Vertebrate ecology in caatinga: A. Distribution of wildlife in relation to water. B. Diet of pumas (*Puma concolor*) and relative abundance of felids.

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ABSTRACT

Caatinga is a seasonally dry forest in northeastern Brazil. Despite the strong seasonality of rainfall, the fauna of caatinga is characteristic of mesic biomes and shows no special physiological adaptations for coping with water limitation. Overall, the fauna of caatinga is poor in endemics and species richness is lower than in other systems. This study has two major objectives. First, I describe the seasonal distribution of common medium- and large-sized vertebrates in relation to water sources. Second, I analyze the feeding ecology of a large, widespread predator in caatinga. This study was conducted from October 1999 until August 2000 in Serra da Capivara National Park. The first part of this study describes the seasonal distribution of tegu lizards (*Tupinambis teguixin*), rusty-margined guans (*Penelope superciliaris*), seriemas (*Cariama cristata*), crab-eating foxes (*Cerdocyon thous*), pumas (*Puma concolor*), gray brocket deer (*Mazama gouazoubira*), white-collared peccaries (*Tayassu tajacu*) and agoutis (*Dasyprocta prymnolopha*) based on observational data. During the dry season, foxes and seriemas moved from the dry plateau of the park to valleys where water holes are present. Other species showed seasonal site fidelity and were observed mostly at lower (deer) or higher (agouti) elevations. With the exception of pumas and agoutis, all species showed close association with available water sources, at least during the dry season. The year-round availability of water at lower elevations and overall differences in vegetation along the elevational gradient influenced the distribution of species are discussed. The second part of this study analyzes the diet of pumas in relation to the relative abundance and biomass of prey. The relative abundance of felids in caatinga is compared with other neotropical systems. Relative abundance of prey and felids were estimated using remote cameras.

Puma diets were described following analysis of scats. Nine-banded armadillos (*Dasypus novemcinctus*) accounted for 70 % of prey items and 69 % of the biomass consumed. Pumas preyed on armadillos and lesser anteaters (*Tamandua tetradactyla*) more than expected based on their relative abundance. Pumas selected against large prey, such as peccaries and deer, and took agoutis and skunks (*Conepatus semistriatus*) in proportion to their relative abundance and biomass. Pumas do not act as energy maximizers, but rather as number maximizers, taking prey on encounter. Habitat structure is suggested as an explanation for the observed prey selectivity, although competition with jaguars and differences in prey vulnerability could also play a role. Pumas and oncillas (*Leopardus tigrina*) are more abundant than jaguars (*Panthera onca*) and ocelots (*L. pardalis*) in this system. Greater abundance of pumas than jaguars is explained by the scarcity of large prey in this system, which favors the smaller puma. Low abundance of ocelots could be due to low density of small mammals in caatinga and competition with pumas for medium-sized prey.

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CHAPTER I

SPATIAL DISTRIBUTION OF COMMON MEDIUM- AND LARGE-SIZED VERTEBRATES IN RELATION TO AVAILABLE WATER RESOURCES IN SERRA DA CAPIVARA NATIONAL PARK

INTRODUCTION

Availability of water largely determines the distribution and abundance of animals in arid and semi-arid environments and as a consequence, distribution and quality of water are factors that influence carrying capacities of protected areas in such environments (Thrash et al., 1995). Water availability depends on rainfall, which varies greatly among and within years in arid and semi-arid environments, with most of the annual precipitation falling within only a few months each year (Mares, 1999). Variability of rainfall not only directly influences availability of water on a landscape scale but also has strong impacts on the availability of animal food resources and microclimatic conditions (Frankie et al., 1974; Bullock and Solis-Magallanes, 1990; James et al., 1999; Griz and Machado, 2001).

Water is available to animals from three different sources including free water (i.e., streams, lakes, puddles, water holes), preformed water (i.e., water contained in food), and oxidative or metabolic water (i.e., water produced as a product of the oxidation of organic compounds containing hydrogen). Highly seasonal patterns of rainfall directly determine the water levels of water holes and rivers (i.e., free water), and cause seasonal changes in the availability of food, which, in return, leads to changes in the availability of preformed water in the form of fruit pulp and fresh leaf material. In tropical dry forests, in particular, fleshy fruits are available nearly exclusively during the wet season (Griz and Machado, 2001) and water content of grasses and leaves decreases dramatically during the dry season and disappears altogether over large areas as most shrubs and trees shed their leaves and as the herbaceous layer that covers the forest floor during the wet season disappears (Bullock et al., 1995).

Water requirements and the availability of preformed water vary substantially among species and are strongly influenced by basal metabolic rates, diet, body size, and activity patterns (Robbins, 1993). In general, water requirements are highest for herbivores, intermediate for omnivores, and lowest for carnivores and granivores. Water requirements also increase with decreasing body size, because increasing metabolic rates per unit of weight and higher surface/volume ratios increase water loss through evaporation. Evaporation is also higher for diurnally active species because of higher ambient temperatures during daytime. The intake of preformed water varies substantially with diet, being highest for animal tissue and fruit (up to 70 %) and lowest for dry seeds (2 – 3 %). These differences in water content of food indirectly influence the dependence of animals on free water.

