, primates	15, 094
Serengeti Unit, Tanzania	Primarily ungulates	4,222
Manyara, Tanzania	Primarily ungulates	7,785
Ngorongoro Crater, Tanzania	Primarily ungulates	10,363
Manyara, Tanzania Ngorongoro Crater, Tanzania	Primarily ungulates Primarily ungulates	7,785 10,363

Sources are as follows: Missouri River Breaks, Hato Masaguaral, Barro Colorado, Guatopo (Eisenberg 1980); Urucu (Peres 1999); Pantanal (Schaller 1983) Wilpattu (Eisenberg and Lockhart 1972, McKay and Eisenberg 1974, Eisenberg and Seidensticker 1976); Kanha (Schaller 1967 adapted by Eisenberg and Seidensticker 1976); Nagarahole (Karanth and Sunquist 1992) Serengeti, Manyara, and Ngorogoro Crater (Schaller 1972).

Table 67. Gross productivity of major mammalian prey at Hato Piñero.

MAJOR PREY						
Species	Abundance	Standing crop	Annual addition of biomass per 100 animals (kg)	Annual Gross productivity By Species (kg)		
capybara	547	20,315-22,654	2,295.00	12,554 capyhara		
white-lipped peccary	167	5,005	1,615.60	2,698 white-lipped peccary		
white-tailed deer	2,235	78,890	1,292.50	28,88 7 white-tailed deer		
collared peccary	1,760	35,835	1,660.00	29,224 collared peccary		
Increments of biomass added j Subtractions (adult mortality &	per year. 2 otherwise) not incl	uded.		7 3,363 Gross Productivity Estimate		
Estimated Annual Kill to Su	innort Drecent Rec	ident Cate		Cats Needs $24.215 = 3396$ CP		
MINOR PREY						
cottontail	228	183	250	570		
agouti	282	1,072	109.4	308		
armadillo	937	3,561		2,956		

CHAPTER 5 REFLECTIONS ON WILDLIFE MANAGEMENT IN LOS LLANOS ALTOS IN GENERAL AND HATO PINERO IN PARTICULAR

Humans control all regions on Earth offering them accessible high levels of primary productivity. Carnivore conservation usually translates to compromises involving the best of what is left. Every breadbasket of this world once supported large carnivores. Not every wilderness remaining can. Yet, most wild places on earth, subarctic, temperate, and tropical, provide large carnivores high values in the parameter now almost more important than habitat quality: freedom from persecution from humans, whether direct or via prey depletion. In Venezuela, vast tracts of Amazonian rain forest south of the Orinoco river provide a reservoir of jaguars. Yet, the optimal jaguar habitat in Venezuela was probably originally Los Llanos [Hoogesteijn, 1993 #82; 1996 #99; Mondolfi, 1986 #19]. Persistence of carnivores on private lands indicates that those lands are productive and important for conservation. This is the case for the Florida panther (Maehr 1997b). The Everglades National Park contains approximately one million acres of marginal panther habitat. Conversely, some private ranches, productive in upland game, constitute desirable, and fought-over puma home ranges (Maehr 1997b).

In Los Llanos Altos of Venezuela, a series or large interconnected cattle ranches have allowed rare large mammals such as tapir, white-lipped peccary, and jaguar to persist in an agricultural mosaic. Hato Corralito is connected to Hato Piñero which is connected to Hato Socorro and so on. Piñero's white-lipped peccaries travel along the bed of Caño Caujaral, and have been seen Hato Mata Clara to the north. Further

northwest in Cojedes, Hato San Ignacio's riparian forests along Rio Tinaco also support white-lipped peccaries and jaguars. A metapopulation (McCullough 1996) of jaguars has survived in Los Llanos Altos (Estados Guarico, Cojedes, Portuguesa). There are no public protected areas in the area where this study took place. The wildlands are all in ranches dedicated to cattle ranching, with forests retained for building materials and fence posts. Rarely stated as such, these ranch owners also seek to preserve a way of life. Jaguar numbers could be higher. Adult mortality, often associated with conflicts with ranchers, reduces the rate of growth of these populations. There are, at least on the short term, some vacancies in potential jaguar ranges. Yet, there are jaguars, and money is being made. This is a factor of attitude and economy, a success story of the buzzword "sustainable development" that needs to be encouraged to continue. Rather than saving the best of what is left, working with these ranches entails saving what is left in the best. The stakes are important. Some suggestions intended to help are outlined in this chapter.

A number of workers have studied jaguars on working cattle ranches (Crawshaw In Press; Crawshaw & Quigley 1991; In Press; Farrell 1999; Gonzalez-Fernandez In Press; Hoogsteijn et al. 1993; In Press; Hoogesteijn & Mondolfi 1993; 1996; Mondolfi & Hoogesteijn 1986; Quigley & Crawshaw 1992; Schaller & Crawshaw 1980; Scognamillo et al. In Press; Sunquist et al. 1999b). Some have commented on the potential of these ranches as "tools" for conservation (Hoogesteijn & Chapman 1997; Quigley & Crawshaw 1992). It might seem ironic to consider areas subject to episodic extreme conflicts between ranchers and cats as "tools" for conservation, until one understands that there is scant wildlife outside these large tightly controlled landholdings. Ranches might also seem inherently instable compared to federally designated parks. Ownership can

change hands. Inheritors can choose to subdivide. Inflation may spur forest clearing. Yet, vast areas of significant wildlife habitat lie in private lands, with no public protected areas nearby. Any wildlife management program ultimately requires enforcement to succeed. No matter the mechanism, the need for enforcement is inevitable, even in community management schemes. In many national parks in Latin America, enforcement capabilities are minimal. Too often, the degree of protection afforded wildlife habitats is related to distance from human travel routes and population centers, not administrative designation. This is where the large ranches seem to excel. The socioeconomic system in Los Llanos Altos possesses land and income disparities, but can provide a strong arm approach, namely effective enforcement, to protect wildlife. Some ranches use hired enforcers. Others rely on local branches of the National Guard to respond to complaints. To be certain, some poaching occurs, some originating inside the ranches, but more often as incursions along property borders. Ironically, this system, which is the antithesis of programs for equitable land and income distribution, has much in common with community conservation. Both are borne out of the current inability of public institutions to adequately manage wildlife and wildlands. Both rely on vested private interests as an incentive to manage and protect. And ultimately a key to the success of both is enforcement.

(Ojasti 1973; 1983; 1991) has commented on the management potentials of capybara on private ranches. Thorbjarnarson and Velasco (1998; 1999), Thorbjarnarson (1991b), and Velasco and Ayarzagüena (1995) have commented on the potentials of caiman management on ranches and the strengths and weaknesses of the programs in Venezuela. Water retention pits, excavated during road construction, and ponds

excavated to provision cattle during the dry season have expanded caiman and capybara habitats in Los Llanos (Ojasti 1991; Thorbjarnarson 1991b). Spectacled caiman represent no conflict with cattle ranching.

A simplified summary of mixed open-area capybara habitats is as follows: 1) esteros (shallow ponds which may dry up in the dry season, dominated by aquatic vegetation, Cyperacaeae, and semi-aquatic grasses); 2) bajios (up to 0.5 m higher than esteros – flood 10-120 cm in wet season- predominately grasses); 3) bancos (rarely flood, though interspersed with habitats that flood, dominated by tall grasses, bushes, patches of forest, more dicotyledons). Cattle and horses prefer to use bancos, which capybara usually only use in June and July (Escobar & Gonzalez-Jiminez 1976; Herrera & MacDonald 1989). The capybara make higher use of aquatic vegetation and Cyperaceae than do cattle (Escobar & Gonzalez-Jiminez 1976; Herrera & MacDonald 1989). Competition is low in bajios. The greatest potentials for competition are in esteros in the dry season, particularly when pastures have been overgrazed (Escobar & Gonzalez-Jiminez 1976; Ojasti 1973). If pastures are managed well, the potentials for competition are low. Cattle management facilitates the capybara through retention ponds, improving savanna forages by burning, and poaching control (Ojasti 1973).

In Los Llanos, white-tailed deer are more browsers than grazers (Brokx 1972; Danields 1991). This varies. At points, the deer consume enough fruit fall from trees that one might call them frugivores (*Genipa, Spondias, Guazuma*) or granivores (*Caesalpina, Enterolobium, Pithecellobium*). In some areas and seasons they make heavier use of graminoids, but overall, dicotyledons figure heavily in deer diets (Brokx 1972; Danields 1991). In southeastern Texas, deer avoid close association with cattle

without abandoning their home ranges, and use pastures more heavily after cattle are removed than prior to or during the cattle's occupancy (Adams 1978). In Los Llanos Altos, the competition between deer and cattle is low, though it can increase during the dry season, particularly in overgrazed areas.

In the Northern Rocky Mountains of the United States and southern Canada, people killed 77-85% of grizzly bears that died while radio-collared (McClellan et al. 1999). Crawshaw experienced 100% human related mortality of radio-collared jaguars in the area of Iguazu National Park (Crawshaw 1995). Sunquist (In Press) pointed out that a high proportion of study animals have been killed by poachers and ranchers in every jaguar study to date. At Piñero, we observed puma control. Losses were tolerated when sporadic. When chronic, the specific animal responsible was eliminated. Regardless of legal protection afforded cats, in these remote fiefdoms in the savannas of tropical America, some of this is to be expected. If removals affect female survivorship, at either adult or juvenile stages, they will affect rates of recruitment and dispersal.

Piñero kept better books than most ranches. They indicated that in 14 years 20 puma and 2 jaguar had been removed (Scognamillo et al. In Press). The legalities of removing jaguar without appropriate authorization and clearances do carry severe penalties. For puma, a licence to kill in response to livestock losses can be issued. No such permit is issued for jaguar. Venezuela experimented with a capture-relocation scheme, but resources (i.e. political will) were inadequate to sustain it in the manner planned. Further, it is expensive to catch and move and monitor problem cats. For now the program is stalled. Although ranchers in Estados Cojedes and Portuguesa participated while it thrived, providing 80% of the complaints (requests to relocate jaguars), it is safe to assume that old-fashioned but effective controls have resumed.