Animals may persist in water-limited environments by concentrating in areas with relatively constant supplies of water, by producing resistant life forms to overcome periods of water limitation, through dormancy, by seasonal resource tracking and movements, or because of a high degree of tolerance of low-water conditions, through behavioral and physiological adaptations (Robbins, 1993; Schmidt-Nielson, 1997;

Valenzuela and Ceballos, 2000). Although physiological adaptations to extreme water deprivation have been documented in a variety of taxa restricted to dry environments, many other, more widespread species, exclusively rely on behavioral strategies to avoid dehydration (Schmidt-Nielsen, 1997; Bothma, 1998). For example, seasonal movements from and to areas with high abundance of free water are a commonly observed behavioral strategy of medium- to large-sized vertebrates for overcoming water limitation during the dry season (Western, 1975; Rautenstrauch and Krausman, 1989; Thrash et al., 1995).

Behavioral adaptations to water limitation are expected to be particularly prevalent for animals in caatinga, a seasonally dry deciduous forest, situated in the northeast of Brazil (Sampaio, 1995). The fauna of caatinga is very poor in endemics (Vanzolini, 1976; Fonseca et al., 1999) and is characteristic of mesic environments, showing no physiological adaptation for water conservation (Mares et al., 1985). In the absence of physiological adaptations to aridity, rodents and bats, for example, continue to inhabit caatinga by persisting in mesic enclaves during droughts, recolonizing dry scrub forests during moist portions of the year (Mares et al., 1985).

Serra da Capivara National Park, the largest protected area of caatinga and the study site of this project, has no rivers and free water is available only at very unevenly distributed small water holes situated in valleys and canyons (Figure 1.1.), leaving extensive areas at higher elevations with virtually no free water (FUMDHAM, 1998). As a consequence of the spatial distribution of free water in Serra da Capivara NP, animals are expected to either engage in seasonal movements along the elevational gradient or be resident in areas with high or low availability of water, depending on their water requirements and mobility.

The ecology of vertebrates, as well as invertebrates, in caatinga is very poorly understood and many large animals have been extirpated over vast areas due to habitat alteration and hunting (Sampaio, 1995). The persistence of many species will depend on sound management practices in protected areas, which requires a better understanding of animal water requirements, likely the major limiting factor of animal distribution in this system (Mares et al. 1985). The overall goal of this study is to describe the distributional patterns of the most common medium to large vertebrate species in relation to water sources in caatinga. The focal species of this study are tegu lizards (*Tupinambis teguixin*), rusty-margined guans (*Penelope superciliaris*), seriemas (*Cariama cristata*), crab-eating foxes (*Cerdocyon thous*), pumas (*Puma concolor*), gray brocket deer (*Mazama gouazoubira*), white-collared peccaries (*Tayassu tajacu*), and agoutis (*Dasyprocta prymnolopha*).

Seasonal changes in distance to the nearest waterhole are often considered an indication of seasonal movements in relation to water availability (Western, 1975; Rautenstrauch and Krausman, 1989; Thrash et al., 1995). This distance measure does not, however, account for overall water availability to animals and ignores the local influence of water holes, other than the one closest to each animal location, on the distribution of species. In this paper, I will compare mean distance to the nearest and to the ten closest water holes between seasons. I will interpret mean distance to the nearest water hole as an approximation of how far animals are able to venture from any single water source, whereas the mean distance to the ten closest water holes will be viewed as an index of water density.

Specifically, the objectives of this study are: 1) to compare the distribution of animal locations between wet and dry seasons along the elevational gradient of the park; 2) to make a seasonal comparison of the distribution of animals in relation to the nearest water hole; 3) to determine if animals tend to be found in areas with different densities of water holes among seasons; and, 4) to extrapolate observed patterns of animal distribution in relation to water from an intensive study area to the entire park, using different water requirement models, to predict areas of occupancy by different species.

STUDY SITE

Serra da Capivara National Park (SCNP) covers approximately 130,000 ha in the southeast of the state of Piaui, Brazil (approx. 8°30-8°50' S and 42°20-42°50' W; Figure 1.1.) within the semi-arid caatinga biome. Annual rainfall in caatinga may vary from close to zero to as much as ten times the long-term annual average and deviation from the normal rainfall may be higher than 55 %. Usually, 20% of the annual rainfall occurs on a single day and 60% in a single month (de Andrade Lima, 1981; Sampaio, 1995). Most rain falls between September and March. Average annual rainfall is 644 mm, with a 50-year maximum of 1,131 mm and minimum of 250 mm (Emperaire, 1984). Mean annual temperature is 27.6° C. SCNP is the largest caatinga preserve and likely represents the last area in the entire ecosystem where jaguars (*Panthera onca*), giant anteaters (*Myrmecophaga tridactyla*), and white-lipped peccaries (*Tayassu pecari*) co-occur (Olmos, 1992; FUMDHAM, 1998).

Eight vegetation types have been described in SCNP (Emperaire, 1984). Most of the park, including the central plateau, is covered by old-growth, species-rich, arboreal-arbustive (i.e., shrubby) vegetation (6-10 m tall). Other vegetation types range from mesic 30-m tall, semi-deciduous forests located in canyons to bushy formations rich in cacti and bromeliads that occupy rocky areas (Olmos, 1992). Areas previously occupied by human settlements are covered by secondary vegetation, predominantly composed of *Croton* sp. and *Senna fannesiana*. Secondary caatinga vegetation is found mainly at intermediate elevations around 480 – 520 m.

Topographically, the park is composed of a main plateau, which is bounded by cliffs, 50 to 200 m high, and dissected by valleys and canyons, mostly near the boundaries of the park. The elevational gradient in the park ranges from 280 m to more than 600 m above sea level (Figure 1.1.). The central plateau lies between 520 and 600 m. Soils on the plateau are mainly yellow-red latosols, whereas in the canyons, soils are mainly composed of white sand. Extensive areas of shallow soils and exposed rock can be found along the borders of the plateau. My study area covered ~ 300 km^2 (23 % of the park) along the eastern border of the park, following a northeast - southwest roadway and its branches (Figure 1.1).