Actually, 10 jaguar were removed from Piñero in the seven years preceding our study. One of those was removed non-lethally, but died during translocation. An 11th was removed from nearby Hato Samanote, weeks before our field work began in 1996. One female may not have been involved in cattle attacks but was associated with a large male that had been when she was killed. The remainder had been involved in attacks on livestock to varying degrees. No jaguars were removed during our study period. In fact, jaguar attacks on livestock were sporadic and relatively infrequent during our tenure. The ten year picture would be different than the three year picture. No doubt, puma cause more losses than do jaguar in Los Llanos Altos in general and Hato Piñero in particular. However, the long-term proportions of puma to jaguar livestock kills would be slightly different than what our three year window captured. Logan et al. (1996) experimentally reduced (58%) adult and subadult pumas on half of their study area in Mexico. It took 31 months for the adult segment of the population to recover.

In west-central Estado Cojedes and eastern Portuguesa, 0.4% of 92,043 head of cattle were lost to jaguar and puma. The maximum loss experienced by any ranch in the region was 2.4% annually. In only 4 of 37 ranches were losses over 1% annually (Gonzalez-Fernandez In Press). However, if those losses were all calves, they could represent 2.5-5% of annual recruitment (Gonzalez-Fernandez In Press). In Hato Piñero, the percentage of all calf mortality attributable to felids was 9% for 1981-1990, 15% for 1986-1990 (Hoogesteijn et al. 1993) and 13.3% for 1991-1997 (Sunquist et al. 1999b). Of the latter figure, 11.5% were lost to puma and 1.8% to jaguar. Losses to jaguar may

have been slightly higher than recorded, for reasons discussed previously. Calves vary in value. With some, investments in breeding (selective artificial insemination) have been high. Further, a calf represents economic potential. A young calf may not be that valuable. The rancher is raising it for its price at maturity. In July 2000, the approximate prices for adult cattle from Los Llanos were as follows: commercial cows \$380; fattened steers \$ 550; registered breeding cows from \$ 600 to 800; and registered breeding bulls between \$ 1,000-1,500 (Rafael Hoogesteijn pers.comm.). There will always be some losses to felids. When those become frequent, and particularly when they focus on expensive stock, they generate lethal antipathy. The fabric of the jaguar metapopulation is thin. Each subpopulation could be more robust and there are hazards between every patch. Every piece is needed. The best that can be hoped for is deterrence. How can we keep the losses low? The following section discusses options, focusing on Piñero in more detail.

Hoogesteijn et al. (In Press) proposed the establishment of cooperative conservation programs linking non-government organizations and ranchers to 1) improve cattle management; 2) formalize control of problem cats; 3) develop compensation programs for livestock losses; 4) coordinate private vigilance. Such a program would need the informed blessing of the government and assurances of in-field government support (Hoogesteijn et al. In Press). As recent as the 1980s, Venezuela was one of Latin America's most stable countries. Yet, inflation was 103% the first year we conducted field work. Buying power of any currency was halved in less than one year. During the last year of our study, Cesar Chavez, a former coup leader, was elected President of Venezuela in what election observer former U.S. President Jimmy Carter called a

"peaceful revolution". That peaceful revolution has had mixed success. Restructuring the government has delayed progress on numerous fronts and social tensions are perhaps higher than ever. In unstable political environments, private enterprises will have to take the lead. A cluster of ranches in the Cojedes/Portuguesa area in Venezuela (including Corralito, Socorro, Samanote, Mata Clara, San Ignacio, Santo Domingo and others) offer an excellent opportunity to advance the idea of a consortium. The facilitator(s) of this program will have to be skilled at consensus building: strong personalities are involved. Some ranch owners are wealthy enough to spend time in New York and/or Europe. Meetings will require some planning.

Nature oriented tourism can provide an incentive to preserve wildlife. This works in Hato Piñero, and is working in several other ranches in Los Llanos. It has also had a positive impact for conservation in the Pantanal of Brazil (Crawshaw In Press). The market for high paying foreign tourists (prices at these lodges are too high for many Venezuelans) may be exhausted. The open niche is in lower-priced yet comfortable lodging and tours oriented towards more of the Venezuelan public.

Some general suggestions for maintenance of both cats and cattle on the ranches of Los Llanos Altos and other savanna/forest mosaics of the tropical Americas are:

- 1) Protect all principal prey of the large cats by preventing poaching;
- Avoid commercial harvests of capybara and caiman. If harvests are conducted, exert strict control, particularly with capybara;
- When feasible impede the ability of cattle to enter forest. If possible, fence them out of gallery forest;

- Concentrate calving seasons via artificial insemination. A shorter calving season facilitates control;
- 5) When possible, locate maternity pastures at a distance from cover that cats may prefer;
- Explore the application of electric fence around maternity pastures, as developed by (Scognamillo et al. In Press);
- If practical, move calves from pastures with chronic depredation problems and replace with older animals, over 1-2 years of age.
- Move all cattle out of lowland flooding areas before waters rise to avoid isolation and crowding in forest islands amidst flooded savannas;
- Where possible, stock low flooding savannas with water buffalo (less vulnerable to jaguar);
- Keep good clear records of losses from all causes to facilitate planning and decision making;
- 11) Do not clear all forests. The clearing of upland forests has recently increased in Los Llanos Altos (Gonzalez-Fernandez In Press);
- 12) Excavate water retention ponds specifically for prey to elevate prey numbers, direct their spatial distribution, and thereby focus cats activities.

There is risk that maintenance of a healthy natural prey base will facilitate a healthy cat population that will do some prey switching onto cattle (Hoogesteijn et al. 1993). If we are serious about jaguar conservation, that risk will have to be assumed. If cats possess adequate alternatives to livestock they will be less likely to learn self-

destructive habits. An elevated natural prey base will decrease the relative profitability of domestic prey.

The natural prey base in Piñero was adequate to support resident jaguar and puma. However, there is cause to be concerned about capybara numbers. Both large cats demonstrated a strong preference for capybara. Llaneros demonstrated the same preference. Crew members found slaughtered capybara near Caño La Iguana, Laguna Cerritos, and other areas. The ranch owner allows select ranch employees to take some capybara before Semana Santa (Easter week). There are reasons to believe that the internal take exceeds the level permitted. Further there are incursions in some important capybara habitats near the Rio Portuguesa. And, numbers could also be higher along Rio Pao.

In February of 1985, Allan Woodward and Dennis David counted 198 capybara during one visit in a boat in Caño Manglarito (unpublished observations). Following counts from boats, vehicles, and foot in April 1997 and April 1998, my maximum count for Caño Manglarito was 65. If the strip of wet savanna that leads to Caño Manglarito (its shallow tributary) is included that total could be elevated to 90. The impressions of capybara specialists Juhani Ojasti (UNELLEZ) and Diego Giraldo (UCV) were that the specific area could support more animals. This deep palm-lined caño lies near Rio Portuguesa, and near one of the Fundaciónes, an outpost staffed to defend Piñero. My interpretation is that, at best, the ranch employees at the Fundación may turn a blind eye. Caño La Iguana is fairly large, but by the dry season's end some sections dry out. Some of its capybara may move to the deeper Manglarito in the final scorching weeks of the dry season (which is when we made our counts). Capybara were few at La

Iguana (maximum 20) and extremely cautious. They had to be counted at night. Remains of slaughtered animals were encountered there in 1997 and 1998. La Iguana is remote from any outpost and also near the river. The hunting pressure on these two southern habitats appears to come from outside the ranch, but that is an assumption. The two caños lie inside the ranch and are thus defendable. More problematic is the heavy fishing traffic along Rio Pao with its incidental take exploiting anything that moves (except anacondas). The most intense traffic is primarily oriented towards fish and is limited in time, peaking before Semana Santa. The banks of Rio Pao are for the most part devoid of game tracks. The few capybara that do use the river are so furtive that their numbers had to be inferred from tracks. Caiman poachers and turtle hunters ply these waters, which run north-south through the east side of the property. The river being a public thoroughfare, an aquatic highway, there are limits to what can be done. However, in two cases, when notified of poachers carrying Piñero game down river (one time caiman, another time deer), Branger's bodyguards (ex-National Guardsmen) enlisted the assistance of the National Guard in El Baúl. The poachers not only lost everything they had (boat, motor, skins, meat) they also faced non-trivial jail sentences. Perhaps this seems severe. It can be assumed that it did make other potential poachers think twice.

In the northern part of the ranch, on a low rise between Laguna Cerritos and Laguna Grande lives a family, with Branger's permission, and with no visible means of support. One member was a pleasant half-wit with a half dozen dogs that knew how to hunt. Laguna Cerritos, a beautiful park-like habitat, has fewer capybara than the area could support. True, the puma that use the area may be responsible, but I suspect there is more to it than that. Maximum for the Laguna Cerritos/Alta system in 1996 was

approximately 70 animals. In 1998, it was 41. I feel for these people, a pleasant sort of penniless Appalachia family in Los Llanos. For conservation purposes they should be moved out.

In numerous parts of Piñero, ranch employees take capybara before Semana Santa and smuggle out the dried and salted meat. In the middle of Piñero, the capybara around Los Patos/Puente Benjamin, near Fundación Charco Azul, sometimes show a nervousness indicative of low level hunting. The capybara around Los Venados/Juncal are uniformly calm by comparison.

Hoogesteijn and Chapman (1997) published estimates for Piñero of 90,000 ha of available capybara habitat, 36,000 ha of optimal habitat, an average density of 100 capybara/km² (or 1 capybara/ha), that would provide 36,000 capybara, for a sustainable harvest of 10,800/year. There is a total of approximately 547 capybara in Hato Piñero, providing a crude density estimate of .00865/ha, compared to 1.84-2.06/ha in an optimal area (Cordero & Ojasti 1981) and a crude average density estimate over a large study area (more comparable) of .18/ha (range .07-.34/ha) in Apure (Ojasti 1973). Ecological densities in the same area in Apure averaged 1.03/ha (range .43-2.08/ha). Piñero can handle an occasional caiman harvest. For capybara, no harvest is suggested and it is further suggested that all external and internal take of capybara be stopped immediately.

Piñero is not ideal habitat for capybara. It has much less surface water and much more forest than the study areas in Apure (Cordero & Ojasti 1981; Herrera & MacDonald 1989; Ojasti 1973; 1983; 1991). Hato Piñero is better habitat for peccaries than capybaras. Still, the habitat probably could support more capybara than are present.

The convergent pressures put capybara at risk of a decline. Since the cats like capybara so much, reserve it for them.

There are additional poaching pressures on other game species all along Rio Cojedes and Rio Portuguesa. In Piñero's northwest corner, associated with the squatter community of Quebrada de Agua, there are incursions fairly far into Piñero's interior. Hunting is common-place in Valle Hondo. The owner presumably knows much of this, and balances the potential costs of increasing his vigilance against the revenues generated by eco-tourism, concluding that, since the tourists are oblivious to these details, no further investments are warranted. While this nibbling at Piñero's frontiers may be unavoidable, the special attention to capybara previously suggested is reaffirmed. It is possible that the owner's attentiveness to an internal take, which when added up could be considerable, has slipped. If so, let this serve as a reminder.

Quigley and Crawshaw (1992) mentioned how cattle were sometimes left in low-lying areas in the Pantanal during floods, where they fell prey to jaguar. Crawshaw (In Press) stated that some of this still occurs in the Pantanal. For the most part, Piñero cattle are not abandoned in heavily-flooded areas to fend for themselves. Although this modification was oriented towards increased calf survivorship (calves cannot forage in water and are more susceptible to diseases in wet conditions) it presumably reduces the frequency of attacks. Piñero does stock its lowest, wettest areas with buffalo, though a bit more as a hobby than as a profit generator. Piñero also does keep clear records of dates, locations, and conditions of cattle losses. Its calving season is fairly concentrated temporally, though it could perhaps be even slightly more compressed.

The forests along the northeastern boundary of Piñero seemed to have less prey than those in Piñero's center. Some of this is probably related to availability of surface water in the dry season. Piñero's central region is dotted with prestamos, some fairly large. Caño Caujaral runs through its center. Windmills and water tanks are scattered through much of the areas. There are hardly any prestamos in the Northeast. Cano Matajei is seasonal. Caño Rosario dries early. The banks of Rio Pao carry hazards. In the dry season of the llanos, water becomes very important. Deer and both peccaries visit water holes regularly. Capybara home ranges include at least a segment of a water body, with a terrestrial polygon extending into suitable grazing habitats (Herrera & MacDonald 1989). I propose that deer and collared peccary home ranges have similar limitations, though the water bodies can be far smaller and the terrestrial component much more important. I suggest the excavation of some water bodies specifically for prey. This could elevate prey numbers, spatially focus prey distributions, and direct cats' use of space. In Kruger National Park in South Africa artificial water points, intended to help wildlife, had unforeseen negative side effects. Zebra (Equus burchelli) and wildebeest (Connochaetes taurinus) numbers built up in habitats previous mostly limited to endangered roan (*Hippotragus equinus*). Lions (*Panthera leo*) followed, and their predation on adult roan caused a sharp decline. Following the closure of waterpoints in a section of the roans range, roan herds in that area started to recover (Harrington et al. 1999). Water provisioning expanded the range of large herbivores in South Africa. In Piñero several water bodies could be developed to increase and focus collared peccary numbers in the northeast where few cattle are maintained. If the water bodies were adequate and poaching was controlled, capybara would probably occupy the area. In the

dry season, Piñeros jaguars make rounds among prey-productive patches. Make a new patch, a new pond, and you influence a dry season home range. Dry season home ranges do not define wet season home ranges, but the two are not independent.

Finally, Scognamillo et al. (In Press) experimented with electric fence as a deterrent circling maternity pastures. Their results were encouraging and Piñero continues to explore this surprisingly cost-effective alternative. It will be impossible to entirely eliminate cat attacks on livestock. With dedication and ingenuity, cattle losses can be reduced, and thereby cat losses as well.

APPENDIX A

LIST OF PLANTS IDENTIFIED DURING SAMPLING AT HATO PINERO, SORTED BY LOCAL COMMON NAMES AND FIELD NUMBERS.

SAMPLING EMPHASIZED FORESTS. BEJUCO = VINE. S/H/U/G = SHRUB/HERBACEOUS/UNDERSTORY/GRASS < 4 M IN HEIGHT. SOME TREES CAN BE SHRUBS (< 4 M IN HEIGHT) AND VICE VERSA. Appendix A. List of plants identified during sampling at Piñero, sorted by local common names and field numbers. Sampling emphasized forests. Bejuco = vine. S/H/U/G = shrub/herbaceous/understory/grass < 4 m in height.

Some trees can be shrubs (< 4 m in height) and vice versa.

COMMON NAME AND/OR FIELD NUMBER	SCIENTIFIC NAME	AUTHOR	FAMILY	FORM
# 158	Cyperus meyenianus	(Ness.) Kunth.	Cyperaceae	S/H/U/G
#138	Sacciolepsis myoros	(Lam.) Chase	Gramineae	S/H/U/G
#144	U	U	Ebenaceae	Tree
Aceite	Copaifera officianalis	L.	Leguminosae	Tree
Agallon	Guapira olfersiana	(L.K.O.) Lundell	Nyctaginaceae	Tree
Alado, # 155	Paspalum	U	Gramineae	S/H/U/G
Alcornoque	Bowdichia virgiloides	H.B.K.	Leguminosae	Tree
Algorrobo	Hymenaea courbaril	L.	Leguminosae	Tree
Almendrion, almendro	Machaerium caicarense	Pitt.	Combretaceae	Tree
Amargoso	Aspidosperma cuspa	(H.B.K.) Blake & Pittier	Apocynaceae	Tree
Anoncillo	Dugetia riberensis	Arist.	Annonaceae	Tree
Arbolito Espinoso #42	Machaerium sp.	U	Leguminosae	Tree
Aserrado, # 153	Alchornea schomburgkii	(K.L.)	Euphorbaceae	Tree
Balsamo	Bursera tomentosa	(Jacq.) Tr. & Pl.	Burseraceae	Tree
Bambucillo, carricillo	Lasiacis anomala	Hitch.	Gramineae	S/H/U/G
Barbasco	Piscidea cartaginensis	Jacq.	Leguminosae	Tree
Bejuco	Paullinia leicocarpa	Griseb.	Sapindaceae	Bejuco
Bejuco A #21, Bejuco Cuatro Canales #37	Cydista aequinoctialis	(L. Miens)	Bignoniaceae	Bejuco
Bejuco Cuatro Filos	Cydista diversifolia	(H.B.K.) M.	Bignoniaceae	Bejuco
Bejuco FD 171169	U	U	Bignoniaceae	Bejuco
Bejuco Fruta Alado #67	Banisteriopsis muricata	(Cav.) Cuatr.	Malphigiaceae	Bejuco
Bejuco Guaica	Combretum alternifolium	Pers.	Combretaceae	Bejuco
Bejuco Paullinia Negro	Paullinia pinnata	L.	Sapindaceae	Bejuco
Bejuco Poly, Bejuco p16 NB3	Securidaca pubescens	D.C.	Polygalaceae	Bejuco
Bejuco Sangrito	Machaerium humboldtianum	Vogel	Leguminosae	Bejuco
Bignoniaceae #100	U	U	Bignoniaceae	Tree

COMMON NAME AND/OR FIELD NUMBER	SCIENTIFIC NAME	AUTHOR	FAMILY	FORM
Braquiaria	Braquiaria humidicola	(Rendle) Scheik.	Gramineae	S/H/U/G
Cachicamito, #83, RO 4050, FD17570		U	Rubiaceae	Tree
Cacho de Venado	Godmania aesculifolia	(H.B.K.) Stanl.	Bignoniaceae	Tree
Cadillo	Wissadula periplocifolia	Persl.	Malvaceae	S/H/U/G
Cadillo, #156	Cenchrus echinatus	L.	Gramineae	S/H/U/G
Cajon de Verraco	Tabernaemontana psychotrifolia	H.B.K.	Apocynaceae	Tree
Camaruco	Sterculia apetala	(Jacq.) Karsten	Sterculiaceae	Tree
Campanilla, Celedonia	Ipomea carnea	Jacq.	Convulvaceae	S/H/U/G
Campin Melao	Melinis minutiflora	Beauv.	Gramineae	S/H/U/G
Canafistolo	Cassia moschata	H.B.K.	Leguminosae	Tree
Canilla de Venado	Allophyllus occidentalis	(S.W.) Radlk.	Sapindaceae	Tree
Canoito, Pala de Agua	Ruprechtia tenuiflora	Benth.	Polygonaceae	Tree
Capparis # 96, RO 4052	U	U	Capparaceae	Tree
Carabali	Albizia caribea	(Urb.) Britton & Rose	Leguminosae	Tree
Caramacate	Hirtella racemose	Lamark	Chrysobalanaceae	Tree
Cardon	Cerrus hexagonus	(L.) Miller	Cactaceae	Tree
Cariaquito	Lantana camara	L.	Verbenaceae	S/H/U/G
Carnaval, Bototo	Cochlospermun vitifolium	(Wild.) Spreng	Cochlospermaceae	Tree
Carne asada	Roupala montana	Aubl. Var Dentata	Proteaceae	S/H/U/G
Caro Caro	Enterolobium cyclocarpum	(Jacq.) Griseb.	Leguminosae	Tree
Carricillo	Olyra ciliatifolia	Redd.	Gramineae	S/H/U/G
Carricillo	Olyra latifolia	L.	Gramineae	S/H/U/G
Cartan	Centrolobium paraense	Tul.	Leguminosae	Tree
Caruto	Genipa americana var caruto	(H.B.K.) Schum	Rubiaceae	Tree
Caujaro Candilero, #148	Cordia collococca	(Sandmark) L.	Boraginaceae	Tree
Caujate	Entada polystacha	D.C.	Leguminosae	Bejuco
Ceiba	Ceiba pentandra	(L.) Gaertn.	Bombacaceae	Tree
Cereipo	Myospermom frutescens	Jacq.	Leguminosae	Tree
Chaparro	Curatella americana	L.	Dilleniaceae	Tree
Chaparro de Agua, Bejuco #52, Bejuco Chaparillo, Trep. Chaparillo #36	Tetracera volubilis	L.	Dilleniaceae	Bejuco
Charo, 149	Soracea sprucei	(Baill.) Macbr.	Moraceae	Tree
Charrasco #39	Pithecoctenium crucigenum	(L.) Gentry	Bignoniaceae	Bejuco