There is no permanent watercourse in the park. Free water is found in natural and manmade water holes and ponds distributed unevenly throughout the park (Figure 1.1.). During the wet season, water temporarily accumulates in shallow rocky depressions and puddles, which evaporate within a few days without rain. Water holes in the study area form four distinct aggregates of approximately 10 water holes each (Figure 1.1.). Rainfall is the major source of water, although several natural water holes benefit from a continuous supply of water through infiltration. I do not know the amount, quality, and persistence of water within water holes. However, just a few of those water holes that I visited regularly dried out during the dry season. Those that did dry out were artificially supplemented by the park's management shortly thereafter.

METHODS

Data collection

Data were collected from October 1999 until August 2000. Seasons were defined based on precipitation data collected during this study. November through April are referred to as wet, whereas October and May through August are dry (Figure 1.2.). Data on animal locations in both seasons are based on direct observations and tracks, recorded while driving or on foot. Observations and track records were made on 108 days during the wet season and 90 during the dry season. I used 55.8 km of roads and trails for animal observations; 10.7 km were covered on foot and 45.1 km by car. I entered the park usually shortly before or after sunrise and used either the Serra Vermelha or BR20 access (Figure 1.1.). I drove at low speed (± 25 km/h), usually from one entrance to the other but I occasionally used the same gate for entering and leaving the park. I did not drive continuously from one entrance to the other but made frequent stops to conduct observations on foot. I used a GPS unit (Garmin-GPS 12) to record UTM coordinates, date and time of observations for all animals or tracks encountered.

GIS and statistical analyses

Elevational data and general GIS layers, such as locations of water holes, park boundaries, and the road and trail system within the park were obtained through the Fundação Museu do Homem Americano (FUMDHAM). I had at my disposition a database of 256 water holes distributed within and around the park. All calculations of distance of animal locations to water sources were made in relation to the 43 water holes within my study site (Figure 1.1.). I used ArcView 3.1 and several public-domain scripts and extensions available at http://gis.esri.com/arcscripts/scripts.cfm (ESRI, Redland, CA) to produce tables relating animal locations with geographic features such as elevation, and distance to water sources.

Due to the dense vegetation of caatinga, observations of animals are mostly limited to trails and roads. Restriction to roads can bias observational data towards species that commonly use roads as traveling routes (Wolff , unpublished data), and may also creates a bias in the geographic information attributed to these observations. Indeed, values for distance to the nearest water hole or elevation are constrained by where roads are found, which is rarely representative of the overall landscape. To account for such biases, I compared all observed results on elevational distribution and mean distance to water holes to the geographic attributes of a set of computer-generated regularly spaced points along roads and trails used for animal censuses. For this comparison, I created a total of 579 points separated by 100 m along the census network, "using the route hatch 1.1." extension for ArcView 3.1 (see web site address above).

All variables were tested for normality (Shapiro-Wilk test) and equality of variances (Barlett's test) before statistical analyses. Variables that did not meet these assumptions were analyzed with appropriate non-parametric tests. All statistical tests are described in Zar (1999).

Elevational distribution The available elevational gradient of the park was subdivided in six belts of 40 m each. Thus, I expressed elevational distribution as the number of observations per species and season per 40 m elevational belt. I used a Spearman rank correlation for comparing observed frequency distributions of animal sightings at different elevations with expected values derived from the distribution of computer-generated points. The same statistical procedure was used when comparing observed frequency distributions of animal sightings at different elevations across seasons with the elevational distribution of water holes in the study area. Sample size for all correlations was six, i.e., the number of elevational belts. Significant positive correlation between the observed and expected elevational distributions indicates close to random distribution along the elevational gradient. Correlation between observed and expected should be weaker during the dry season, when the distribution of animals is most likely to be influenced by the availability of water at particular elevations. Strong significant positive correlation between the elevational distribution during the wet and the dry season is an indication of little or no changes in distribution between seasons, whereas no correlation or a negative correlation are indicative of seasonal movements.

Distance to water: Distance to water (x_{ij}) was calculated for the ten closest water holes ($1< i \leq 10$) for each animal location (j), using the “Nearest Feature v.3.3” extension. Subsequently, mean distance to the i^{th} water hole ($\Sigma x_{1j}/n_y$, Σ_{2j}/n_y,…, $\Sigma x_{10j}/n_y$) and the overall mean distance to the 10 closest water holes ($\Sigma x_{ij}/n_y$) were calculated for each species (y) for both seasons. Mean distance was calculated for the 10 closest water holes because water holes within the study area were found in four distinct aggregates of approximately 10 water holes each (Figure 1.1.). To compare the mean distance to water for animal locations between seasons and across species, I used a Kruskall-Wallis test. Multiple comparisons of mean distance to water were made using a non-parametric multiple comparisons test with unequal sample sizes (Zar, 1999). The mean distance of water holes and computer-generated points to the park's border were compared using a Mann Whitney U test.

Modeling of animal distribution: Water requirements and mobility vary among focal species and, consequently, animals are expected to perceive the distribution of water holes (i.e., density) in their surroundings at different scales. The extrapolation of potential habitat for different species from the intensive study site to the entire park was based on the spatial attributes of a set of evenly spaced points that covered the park and a 5 km buffer zone. This point file was created using a set of straight vertical lines, separated by 100 m (extension: Grmake2) that covered the park and the 5 km buffer zone. I then used the "route hatch 1.1" extension (see above) to create a total of 330,180 points, separated by 100 m, along these lines. The distance from any of these points to the i^{th} ($1< i \leq 10$) nearest water hole (using all 256 mapped water holes) was calculated using the Nearest Feature V.3.3 extension.