COMMON NAME AND/OR FIELD NUMBER	SCIENTIFIC NAME	AUTHOR	FAMILY	FORM
Chiguichigue	Bromelia pinguin	L.	Bromeliaceae	S/H/U/G
Chinchorro	Ronchefortia spinosa	(Jacq.) Willd.	Boraginaceae	Tree
Chupa Chupa	Combretum fruticosum	(Loefl.) Stuntz.	Combretaceae	Bejuco
Clavellina	Jacaranda obtusifolia	H.& B.	Bignoniaceae	Tree
Clavellina	Sesbania exasperata	H.B.K.	Leguminosae	Tree
Cochinito	Margaritaria nobilus	L.F.	Euphorbaceae	Tree
Coco de Mono	Lecythis ollaria	Loefl.	Lecythidaceae	Tree
Cojon de verraco	Tabernaemontana cymosa	Jacq.	Apocynaceae	Tree
Cola de Mula	Sporobolus jacquemontii	Kunth.	Gramineae	S/H/U/G
Cola de Zorro, Cola de Mula	Andropogon bicornis	L.	Gramineae	S/H/U/G
Coloradito	Trichilia unifoliata	(Blake & Standl.)	Meliaceae	Tree
Coloradito de Cerro, Hayo	Erythroxylum orinocense	H.B.K.	Erythroxylaceae	Tree
Contrahierba	Dorstenia contrajerva	L.	Meliaceae	S/H/U/G
Cordoncillo, #110	Piper tenue	U	Piperaceae	S/H/U/G
Corozo	Acromia aculeata	(Jacq.) Lood. Mart.	Arecaceae	Tree
Cortadera, #109, #137	Scleria pterota	Persl.	Cyperaceae	S/H/U/G
Cruceto	Randia hebecarpa	Griseb.	Rubiaceae	S/H/U/G
Crucetta, Cruceto	Coutarea hexandra	(Jacq.) Schum	Rubiaceae	Tree
Cuji Blanco	Pithecellobium tortum	Mart.	Leguminosae	Tree
Diente de Perro	Randia formosa	(Jacq.) Schum.	Rubiaceae	Tree
Dividive	Caesalpina coriaria	(Jacq. Willd.)	Leguminosae	Tree
Dormidera	Mimosa pudica	L.	Leguminosae	S/H/U/G
Drago	Pterocarpus acapulcense	Rose	Leguminosae	Tree
Escoba	Sida acuta	Burm. F.	Malvaceae	S/H/U/G
Espinito, Cabrito, # 95	Guettardia divaricata	(H.G.B.) Standl.	Rubiaceae	Tree
Espuela de Gallo	Strychnos fendleri	Sprague & Sandw.	Loganaceae	Tree
Flor amarilla	Tabebuia ochracea	(Cham.) Standl.	Bignoniaceae	Tree
Fruta de Guaro, Pico de Loro	Connarus venezuelanus	Baillon	Connaraceae	Tree
Gamelote Chiguirero	Paspalum fasciculatum	Willd. Ex. Flugge	Gramineae	S/H/U/G
Gamelote, #115	Panicum laxum	Swartz	Gramineae	S/H/U/G
Gateado	Astronium graveolens	Jacq.	Anacardiaceae	Tree
Guacimo	Guazuma tomentosa	Kunth.	Sterculiaceae	Tree

COMMON NAME AND/OR FIELD NUMBER	SCIENTIFIC NAME	AUTHOR	FAMILY	FORM
Guacimo cimarron	Luehea candida	(D.C.) Mart.	Tiliaceae	Tree
Guamacho	Pereskia guamacho	Fac. Weber	Cactaceae	Tree
Guamo	Inga spuria	Willd.	Leguminosae	Tree
Guarataro	Vitex capitata	Vahl.	Lamiaceae	Tree
Guayabito	Myrcia guianensis	(Aubl.) D.C.	Myrtaceae	Tree
Guayabito de Cerro, Guayaba de Cerro	Psidium salutare	(Kunth.) Berg.	Myrtaceae	S/H/U/G
Guayabito Sabanero	Psidium guianensis	S.W.	Myrtaceae	Tree
Guayabo Pauji	Pseudonamonis umbillifera	(U.B.K.) Kausel	Myrtaceae	Tree
Hayito	Trichilia trifolia	L.	Meliaceae	Tree
Jobillo	Sciadodendron excelsom	Griseb.	Araliaceae	Tree
Jobo	Spondias mombin	L.	Anacardiaceae	Tree
Junco	Eleocharis elegans	(Vahl.) R. & S.	Cyperaceae	S/H/U/G
Lagunero, Fruta de Paloma, # 86	Hecatostenon completus	(Jacq.) Sleumer	Flacourtaceae	Tree
Lairen	Maranta arundinacea	L.	Marantaceae	S/H/U/G
Lechero	Sapium biglandulosum	(L.) M. Arg.	Euphorbaceae	Tree
Limoncillo	Zizyphus cyclocardia	Blake	Rhamnaceae	Tree
Mahomo Blanco, Mahomo Morado, #147	Lonchocarpus pictus	Pittier	Leguminosae	Tree
Mahomo Negro	Lonchocarpus crucis-rubierae	Pittier	Leguminosae	Tree
Majagua	Cassia reticulata	(Willd.) Pittier	Leguminosae	S/H/U/G
Majomo Blanco	Lonchocarpus fendleri	Benth.	Leguminosae	Tree
Mangle macho, #146	Trichilia singularis	C.D.C.	Meliaceae	Tree
Mango	Mangifera indica	L.	Anacardiaceae	Tree
Manirito	Annona jahnii	Safford	Annonaceae	Tree
Manirote	Annona purpurea	Moc. & Sesse	Annonaceae	Tree
Manteco	Byrsonima crassifolia	(L.) Rich.	Malphigaceae	Tree
Mapurite	Zanthoxyllum caribaeum	Lam.	Rutaceae	Tree
Masaguaro	Albizia guachapele	(H.B.K.) Dugand	Leguminosae	Tree
Masamasa Bejuco B, Paradito, FD 17619, #79, RO 4057	Xylophragma seemannianum	(O.Ktze.) Sandw.	Bignoniaceae	Bejuco
Masamasa Peludo #53	Arrabidaea mollisima	(H.B.K.) Bur. & K. Schum	Bignoniaceae	Bejuco
Mastranto, Mastrento	Hyptis suaveolens	(L.) Poit.	Lamiaceae	S/H/U/G
Matapalo	Ficus maxima	P. Miller	Moraceae	Tree
Maya	Bromelia chrysanta	Jacq.	Bromeliaceae	S/H/U/G

COMMON NAME AND/OR FIELD NUMBER	SCIENTIFIC NAME	AUTHOR	FAMILY	FORM
Menudito	Derris moniliformis	(L.F.) Ducke	Leguminosae	Tree
Merecure	Licania pyrifolia	Griseb.	Chrysobalanaceae	Tree
Naranjillo	Bravaisia integerrima	(Spreng.) Standl.	Acanthaceae	Tree
Olivo	Capparis odoratissima	Jacq.	Capparaceae	Tree
Olivo Negro, #86	Capparis flexuosa	(L.) L.	Capparaceae	Tree
Orare, Orore	Pithecellobium ligustrium	(Jacq.) Klotzsch.	Leguminosae	Tree
Orosul	Marsdenia macrophylla	(H.B.K.) Fourn.	Asclepiadaceae	Bejuco
Paja de Agua	Hymenachne amplexicaulis	(Rudge) Nees.	Gramineae	S/H/U/G
Pala de Agua, Majomo (Caujaral)	Pouteria glomerata	(Miq.) Radlk.	Sapotaceae	Tree
Palma Llanera	Copernicia tectorum	(H.B.K.) Mart.	Arecaceae	Tree
Palotal	Vernonia brasiliana	(L.) Druce	Asteraceae	S/H/U/G
Para para	Sapindus saponaria	L.	Sapindaceae	Tree
Pardillo	Cordia hirta	Johnst.	Boraginaceae	Tree
Paspalum, # 157	Paspalum	U	Gramineae	S/H/U/G
Pata de Venado, Pato Venado	Callichlamys latifolia	(Rich.) Schum	Bignoniaceae	Bejuco
Paullinia	Serjania adjusta	Radlk.	Sapindaceae	Bejuco
Pavonia, U	Pavonia cancellata	(L.) Cav.	Malvaceae	S/H/U/G
Picapica	Mucuna pruriens	(L.) D.C.	Leguminosae	Bejuco
Picaton	Philodendron acutatum	Schott	Araceae	S/H/U/G
Pico de Loro, Pico de Guaro, #75	Swartzia pittieri	Schery.	Leguminosae	Tree
Piritu	Bactris guineensis	(L.) E. Moore	Arecaceae	Tree
Pitahaya	Acantocerus tetrogonus	(L.) Hummelinck	Cactaceae	S/H/U/G
Platanico	Thalia geniculata	L.	Marantaceae	S/H/U/G
Punteral #74	Randia venezuelensis	Steyermark	Rubiaceae	Tree
Quiribijul	Bromelia plumieri	(E. Morr.)	Bromeliaceae	S/H/U/G
Ramon Blanco	Brosimium alicastrum	S.W.	Moraceae	Tree
Roble	Platymiscium diadelphum	Blake	Leguminosae	Tree
Sabrosoacure	Trichilia martiana	C.D.C.	Meliaceae	Tree
Saeta	Axonus canescens	(Nees. & Trin.) Pilger	Gramineae	S/H/U/G
Saeta	Trachypogon plumosus	(H.B.K.) Nees	Gramineae	S/H/U/G
Saeta de Cerro, FD 17585	Andropogon angustatus	(Porsl.) Steud.	Gramineae	S/H/U/G
Salado	Vochysia venezuelana	Stafleu	Vochysiaceae	Tree

COMMON NAME AND/OR FIELD NUMBER	SCIENTIFIC NAME	AUTHOR	FAMILY	FORM
Saman	Pithecellobium saman	(Jacq.) Benth.	Leguminosae	Tree
Saquisaqui	Bombacopsis quinata	(Jacq.) Dugand	Bombacaceae	Tree
Selaginella	Selaginella horizontalis	A. Braun	Selaginaceae	S/H/U/G
Sierrito, Ouratea, Hierrito, #135	Ouratea grossourdii	(Vt.) Steyermark	Ochnaceae	S/H/U/G
Tacamajaco	Protium heptaphyllum	(Aubl.) March	Burseraceae	Tree
Taguapire, Une de Gato	Pithecellobium dulce	(Willd.) Benth.	Leguminosae	Tree
Tapaculo	Caesaria mollis	H.B.K.	Flacourtaceae	S/H/U/G
Tapocho de Monte	Calathea latifolia	(Link.) Kl.	Marantaceae	S/H/U/G
Tapocho de Monte	Calathea propinqua	(P.&E.) Koern	Marantaceae	S/H/U/G
Tiamo	Acacia glomerosa	Benth.	Leguminosae	Tree
Tornillo	Helicteres guazumaefolia	(H.B.K.)	Sterculiaceae	S/H/U/G
Tortalito	Casearia sylvestris	S.W.	Flacourtaceae	S/H/U/G
Trompillo	Tetragastris panamensis	(Engl.) Kuntze	Burseraceae	Tree
U	Blechnum brownei	Juss.	Acanthaceae	S/H/U/G
U	Ruellia paniculata	L.	Acanthaceae	S/H/U/G
U	Echinodorus grandiflorus	(Ch. & Sch.) Mich.	Alismataceae	S/H/U/G
U	Chromolaena odorata	(L.) K.& R.	Asteraceae	S/H/U/G
U	Elephantopus mollis	(H.B.K.)	Asteraceae	S/H/U/G
U	Pectis elongata	H.B.K.	Asteraceae	S/H/U/G
U	Simsia pubescens	Tr.	Asteraceae	S/H/U/G
U	Cyperus iria	L.	Cyperaceae	S/H/U/G
U	Cynodon dactylon	(L.) Pers.	Gramineae	S/H/U/G
U	Oplismenus burmanni	Beauv.	Gramineae	S/H/U/G
U	Panicum trichoides	S.W.	Gramineae	S/H/U/G
U	Pharus latifolia	L.	Gramineae	S/H/U/G
U	Schrankia leptocarpa	D.C.	Gramineae	S/H/U/G
U	Hydrolea spinosa	L.	Hydrophyllaceae	S/H/U/G
U	Hyptis pulegioides	Pohl.	Labiataceae	S/H/U/G
U	Galactia jussiaeana	Kunth.	Leguminosae	S/H/U/G
U	Sesbania sericea	(Willd.) Link	Leguminosae	S/H/U/G
U	Kosteletzka depressa	(L.) Blanchard Frix & Batis	Malvaceae	S/H/U/G
U	Malachra heptaphylla	Fisch.	Malvaceae	S/H/U/G

COMMON NAME AND/OR FIELD NUMBER	SCIENTIFIC NAME	AUTHOR	FAMILY	FORM
U	Peltaea speciosa	(H.B.K.) Standl.	Malvaceae	S/H/U/G
U	Clidemia rubra	(Aubl.) Mart.	Melastomaceae	S/H/U/G
U	Lygodium venuston	(S.W.)	Schizaeaceae	S/H/U/G
U	Melochia villosa	(Mill.) Fawc. & Kendl.	Sterculiaceae	S/H/U/G
Una Gavilan	Machaerium aculeatum	H.B.K.	Leguminosae	Tree
Uvero	Coccoloba caracasana	Meisn.	Polygonaceae	Tree
Vera Macho	Pithecellobium pistaciaefolium	(Willd.) Dugand	Leguminosae	Tree
Verrucoso (same sp. as crucetta)	Coutarea hexandra var hexandra		Rubiaceae	Tree
Yagrumo	Cycropia peltata	L.	Moraceae	Tree
Yagrumo Macho	Didymopanax morototoni	(Aubl.)D.C.	Araliaceae	Tree
Yaragua	Hyparrhenia rufa	(Ness.) Stapf.	Gramineae	S/H/U/G
Zapatero	Cupania americana	L. var Sativa D.C.	Sapindaceae	Tree

APPENDIX B

LIST OF PLANTS IDENTIFIED DURING SAMPLING AT HATO PINERO, SORTED BY: 1) FORM; 2) FAMILY; 3) GENUS AND SPECIES.

SAMPLING EMPHASIZED FORESTS. BEJUCO = VINE. S/H/U/G = SHRUB/HERBACEOUS/UNDERSTORY/GRASS < 4 M IN HEIGHT. SOME TREES CAN BE SHRUBS (< 4 M IN HEIGHT) AND VICE VERSA. Appendix B. List of plants identified during sampling at Piñero, sorted by: 1) form; 2) family; 3) genus and species.

Sampling emphasized forests.

Bejuco = vine. S/H/U/G = shrub/herbaceous/understory/grass < 4 m in height.

Some trees can be shrubs (< 4 m in height) and vice versa.

COMMON NAME AND/OR FIELD NUMBER	SCIENTIFIC NAME	AUTHOR	FAMILY	FORM
Orosul	Marsdenia macrophylla	(H.B.K.) Fourn.	Asclepiadaceae	Bejuco
Masamasa Peludo #53	Arrabidaea mollisima	(H.B.K.) Bur. & K. Schum	Bignoniaceae	Bejuco
Pata de Venado, Pato Venado	Callichlamys latifolia	(Rich.) Schum	Bignoniaceae	Bejuco
Bejuco A #21, Bejuco Cuatro Canales #37	Cydista aequinoctialis	(L. Miens)	Bignoniaceae	Bejuco
Bejuco Cuatro Filos	Cydista diversifolia	(H.B.K.) M.	Bignoniaceae	Bejuco
Charrasco #39	Pithecoctenium crucigenum	(L.) Gentry	Bignoniaceae	Bejuco
Bejuco FD 171169	U	U	Bignoniaceae	Bejuco
Masamasa Bejuco B, Paradito, FD 17619, #79, RO 4057	Xylophragma seemannianum	(O.Ktze.) Sandw.	Bignoniaceae	Bejuco
Bejuco Guaica	Combretum alternifolium	Pers.	Combretaceae	Bejuco
Chupa Chupa	Combretum fruticosum	(Loefl.) Stuntz.	Combretaceae	Bejuco
Chaparro de Agua, Bejuco #52, Bejuco Chaparillo, Trep. Chaparillo #36	Tetracera volubilis	L.	Dilleniaceae	Bejuco
Caujate	Entada polystacha	D.C.	Leguminosae	Bejuco
Bejuco Sangrito	Machaerium humboldtianum	Vogel	Leguminosae	Bejuco
Picapica	Mucuna pruriens	(L.) D.C.	Leguminosae	Bejuco
Bejuco Fruta Alado #67	Banisteriopsis muricata	(Cav.) Cuatr.	Malphigiaceae	Bejuco
Bejuco Poly, Bejuco p16 NB3	Securidaca pubescens	D.C.	Polygalaceae	Bejuco
Bejuco	Paullinia leicocarpa	Griseb.	Sapindaceae	Bejuco
Bejuco Paullinia Negro	Paullinia pinnata	L.	Sapindaceae	Bejuco
Paullinia	Serjania adjusta	Radlk.	Sapindaceae	Bejuco
U	Blechnum brownei	Juss.	Acanthaceae	S/H/U/G
U	Ruellia paniculata	L.	Acanthaceae	S/H/U/G
U	Echinodorus grandiflorus	(Ch. & Sch.) Mich.	Alismataceae	S/H/U/G
Picaton	Philodendron acutatum	Schott	Araceae	S/H/U/G
U	Chromolaena odorata	(L.) K.& R.	Asteraceae	S/H/U/G
U	Elephantopus mollis	(H.B.K.)	Asteraceae	S/H/U/G
U	Pectis elongata	H.B.K.	Asteraceae	S/H/U/G