Models were based on observed mean distances to the 10 nearest water holes (x_i) within the intensive study area. For each species, I identified all computer-generated points within the area of the park and the 5-km buffer that satisfied the conditions of mean distance to the i^{th} water hole assigned by the models described below. The area of potential habitat was calculated by summing the area covered by all points.

Model 1. Animals are found exclusively within x_1 m of the nearest water hole, independently of all other water holes. This scenario describes the movements and distribution of water-dependent species, whose home range is centered around a single water hole.

Model 2. Animals are found in areas that are within x_1 OR x_2, ….,OR x_{10} m from the i^{th} water hole ($1 < i \leq 10$). This least-restrictive scenario describes the distribution and movement pattern of a water-independent species that occasionally drinks when water is available.

Model 3. Animals are found in areas that are within x_1m of the nearest water hole AND within x_2 OR x_3, …., OR x_{10} m or the i^{th} water hole. This model is similar to the first one, in that species need to be in the vicinity of water at all times but their home ranges exceed the immediate vicinity of a single water hole and need to comprise more than one water hole.

RESULTS

Elevational distribution

Overall, I obtained 165 animal locations during the dry and 229 during the wet season (Table 1.1.). Seriemas, pumas, and guans were recorded more frequently during the dry season. Tegu lizards showed the largest difference between seasons, with 95 % of all records made during the wet season.

The elevational distributions of foxes, peccaries, guans, deer and tegu lizards were significantly correlated with the elevational distribution of computer-generated points (i.e., points along census network) during the wet season (Figure 1.3., Figure 1.4., Table 1.2.) indicating that their distribution was not different from random. The guan was the only species showing significant correlation with expected during the dry season (Table 1.2.).

Observed patterns of elevational distribution between wet and dry season were significantly correlated for guans and deer. Lack of correlation between seasons for all other species, suggest seasonal differences in distribution. The distributions of seriemas (dry season: $r = 0.986$, $p < 0.001$) and deer (dry season: $r = 0.985$, $p < 0.001$; wet season: $r = 0.896$, $p = 0.016$) were significantly correlated with the distribution of water holes along the elevational gradient of the study site. No seasonal analysis of the elevational distribution of tegu lizards was attempted because of the limited number of observations during the dry season (Table 1.1.). Both foxes and seriemas show clear evidence of a downward movement during the dry season, when they were observed particularly more than expected between 440 and 480 m (Figure 1.3.).

Distance to nearest water source

There was no significant difference in either season between observed and expected mean distance to the nearest water hole for all species combined (dry season: 1389 m ± 86 (S.E.); wet season: 1282 m ± 64 (S.E.); expected: 1323 m ± 44; Kruskall-Wallis $\chi^2 = 0.455$, df = 2, p = 0.792). Nevertheless, significant differences among species within and between seasons and between species and expected values existed (Kruskall-Wallis $\chi^2 = 57.8$, df = 16, $p < 0.001$). Agoutis occur farther than expected from water holes during the dry season and were found farther from the nearest water hole than any other species, except for peccaries, during both wet and dry seasons. Despite the lack of significant seasonal differences in distance to the nearest water hole, species could be classified in three groups, based on their observed distribution in relation to the nearest water hole (Figure 1.5., Table 1.3.): 1. Species with more than 75 % of observations within 1500 m of the closest water hole during both seasons (tegu, seriema, deer); 2. Species with more than 75 % of observations within 1500 m of the nearest water hole during the dry season and less than 75 % of observations within 1500 m during the wet season (fox, guan); 3. Species with less than 50 % of observations within 1500 m of the closest water hole during both seasons (agouti).

Density of water holes

Mean distance to the 10 nearest water holes was different from expected during the dry season for all species combined (dry season: 3158 ± 39 (S.E.); wet season: 3060 ± 31 (S.E.); expected: 2981 ± 20 (S.E.); Kruskall-Wallis $\chi^2 = 14.5$, df = 2, p = 0.001).

Mean distance to the 10 closest water holes differed among species, between seasons (Kruskall-Wallis $\chi^2 = 353.95$, df = 16, $p < 0.001$) (Table 1.4.). Agoutis were found in areas with fewer water holes than any other species in both seasons. During the wet season, guans occupied areas with fewer water holes than did pumas, tegu lizards, and seriemas. During the wet season tegu lizards and deer were found in areas with more water holes than expected; guans were found in areas with fewer water holes than expected during the wet season. Seriemas were found in areas with more, and agoutis in areas with fewer water holes than expected during both seasons. No significant differences in mean distance to the 10 nearest water holes between seasons could be detected for any of the species.

Modeling of animal distributions

Models differ in terms of total area of potential habitat they define, and in the degree of fragmentation of identified areas (i.e., the number of distinct patches) within the park (Table 1.5., Figure 1.6.). Independent of the model, total area of potential habitat increases and the degree of fragmentation decreases with increasing mean distance from water. Model 3 (water-dependent species with large home ranges, including deer, foxes, seriemas) provides the smallest area of distribution, and an intermediate level of fragmentation. Model 1 (water-dependent species with small home ranges, including tegu lizards) produced the highest degree of fragmentation and the second largest overall area. Finally, Model 2 (species less dependent on water with large home ranges, including pumas, peccaries, agoutis and guans) produces the largest overall area and the lowest degree of fragmentation.