COMMON NAME AND/OR FIELD NUMBER	SCIENTIFIC NAME	AUTHOR	FAMILY	FORM
U	Simsia pubescens	Tr.	Asteraceae	S/H/U/G
Palotal	Vernonia brasiliana	(L.) Druce	Asteraceae	S/H/U/G
Maya	Bromelia chrysanta	Jacq.	Bromeliaceae	S/H/U/G
Chiguichigue	Bromelia pinguin	L.	Bromeliaceae	S/H/U/G
Quiribijul	Bromelia plumieri	(E. Morr.)	Bromeliaceae	S/H/U/G
Pitahaya	Acantocerus tetrogonus	(L.) Hummelinck	Cactaceae	S/H/U/G
Campanilla, Celedonia	Ipomea carnea	Jacq.	Convulvaceae	S/H/U/G
#116	Cyperus	U	Cyperaceae	S/H/U/G
U	Cyperus iria	L.	Cyperaceae	S/H/U/G
# 158	Cyperus meyenianus	(Ness.) Kunth.	Cyperaceae	S/H/U/G
Junco	Eleocharis elegans	(Vahl.) R. & S.	Cyperaceae	S/H/U/G
Cortadera, #109, #137	Scleria pterota	Persl.	Cyperaceae	S/H/U/G
# 159 Cyperus	U	U	Cyperaceae	S/H/U/G
Tapaculo	Caesaria mollis	H.B.K.	Flacourtaceae	S/H/U/G
Tortalito	Casearia sylvestris	S.W.	Flacourtaceae	S/H/U/G
Saeta de Cerro, FD 17585	Andropogon angustatus	(Porsl.) Steud.	Gramineae	S/H/U/G
Cola de Zorro, Cola de Mula	Andropogon bicornis	L.	Gramineae	S/H/U/G
Saeta	Axonus canescens	(Nees. & Trin.) Pilger	Gramineae	S/H/U/G
Braquiaria	Braquiaria humidicola	(Rendle) Scheik.	Gramineae	S/H/U/G
Cadillo, #156	Cenchrus echinatus	L.	Gramineae	S/H/U/G
U	Cynodon dactylon	(L.) Pers.	Gramineae	S/H/U/G
Paja de Agua	Hymenachne amplexicaulis	(Rudge) Nees.	Gramineae	S/H/U/G
Yaragua	Hyparrhenia rufa	(Ness.) Stapf.	Gramineae	S/H/U/G
Bambucillo, carricillo	Lasiacis anomala	Hitch.	Gramineae	S/H/U/G
Campin Melao	Melinis minutiflora	Beauv.	Gramineae	S/H/U/G
Carricillo	Olyra ciliatifolia	Redd.	Gramineae	S/H/U/G
Carricillo	Olyra latifolia	L.	Gramineae	S/H/U/G
U	Oplismenus burmanni	Beauv.	Gramineae	S/H/U/G
#115	Panicum	U	Gramineae	S/H/U/G
Gamelote, #115	Panicum laxum	Swartz	Gramineae	S/H/U/G
U	Panicum trichoides	S.W.	Gramineae	S/H/U/G
Alado, # 155	Paspalum	U	Gramineae	S/H/U/G

COMMON NAME AND/OR FIELD NUMBER	SCIENTIFIC NAME	AUTHOR	FAMILY	FORM
Gamelote Chiguirero	Paspalum fasciculatum	Willd. Ex. Flugge	Gramineae	S/H/U/G
U	Pharus latifolia	L.	Gramineae	S/H/U/G
#138	Sacciolepsis myoros	(Lam.) Chase	Gramineae	S/H/U/G
U	Schrankia leptocarpa	D.C.	Gramineae	S/H/U/G
Cola de Mula	Sporobolus jacquemontii	Kunth.	Gramineae	S/H/U/G
Saeta	Trachypogon plumosus	(H.B.K.) Nees	Gramineae	S/H/U/G
#140 Hierba/grama	U	U	Gramineae	S/H/U/G
Paspalum, #157	U	U	Gramineae	S/H/U/G
#160	U	U	Gramineae	S/H/U/G
U	Hydrolea spinosa	L.	Hydrophyllaceae	S/H/U/G
U	Hyptis pulegioides	Pohl.	Lamiaceae	S/H/U/G
Mastranto, Mastrento	Hyptis suaveolens	(L.) Poit.	Lamiaceae	S/H/U/G
Majagua	Cassia reticulata	(Willd.) Pittier	Leguminosae	S/H/U/G
U	Galactia jussiaeana	Kunth.	Leguminosae	S/H/U/G
Dormidera	Mimosa pudica	L.	Leguminosae	S/H/U/G
U	Sesbania sericea	(Willd.) Link	Leguminosae	S/H/U/G
U	Kosteletzka depressa	(L.) Blanchard Frix & Batis	Malvaceae	S/H/U/G
U	Malachra heptaphylla	Fisch.	Malvaceae	S/H/U/G
Pavonia, U	Pavonia cancellata	(L.) Cav.	Malvaceae	S/H/U/G
U	Peltaea speciosa	(H.B.K.) Standl.	Malvaceae	S/H/U/G
Escoba	Sida acuta	Burm. F.	Malvaceae	S/H/U/G
Cadillo	Wissadula periplocifolia	Persl.	Malvaceae	S/H/U/G
Tapocho de Monte	Calathea latifolia	(Link.) Kl.	Marantaceae	S/H/U/G
Tapocho de Monte	Calathea propinqua	(P.&E.) Koern	Marantaceae	S/H/U/G
Lairen	Maranta arundinacea	L.	Marantaceae	S/H/U/G
Platanico	Thalia geniculata	L.	Marantaceae	S/H/U/G
U	Clidemia rubra	(Aubl.) Mart.	Melastomaceae	S/H/U/G
Contrahierba	Dorstenia contrajerva	L.	Meliaceae	S/H/U/G
Guayabito de Cerro, Guayaba de Cerro	Psidium salutare	(Kunth.) Berg.	Myrtaceae	S/H/U/G
Sierrito, Ouratea, Hierrito, #135	Ouratea grossourdii	(Vt.) Steyermark	Ochnaceae	S/H/U/G
Cordoncillo, #110	Piper tenue	U	Piperaceae	S/H/U/G
Carne asada	Roupala montana	Aubl. Var Dentata	Proteaceae	S/H/U/G

COMMON NAME AND/OR FIELD NUMBER	SCIENTIFIC NAME	AUTHOR	FAMILY	FORM
Cruceto	Randia hebecarpa	Griseb.	Rubiaceae	S/H/U/G
U	Lygodium venuston	(S.W.)	Schizaeaceae	S/H/U/G
Selaginella	Selaginella horizontalis	A. Braun	Selaginaceae	S/H/U/G
Tornillo	Helicteres guazumaefolia	(H.B.K.)	Sterculiaceae	S/H/U/G
U	Melochia villosa	(Mill.) Fawc. & Kendl.	Sterculiaceae	S/H/U/G
Cariaquito	Lantana camara	L.	Verbenaceae	S/H/U/G
Naranjillo	Bravaisia integerrima	(Spreng.) Standl.	Acanthaceae	Tree
Gateado	Astronium graveolens	Jacq.	Anacardiaceae	Tree
Mango	Mangifera indica	L.	Anacardiaceae	Tree
Jobo	Spondias mombin	L.	Anacardiaceae	Tree
Manirito	Annona jahnii	Safford	Annonaceae	Tree
Manirote	Annona purpurea	Moc. & Sesse	Annonaceae	Tree
Anoncillo	Dugetia riberensis	Arist.	Annonaceae	Tree
Amargoso	Aspidosperma cuspa	(H.B.K.) Blake & Pittier	Apocynaceae	Tree
Cojon de verraco	Tabernaemontana cymosa	Jacq.	Apocynaceae	Tree
Cajon de Verraco	Tabernaemontana psychotrifolia	H.B.K.	Apocynaceae	Tree
Yagrumo Macho	Didymopanax morototoni	(Aubl.)D.C.	Araliaceae	Tree
Jobillo	Sciadodendron excelsom	Griseb.	Araliaceae	Tree
Corozo	Acromia aculeata	(Jacq.) Lood. Mart.	Arecaceae	Tree
Piritu	Bactris guineensis	(L.) E. Moore	Arecaceae	Tree
Palma Llanera	Copernicia tectorum	(H.B.K.) Mart.	Arecaceae	Tree
Cacho de Venado	Godmania aesculifolia	(H.B.K.) Stanl.	Bignoniaceae	Tree
Clavellina	Jacaranda obtusifolia	H.& B.	Bignoniaceae	Tree
Flor amarilla	Tabebuia ochracea	(Cham.) Standl.	Bignoniaceae	Tree
Bignoniaceae #100	U	U	Bignoniaceae	Tree
Saquisaqui	Bombacopsis quinata	(Jacq.) Dugand	Bombacaceae	Tree
Ceiba	Ceiba pentandra	(L.) Gaertn.	Bombacaceae	Tree
Caujaro Candilero, #148	Cordia collococca	(Sandmark) L.	Boraginaceae	Tree
Pardillo	Cordia hirta	Johnst.	Boraginaceae	Tree
Chinchorro	Ronchefortia spinosa	(Jacq.) Willd.	Boraginaceae	Tree
Balsamo	Bursera tomentosa	(Jacq.) Tr. & Pl.	Burseraceae	Tree
Tacamajaco	Protium heptaphyllum	(Aubl.) March	Burseraceae	Tree

COMMON NAME AND/OR FIELD NUMBER	SCIENTIFIC NAME	AUTHOR	FAMILY	FORM
Trompillo	Tetragastris panamensis	(Engl.) Kuntze	Burseraceae	Tree
Cardon	Cerrus hexagonus	(L.) Miller	Cactaceae	Tree
Guamacho	Pereskia guamacho	Fac. Weber	Cactaceae	Tree
Olivo Negro, #86	Capparis flexuosa	(L.) L.	Capparaceae	Tree
Olivo	Capparis odoratissima	Jacq.	Capparaceae	Tree
Capparis # 96, RO 4052	U	U	Capparaceae	Tree
Caramacate	Hirtella racemose	Lamark	Chrysobalanaceae	Tree
Merecure	Licania pyrifolia	Griseb.	Chrysobalanaceae	Tree
Carnaval, Bototo	Cochlospermun vitifolium	(Wild.) Spreng	Cochlospermaceae	Tree
Almendrion, almendro	Machaerium caicarense	Pitt.	Combretaceae	Tree
Fruta de Guaro, Pico de Loro	Connarus venezuelanus	Baillon	Connaraceae	Tree
Chaparro	Curatella americana	L.	Dilleniaceae	Tree
#144	U	U	Ebenaceae	Tree
Coloradito de Cerro, Hayo	Erythroxylum orinocense	H.B.K.	Erythroxylaceae	Tree
Aserrado, # 153	Alchornea schomburgkii	(K.L.)	Euphorbaceae	Tree
Cochinito	Margaritaria nobilus	L.F.	Euphorbaceae	Tree
Lechero	Sapium biglandulosum	(L.) M. Arg.	Euphorbaceae	Tree
Lagunero, Fruta de Paloma, # 86	Hecatostenon completus	(Jacq.) Sleumer	Flacourtaceae	Tree
Coco de Mono	Lecythis ollaria	Loefl.	Lecythidaceae	Tree
Tiamo	Acacia glomerosa	Benth.	Leguminosae	Tree
Carabali	Albizia caribea	(Urb.) Britton & Rose	Leguminosae	Tree
Masaguaro	Albizia guachapele	(H.B.K.) Dugand	Leguminosae	Tree
Alcornoque	Bowdichia virgiloides	H.B.K.	Leguminosae	Tree
Dividive	Caesalpina coriaria	(Jacq. Willd.)	Leguminosae	Tree
Canafistolo	Cassia moschata	H.B.K.	Leguminosae	Tree
Cartan	Centrolobium paraense	Tul.	Leguminosae	Tree
Aceite	Copaifera officianalis	L.	Leguminosae	Tree
Menudito	Derris moniliformis	(L.F.) Ducke	Leguminosae	Tree
Caro Caro	Enterolobium cyclocarpum	(Jacq.) Griseb.	Leguminosae	Tree
Algorrobo	Hymenaea courbaril	L.	Leguminosae	Tree
Guamo	Inga spuria	Willd.	Leguminosae	Tree
Mahomo Negro	Lonchocarpus crucis-rubierae	Pittier	Leguminosae	Tree