The mean distance of water holes from the park's border is significantly smaller than expected based on computer-generated points (water holes: 2,973.4 m ± 356.7 (S.E.); random points: 4,591.2 m ± 153 (S.E); Mann Whitney U = 3,025, P < 0.001), indicating that the distribution of water holes is significantly biased towards the park's edge. The percentage of area of occupancy situated outside of the park's boundaries increases with mean distance form the nearest water hole, varying between approximately 15 % for tegu lizards to more than 20 % for agoutis (Figure 1.7.).

DISCUSSION

Roads and trails in the park are, for the most part, ancient manmade pathways that connect different water holes in the region, which limits the access of people to areas rich in water (FUMDHAM, 1997). As a consequence, large areas of the park (i.e., areas without water) are relatively inaccessible, which limited my ability to observe large-scale movements between water-poor and water-rich areas. The distribution of water in the study site also affects the applicability of the models used for extrapolating species' distributions to the entire park. For species found at greater than expected distances from water, such as pumas, agoutis and peccaries, extrapolations likely underestimate their overall distribution. However, species found at closer than expected distances from water, such as tegu lizards, deer and foxes are very likely to be spatially restricted and, thus, extrapolations to other areas may be justified.

Despite the spatial limitations of the study area, distribution of focal species along the elevational gradient did appear to be influenced by the availability of water. All species, with the exception of pumas and agoutis, showed a close association with available water sources at least during the dry season. Agoutis showed the most distinctive distributional pattern of all species, being observed most frequently at high elevations far away from water. Crab-eating foxes and seriemas seem to undergo seasonal movements to lower elevations. Guans also seemed to expand their range to lower elevations during the dry season, abandoning areas above 600 m. Other species showed seasonal site fidelity and were observed mostly at lower (deer) or higher (agouti) elevations. Although peccaries appeared to be restricted to intermediate elevations during the dry season, documentation of seasonal movements of wide ranging species, such as peccaries and pumas would require sampling over a much greater area.

Whether the distribution of species is driven by the availability of water or other factors such as differences in vegetation and food availability along the elevational gradient remains unclear and requires direct monitoring of animal movements and visitation at water holes (Vaughan and Weis, 1999). Nevertheless, results of this study suggest that deer, seriemas and tegu lizards are restricted to areas close to water holes. Related species are dependent on free water at least during periods of water shortage. For example, guans (*Penelope albipennis*) and deer (*Odocoileus hemonius*) have been reported to drink frequently and to move to areas where water still remains during the driest part of the year (del Hoyo, 1994; Boroski and Mossman, 1996, 1998; Rautenstrauch and Krausman, 1989; Sanchez-Rojas and Gallina, 2000). Tegu lizards, because of their exclusively diurnal activity pattern, which exposes them to higher ambient temperatures and risk of increased water loss, need to derive a significant portion of water from sources other than food (Green et al., 1997), which may explain their close association with free water in Serra da Capivara NP. Increased water loss during the dry season seems to be incompatible with sustained activity of tegu lizards in caatinga, as they go into dormancy during the driest part of the year.

The dependency of frugivores on free water is likely to be affected by seasonal changes in fruit production. Fleshy fruits, rich in preformed water, are produced nearly exclusively during the wet season in caatinga (Griz and Machado, 2001). Species feeding on fleshy fruit may either switch to food poor in preformed water, which increases their requirements for free water, or move to canyons at lower elevations during the dry season where fleshy fruit are still available (Emperaire, 1984; Coimbra-Filho and de Gusmao Camara, 1996). Peccaries in dry forests feed mostly on nutritious and succulent fruits and leaves during the wet season and switch to low quality tubers and roots in the dry season (McCoy et al., 1990; Martinez-Romero and Mandujano, 1995; Mandujano, 1999). When succulent plants are readily available, peccaries can meet their water requirements exclusively through preformed water (Minnamon, 1962 in Sowls, 1997). The relative scarcity of fruit in Serra da Capivara NP, coupled with a low intake of preformed water during the dry season, may make peccaries in caatinga more dependent on free water than in other systems, and may explain their closer association with water when fruit is scarce.

Seasonal changes in diet that are related to fruit avalability may also increase the water requirements of crab-eating foxes during the dry season. During the wet season, foxes feed extensively on fleshy fruit such as *Ziziphus joazeiro* and *Spondias tuberosa* (L. Griz, unpub. data), which are found at high densities within a few areas of the park. Thus, not only do they feed on food that is rich in preformed water, but their energy expenditure may be less due to the local abundance of fruit in relatively small patches. Dry season diets are mainly composed of animal food, which although rich in preformed water, also contains much protein. The metabolism of protein produces nitrogenous waste, excreted as urea in urine, which requires water as a solvent (Robbins, 1993). Agoutis mainly feed on fruit pulp during the fruiting peak and switch to seeds when fruit production is low (Griz, unpublished data, Henry, 1999). Scatter hoarding provides them with sufficient supplies of seeds for periods of low fruit production. Thus, agoutis, as opposed to guans, may not need to move from the plateau to mesic canyons. Exactly how agoutis cope with low water availability remains unclear but may involve physiological adaptations for water conservation and reabsorbtion and/or behavioral strategies (see Morton and MacMillan, 1982).