COMMON NAME AND/OR FIELD NUMBER	SCIENTIFIC NAME	AUTHOR	FAMILY	FORM
Majomo Blanco	Lonchocarpus fendleri	Benth.	Leguminosae	Tree
Mahomo Blanco, Mahomo Morado, #147	Lonchocarpus pictus	Pittier	Leguminosae	Tree
Una Gavilan	Machaerium aculeatum	H.B.K.	Leguminosae	Tree
Arbolito Espinoso #42	Machaerium sp.	U	Leguminosae	Tree
Cereipo	Myospermom frutescens	Jacq.	Leguminosae	Tree
Barbasco	Piscidea cartaginensis	Jacq.	Leguminosae	Tree
Taguapire, Une de Gato	Pithecellobium dulce	(Willd.) Benth.	Leguminosae	Tree
Orare, Orore	Pithecellobium ligustrium	(Jacq.) Klotzsch.	Leguminosae	Tree
Vera Macho	Pithecellobium pistaciaefolium	(Willd.) Dugand	Leguminosae	Tree
Saman	Pithecellobium saman	(Jacq.) Benth.	Leguminosae	Tree
Cuji Blanco	Pithecellobium tortum	Mart.	Leguminosae	Tree
Roble	Platymiscium diadelphum	Blake	Leguminosae	Tree
Drago	Pterocarpus acapulcense	Rose	Leguminosae	Tree
Clavellina	Sesbania exasperata	H.B.K.	Leguminosae	Tree
Pico de Loro, Pico de Guaro, #75	Swartzia pittieri	Schery.	Leguminosae	Tree
Espuela de Gallo	Strychnos fendleri	Sprague & Sandw.	Loganaceae	Tree
Manteco	Byrsonima crassifolia	(L.) Rich.	Malphigaceae	Tree
Sabrosoacure	Trichilia martiana	C.D.C.	Meliaceae	Tree
Mangle macho, #146	Trichilia singularis	C.D.C.	Meliaceae	Tree
Hayito	Trichilia trifolia	L.	Meliaceae	Tree
Coloradito	Trichilia unifoliata	(Blake & Standl.)	Meliaceae	Tree
Ramon Blanco	Brosimium alicastrum	S.W.	Moraceae	Tree
Yagrumo	Cycropia peltata	L.	Moraceae	Tree
Matapalo	Ficus maxima	P. Miller	Moraceae	Tree
Charo, 149	Soracea sprucei	(Baill.) Macbr.	Moraceae	Tree
Guayabito	Myrcia guianensis	(Aubl.) D.C.	Myrtaceae	Tree
Guayabo Pauji	Pseudonamonis umbillifera	(U.B.K.) Kausel	Myrtaceae	Tree
Guayabito Sabanero	Psidium guianensis	S.W.	Myrtaceae	Tree
Agallon	Guapira olfersiana	(L.K.O.) Lundell	Nyctaginaceae	Tree
Uvero	Coccoloba caracasana	Meisn.	Polygonaceae	Tree
Canoito, Pala de Agua	Ruprechtia tenuiflora	Benth.	Polygonaceae	Tree
Limoncillo	Zizyphus cyclocardia	Blake	Rhamnaceae	Tree

COMMON NAME AND/OR FIELD NUMBER	SCIENTIFIC NAME	AUTHOR	FAMILY	FORM
Cachicamito, #83, RO 4050, FD 17570		U	Rubeaceae	Tree
Crucetta, Cruceto	Coutarea hexandra	(Jacq.) Schum	Rubiaceae	Tree
Verrucoso (same sp. as crucetta)	Coutarea hexandra var hexandra		Rubiaceae	Tree
Caruto	Genipa americana var caruto	(H.B.K.) Schum	Rubiaceae	Tree
Espinito, Cabrito, # 95	Guettardia divaricata	(H.G.B.) Standl.	Rubiaceae	Tree
Diente de Perro	Randia formosa	(Jacq.) Schum.	Rubiaceae	Tree
Punteral #74	Randia venezuelensis	Steyermark	Rubiaceae	Tree
Mapurite	Zanthoxyllum caribaeum	Lam.	Rutaceae	Tree
Canilla de Venado	Allophyllus occidentalis	(S.W.) Radlk.	Sapindaceae	Tree
Zapatero	Cupania americana	L. var Sativa D.C.	Sapindaceae	Tree
Para para	Sapindus saponaria	L.	Sapindaceae	Tree
Pala de Agua, Majomo (Caujaral)	Pouteria glomerata	(Miq.) Radlk.	Sapotaceae	Tree
Guacimo	Guazuma tomentosa	Kunth.	Sterculiaceae	Tree
Camaruco	Sterculia apetala	(Jacq.) Karsten	Sterculiaceae	Tree
Guacimo cimarron	Luehea candida	(D.C.) Mart.	Tiliaceae	Tree
Guarataro	Vitex capitata	Vahl.	Lamiaceae	Tree
Salado	Vochysia venezuelana	Stafleu	Vochysiaceae	Tree

APPENDIX C LIST OF FISH SAMPLED IN HATO PINERO.

RG SIGNIFIES VOUCHERS DEPOSITED AT RANCHO GRANDE NATURAL HISTORY MUSEUM

Myliobatiformes

· Po	otamotrygonide
	Potamotryon orbignyi Raya RG
Characif	formes
A	nostomidae
	Leporinus sp. Mije Manteca RG
С	haracidae
	Mylossoma aureus Palometa RG
	Serrasalmus medinai Caribe RG
	Serrasalmus rhombeus Caribe Amarillo RG
	Serrasalmus eigenmanni Caribe Lagunero
	Serrasalmus antoni Caribe Jetudo
	Pygocentris cariba Caribe Colorado RG
E	rythrinidae
	Hoplias malabarilus Guabina
Pı	rochilodontidae
	Prochilodus mariare Coporo RG
Silurifor	mes
А	uchenipteridae
	Parauchenipterus galeatus Apretón RG
С	allichthyidae
	Hoplosternum littorale Curito
D	oradidae
	Agamyxis pectinifrons Sierra RG
	Platydorus costatus Curita/Sierra Rayada RG
L	oricaridae
	Pterygoplichthys punctatus Corroncho
Pi	melodidae
	Microglanis sp. Arlequin RG
	Pimelodus clarias Chorroco
	Pseudopimelodus apurensis Tongo RG
	Pseudoplatystoma tigrinum Bagre Rayada
Percifor	mes
C	ichlidae
	Astronatus sp. Pavona RG

Cichlasoma krausii Pabon

APPENDIX D INDIVIDUAL PASTURES OF HATO PINERO,

PROPERTY OF DON ANTONIO JULIO BRANGER.

Los Potreros Abajo la Vigiliancia del Jefe Domingo Sulbaran (El Hato Norte, Nordeste, Este y Central)

Las Canitas Palmarita Los Tranqueros Maternidad Rancho de Sol Las Culebritas Campechena Banco Guasimito Guaicacito Cayetano Guaical Polvero Los Tres Choques Juncal Escorzonera Los Venados Los Cerritos Los Monos Matajei Las Almendrones (El Rincón de Toro) Tiranitas Merecure Corozito Lagunita Campo Alegre, Campo Alegre II Claro Cerrillo (Humidicola) Humidicola de Cerrillo Los Cartanes Mereyal Viejo Brasiliera III, Brasiliera IIII Piedras Negras I, Piedras Negras II, Piedras Negras III Nüngeral

Los Potreros Abajo La Vigilancia de Catiri Fleta (Fundacion Charco Azul-El Hato Sur, Suroeste, Noroeste)

El Guanabano Cascabel Barranca Amarilla La Canoa
Vellanista I, Vellanista II, Vellanista III La Matica I. La Matica II La Samane Buscaral Tanquecito Valle Hondo Cantanal Chaparral El Zorro Las Penitas I, Las Penitas II Los Patos Mata de Guafa I, Mata de Guafa II, Mata de Guafa III Realidad I, Realidad II, Realidad III, Realidad IV Caro Caro I. Caro Caro II. Caro Caro III El Caribe Embarcadero Los Arenales La Vaquera Carretera Cañaote El Huesero I, El Huesero II, El Huesero III, El Huesero IV Candelaria Naranjillo La Ventana Barco Largo I, Barco Largo II, Barco Largo III

Comment: These colorful place names are the sign posts, the undrawn map of Piñero. Almost all spatial references in a llanero's consciousness are the pastures or caño banks where he and his colleagues have worked. Many references are botanical in origin (Caro Caro, Caujaral, Escorzonera, Mata de Guafa, El Guanabano, Corozito, Merecure, Guasimito). Other names refer to events, some of which are not clear today. El Huesero is not filled with bones, nor is El Polvero resplendent in choking fine dust. It apparently made sense at the time of the naming. Like Popcorn Creek, deep in the pine-clad ridges of North Central Idaho, about 45 miles from the nearest dirt road, where Charlie and I ran into Kurt and Russ. After trying to cut down on food-weight carried, all they had left to eat was popcorn (after nine 10 hour days with pulaskis, pick mattoxes, and shovels, and with 20 miles and 8,000 vertical feet to get back to real food at the airstrip). That name probably didn't stick. Similarly, some of the Piñero place names used during the 1980s were changed and/or obselete by the time we arrived in 1996. What is safe to say is that these names conjure images among us workers: of deer taken by puma, drying ponds peppered with peccary tracks, poached capybaras, calves killed by jaguar, and various animals seen, company kept, and jobs done. They are colorful names, and as toasty as it got, it was colorful time.