Differences in vegetation along the elevational gradient are likely to be another major factor determining the distribution of species described here. The central valley of my study site was used as agricultural land before the creation of the park. As a result, most of the vegetation found at intermediate elevations is composed of secondary vegetation dominated by *Croton* sp. and *Senna fannesiana*. These legumes produce small seeds commonly consumed by deer. Large seeded species such as *Manihot* sp. and *Dioclea*, which are consumed by agoutis and peccaries (Olmos, 1993a) are found nearly exclusively at higher elevations, characterized by primary or old-growth forest. Thus, the distribution of deer and agouti may at least in part be related to the availability of preferred food resources at different elevations.

Modeling has shown that water-dependent species with large home ranges have the smallest amount of suitable area available to them. As a result of the clumped distribution of water holes along the border of the park, the same species are exposed to increased mortality conditions related to human activity along boundaries of protected areas (Woodroffe and Ginsberg, 1998). Water close to the park boundaries also attracts livestock and feral pets (e.g., cows, goats, horses, dogs), which negatively impact native species through predation, competition for water, and possible transmission of diseases. As a consequence, further artificial water holes should be constructed towards the interior of the park, if there were a need for more water developments. Whether more water developments are needed remains unclear, although this study has shown that several species may benefit from such initiatives in the short run. A pilot study on the use of water holes by wildlife species proved that species such as deer, puma, foxes, oncillas (*Leopardus tigrina*), opossums (*Didelphis marsupialis*) and numerous birds including rare species such as King Vultures (*Sarcoramphus papa*) regularly drink at water holes in Serra da Capivara NP. Increased water availability would not create the same problems of overgrazing, soil compactation and consequent stalling of regeneration process observed in many parts of Africa and Australia (Morton, 1990; Parker and Witkowski, 1999; Owen-Smith, 1996), because biomass of browsers and grazers is comparatively low. In the long run, however, increased water availability will benefit local wildlife populations only if water is clearly the main limiting factor (Robbins, 1993).

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Table 1.1. Number of observations of focal species during the wet and dry season in Serra da Capivara NP (October 1999 – August 2000). Observations for peccaries and pumas include direct observations and track records.

Species		Family	Season	
Common name	Scientific name		Dry	Wet
Tegu	*Tupinambis teguixin*	Teidae	4	70
Rusty-margined guan	*Penelope superciliaris*	Cracidae	31	29
Red-legged seriema	*Cariama cristata*	Cariamidae	20	13
Crab-eating fox	*Cerdocyon thous*	Canidae	18	25
Puma	*Puma concolor*	Felidae	41	18
Agouti	*Dasyprocta punctata*	Dasyproctidae	25	28
Gray brocket deer	*Mazama gouazoubira*	Cervidae	14	20
Collared peccary	*Tayassu tajacu*	Tayassuidae	12	26

Table 1.2. Relationship between the elevational distribution of focal species between the wet and dry season and between seasons and expected. Expected values are based on the elevational distribution of computer-generated points along the census network in Serra da Capivara NP. (Spearman rank correlation coefficients (r_s) and P values are given)

	Wet-Dry		Dry-Expected		Wet-Expected	
Species	r_s	P	r_s	P	r_s	P
1. Species showing evidence of seasonal movements along the elevational gradient						
Seriema	0.516	0.29	0.714	0.11	0.395	0.43
Fox	0.185	0.72	0.152	0.77	0.986	0.00
Puma	0.478	0.34	0.771	0.07	0.478	0.34
Peccary	0.216	0.68	0.213	0.69	0.986	0.00
Agouti	0.309	0.55	0.290	0.58	0.725	0.10
2. Species showing no evidence of seasonal movements along the elevational gradient						
Tegu					0.886	0.02
Guan	0.812	0.05	0.886	0.02	0.844	0.04
Deer	0.955	0.00	0.795	0.06	0.883	0.02

Table 1.3. Mean distance (m) and S.E. of animal locations to nearest water hole in the wet and dry season, and both seasons combined. Mean distance (m) to the nearest water hole of computer-generated points along the census network was 1323 ± 44 (S.E.)

Species	Dry season		Wet season		Seasons combined	
	X	S.E.	X	S.E.	X	S.E.
Puma	1356	138	1162	171	1297	109
Peccary	1586	282	1612	264	1618	167
1. Species with more than 75 % of observations within 1500 m of the closest water hole during both seasons						
Tegu[*]					964	79
Seriema	1114	118	1026	154	1080	92
Deer	945	200	906	159	922	123
2. Species with more than 75 % of observations within 1500 m of the nearest water hole during the dry season and less than 75 % of observations within 1500 m during the wet season						
Guan	1269	251	1631	209	1444	164
Fox	1042	211	1328	199	1208	146
3. Species with less than 75 % of observations within 1500 m of the closest water hole during both seasons						
Agouti	2349	260	2029	214	2180	166

[*] Tegus are included in group 1. because they most likely go into dormancy during the dry season within the same area they occupied during the wet season

Table 1.4. Combined mean distance (m) of animal locations to the i^{th} $(1 < i \leq 10)$ water hole between seasons in Serra da Capivara NP (October1999 – August 2000). The expected combined mean distance to the ith water hole of computer generated points along the census network was 2981 ± S.E. 20.

Species	Dry season		Wet season	
	X	S.E.	X	S.E.
Teu	2567	295	2685	55
Seriema	2541*	84	2460*	98
Deer	2750	170	2590*	100
Puma	3220	78	2951	115
Agouti	4042*	102	3881*	72
Peccary	3008	123	3269	94
Guan	3186	88	3415*	86
Fox	2759	115	3329	93

* significantly different from expected

Table 1.5. Area of potential habitat (ha) of different species according to different water requirement scenarios.

	Dry season			Wet season		
Scenario	1	2	3	1	2	3
Tegu				13,531		
Deer			13,170			12,764
Fox			15,505			22,132
Seriema			16,463			14,647
Guan		63,148			66,860	
Puma		65,887			58,402	
Peccary		60,362			67,104	
Agouti		82,922			77,416	

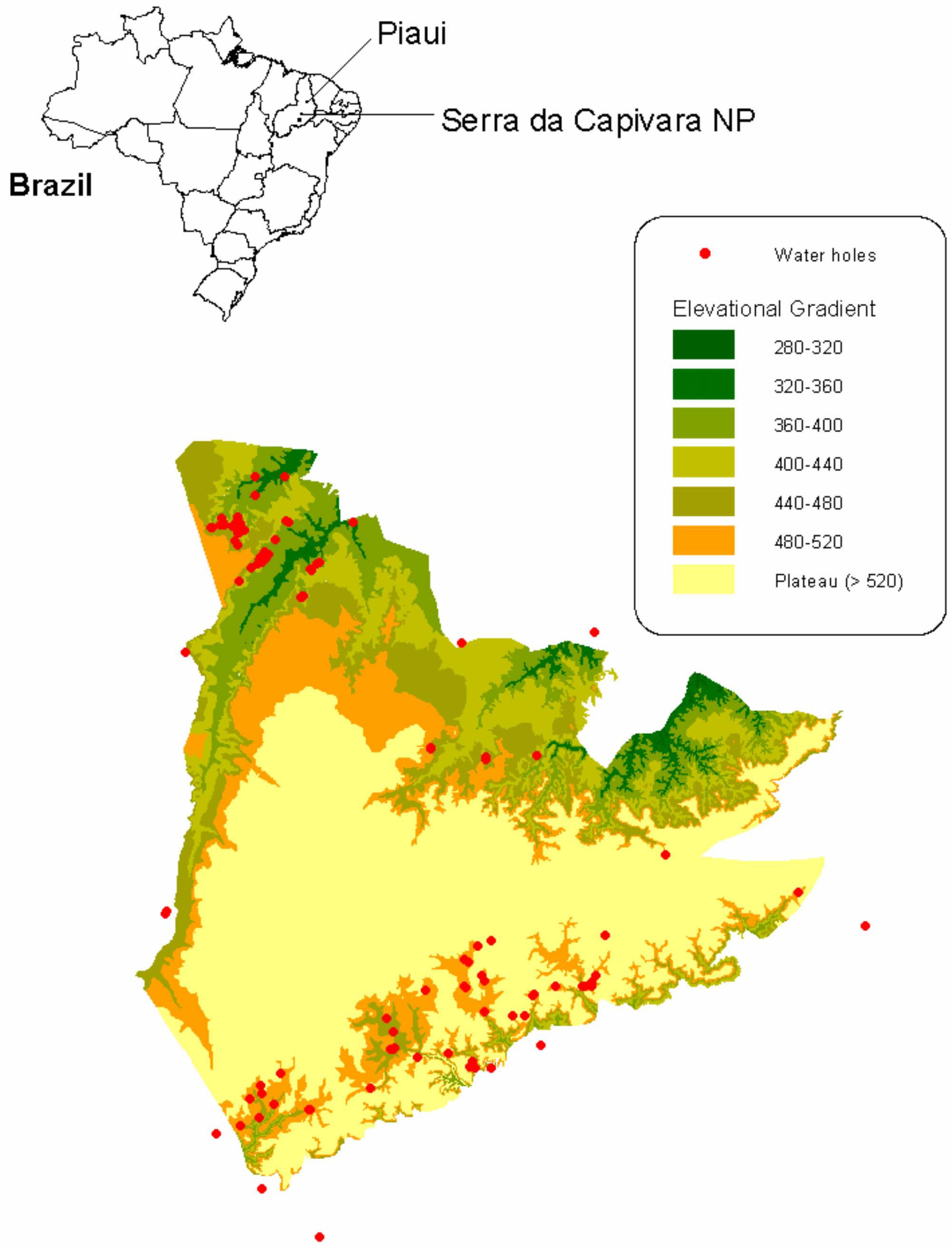

Figure 2.1. Serra da Capivara National Park: A: Location in Brazil, B: Elevational gradient, census network, and distribution of water holes.