APPENDIX E

PARAMETERS USED FOR ANNUAL GROSS PRODUCTION CALCULATIONS

Capybara
Mature at 18 months or slightly more.
Gestation about 5 months.
Some production at 23-24 months.
Using proportions from Piñero estimate 1.23 litters/year, not 1.5 as (Ojasti 1973) found in Estado Apure. Average 4 young per litter.
Adult-juvenile ratio 55-45.
28% females.
4.92 young/year, with 22 kg growth and .6 survivorship.
21.8% subadults (year 1-2) with growth of 18 kg and survivorship .8.
23.2 % juveniles (year 0-1) growth 10 kg and survivorship .7.
Sources: Polisar unpublished data and (Ojasti 1973).

White-lipped peccary
Breed at about 12 months.
Gestation about 8-8.2 months.
1.4 litters/year with 1.6 young/litter
Adult-juvenile ratio 71-29.
36% females.
2.24 young/year, with growth 30 kg and survivorship .5
29% juveniles, with growth 17.5 kg and survivorship .8.
Sources: Polisar unpublished data and (Bodmer et al. 1997; Sowls 1997)

Collared peccary Breed at about 11.5 months. Gestation 4.6-4.9 months. Parturition-gestation cycle may be around 155 days. 1.7 litters/year with 1.9 young/litter. Adult-juvenile ratio 77-23 39% females. 3.23 young per year, with growth 23 kg and survivorship .5. 23% juveniles with growth 11.5 kg and survivorship .8. Sources: Polisar unpublished data and (Bodmer et al. 1997; Hellgren et al. 1995; Sowls 1997) White-tailed deer
Females breed at 10-14 months Males at 12-15 months, 8-10 months 75% with short nubbins or spikes, 11-16 months majority are spikes or in first set cycle.
Implantation/gestation 7-8 months.
Fawn 18-22 months.
Adult-juvenile ratio 76.5-23.5.
Adult sex ratio 32 male-68 female.
52% females.
1.17 young per year, with growth 24.7 kg and survivorship .66.
12.5% young juveniles at t=0 , with growth 22 kg and survivorship .7.
11% older juveniles with growth 7.8 kg and survivorship .8.
6% of total (6/11 older juveniles) fawn, fawn growth 10 kg and survivorship .66.
Sources: Polisar unpublished data and (Brokx 1972; Hayne 1984; Teer 1984)
Spectacled caiman

Females mature in 4 years, around 60 cm SVL, courtship June and July, nesting begins in July, peaks in August, 20-30 eggs/mound, end of incubation October-November, start seeing young in November.

Sources: (Ayarzagüena 1983; Thorbjarnarson 1991; Thorbjarnarson & Velasco 1998)

Cottontail Rabbit High reproductive potential coupled with high mortality rates. Breeds in 2.5 months. Gestation 1 month. 4.6-5.7 litters/year, typically 2 young/litter. Of 22 produced in a young, five survive. Growth age 0-1 is .8 kg. Within one year, complex iteration of production and growth, as the young produced at age 3.5 months, and beyond till age 8.5 months will also produce, as will their young at t = 7 months, and then again, though less so at t = 10.5 months. Source: (Ojeda & Keith 1982)

Agouti

Used production calculations of (Kleiman et al. 1979), weights of (Linares 1998) and juvenile survivorships of (Smythe 1978).

Nine-banded armadillo.

Used (Eisenberg & Redford 1979) in which production emerges as .83 of standing crop biomass.

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APPENDIX F FOREST CLASSIFICATIONS.

Forest classification for Piñero based on 70 500m² plots, in which all trees over 4 m tall identified and enumerated. Classifications based on cluster analyses (Complete Linkage, Furthest Neighbor, Squared Euclidean) run with: 1) all species; 2) species occurring in 2.86% of plots or less removed; 3) species occurring in 4.29% or less of plots removed; 4) numbers 2 and 3 with additional removal of all species occurring in over 50% of plots; 5) numbers 1,2,3,4 with added structural variables of canopy height, mean dbh of 4 overstory trees, substrate classification; elevation classification added. One type, Sabana Seca con Chaparros, was not submitted to cluster analyses. Although populated by trees, none exceeded 4 m in height in these plots. Thus, the type was clear.

A. Sabana Seca con Chaparros (SS/CH)

1. High ridge;

CER14, 600-650; CER15, 750-800; CER16, 900-950; CER17, 1200-1250; CER 18, 1350-1400.

2. Low Ridge:

CER19, 2100-2150; CER20, 2300-2350

B. Bosque Seca (BS)

3. Bosque Seca de Cerros BSC (hillsides and low ridges)

CER5, 1050-1100; CER7, 1650-1700, CER8, 1800-1850; CGT11, 1500-1550; CGT13, 1800-1850; CER12, 2700-2650, CER13, 2600-2550; CGT14, 1950-2000; CGT2, 150-200; CER11,2400-2450; CGT6, 750-800.

4. Bosque Seca de Falda BSF (hill bases, low flanks)

CGT 7, 900-950; CGT9, 1200-1250; CGT5, 600-650; CGT10, 1350-1400; CGT3,300-350; CGT8, 1050-1100; CGT1, 50-100; CGS 3; CGT4, 450-500.

5. Bosque Seca Mezcla BSM (dense short stature forests dominated by (interchangeably) *Protium* and *Erythroxylum*. Can be fairly speciose despite these two species' dominance. A hill type, and surprisingly thick for elevation, presence seems based on aspect/exposure).

CER6, 1500-1550; CER 10, 2000-2050; CER 4, 450-500.

CER9, 1900-1950; stood out in most analyses, an anomaly, being an *Astronium* dominated forest on the back of a hill. May represent one form of transition between BS and BSD. Without saying why, *Cebus* were observed more than once in this forest section in Los Cerritos.

C. Bosque Semi-Deciduo BSD

6. Bosque Semi-Deciduo Seca BSDS (never inundates, where well-drained valleys meet hill bases)

LP1, CGS1, CGS2

7. Bosque Semi-Deciduo Tipico 1 BSDT 1 (variations of this type widespread in Piñero, low elevation forests that seasonally shallowly flood and dry)

CAN 1, 0-50; CAN 4, 550-560; CAU16, 2000-2050; CAN3, 350-400; CAN6, 800-850; CAN9, 1250-1300; CAU6, 500-550; CAN2, 250-300; CAN5, 550-600; CAN13, 1900-1950; CAU14, 1700-1750; CAN8, 1100-1150; CAU12, 1400-1450; CAN10, 1400-1450; CAN11,1550-1600; CAU11, 1250-1300; CAU18,2300-2350; CAU10, 1100-1150; CAU8, 800-850; CAU13, 1550-1600; CAU4, 300-350; CAN12, 1750-1800; CAU2, 100-150; CAN7, 950-1000; CAU9, 950-1000; CAU19, 2450-2500.

8. Bosque Semi-Deciduo Tipico 2 BSDT2 (Very close to BSDT1, seems to be related to micro-elevations in proximity to caño floodplain: of all Caño Caujaral Norte transect plots mean distance to water side was 68 m, in following 5 it was 23.2 m. Perhaps way to think of it is following: In July and August, in these plots if you hadn't recently been wading in fairly deep water, you soon would be. It seems to be a subtle transition, could even be pooled with BSD1).

CAU1, 0-50; CAU5, 450-500; CAU7, 650-700; CAU15, 1850-1900; CAU17, 2150-2200.

9. Bosque Semi-Deciduo Galeria BSDG (plots located so one boundary was edge of Caño Caujaral).

GAL1, GAL2, GAL3, GAL4, GAL5

10. Bosque Semi-Deciduo Quebrada (somewhat unique, and classification could oscillate between BS pool and BSD pool as these very narrow strips of humid forest bordered a seasonal stream set amidst steep hills. Although containing BSD1,2 elements and even BSDG elements, these forests also include some dry forest elements. Being better-drained than most BSD, they also may contain *Mangifera*, In the clusters used for conclusions, these fell amidst other semi-deciduous plots).

QUE1, QUE2

D. 11. Bosque Siempre-Verde BSV Plots in more humid soils in N. Caujaral contained breve-deciduous elements, and Stergios et. al. (1998) make the clear connection between retention of soil moisture in the dry season and frequency of evergreen species in gallery forests in Estado Portuguesa. It is my belief that these sorts of forests are a preferred type for *T. pecari*, whether along a present caño, or where old caño beds are still relatively depressed and rich and bordered by a similar forest community. Nonetheless, under scrutiny it is hard to call the forest bordering Caujaral Norte evergreen (even if parts of La Roseta were lush and green overhead and cool in the late dry season). The *Vochysia* forest at the base of Los Cerritos was a different story. While most of the Rosetta transect was dry by December, the first 300m of Los Cerritos was still a wade through water in January

CER1, 0-50; CER2, 150-200; CER3, 300-350.

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BIOGRAPHICAL SKETCH

John Polisar was born in Decatur, Georgia in 1955, while his father worked with Amalgamated Clothing in the Southern States. He grew up in the Finger Lakes region of New York state, in the town of Ithaca. Many of his younger years were spent in the western states, most often associated with mountains. He cut his teeth on the Sierra Nevadas with an uncle's help and moved on to the Northern Rockies. He received his bachelor's degree in wildlife biology and zoology from the University of Montana in 1985 and his MS degree in wildlife ecology from the University of Florida in 1992. Typically American, he is a blend of Ukrainian and Anglo-Saxon stock, both lines tending to be outspoken critical-thinkers. Married in 1989 to Joanna Persis Hemmat, they had one child, Shane Matthew, born in 1998 in Venezuela. A second child, Sophia Persis, was on the way at the time the dissertation was completed.