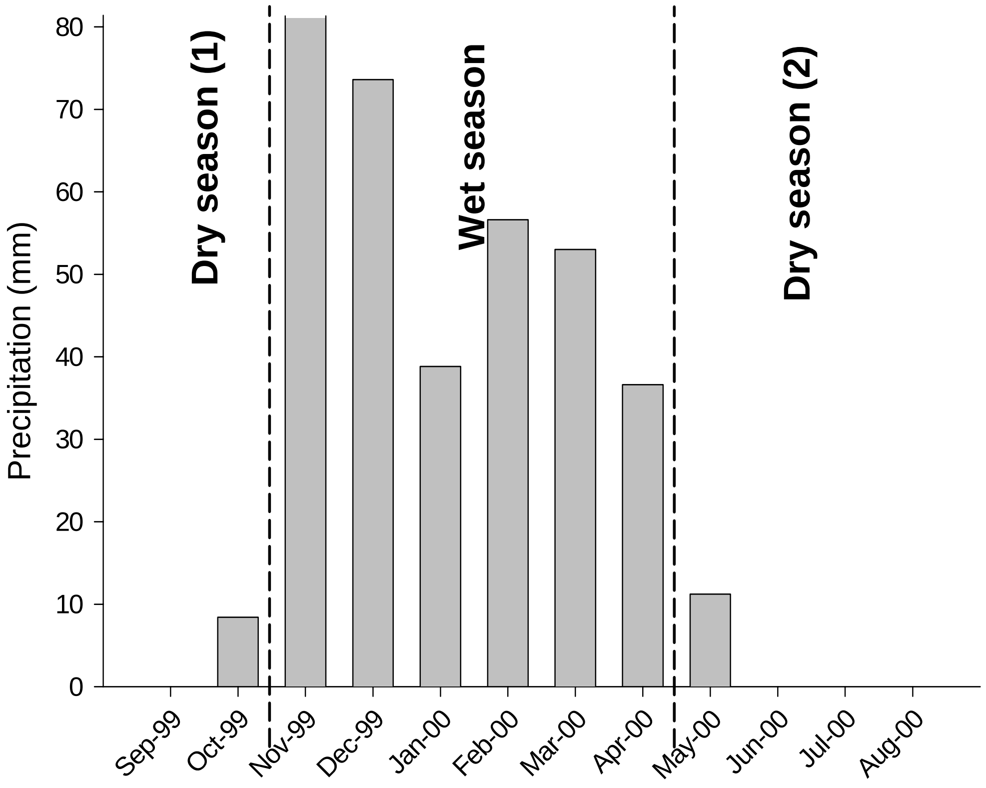

Figure 1.2. Monthly precipitation (mm) recorded in Serra da Capivara NP during the study period (October 1999-August 2000)

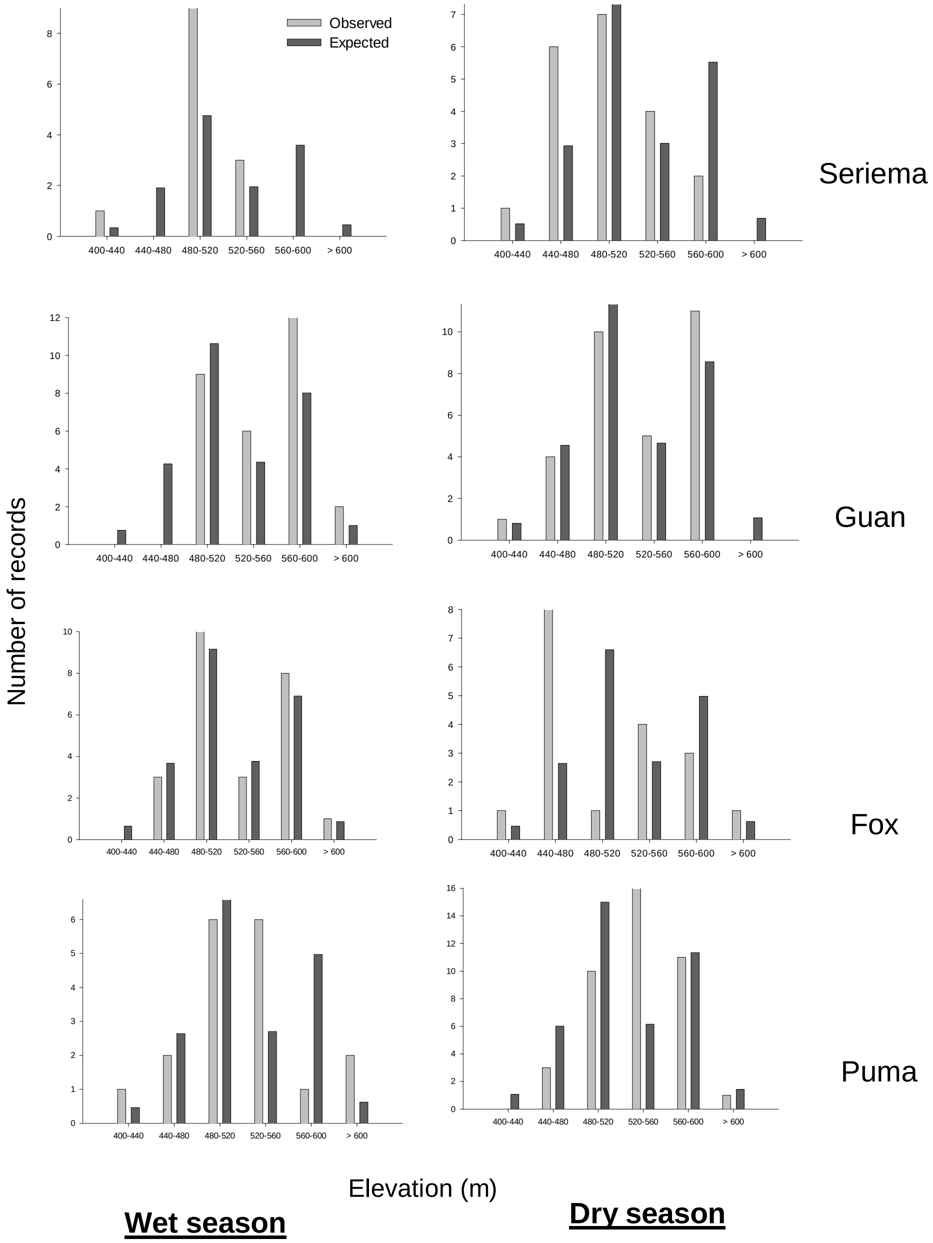

Figure 1.3. Seasonal elevational distribution of seriemas, guans, foxes and pumas in Serra da Capivara NP (October 1999-August 2000)

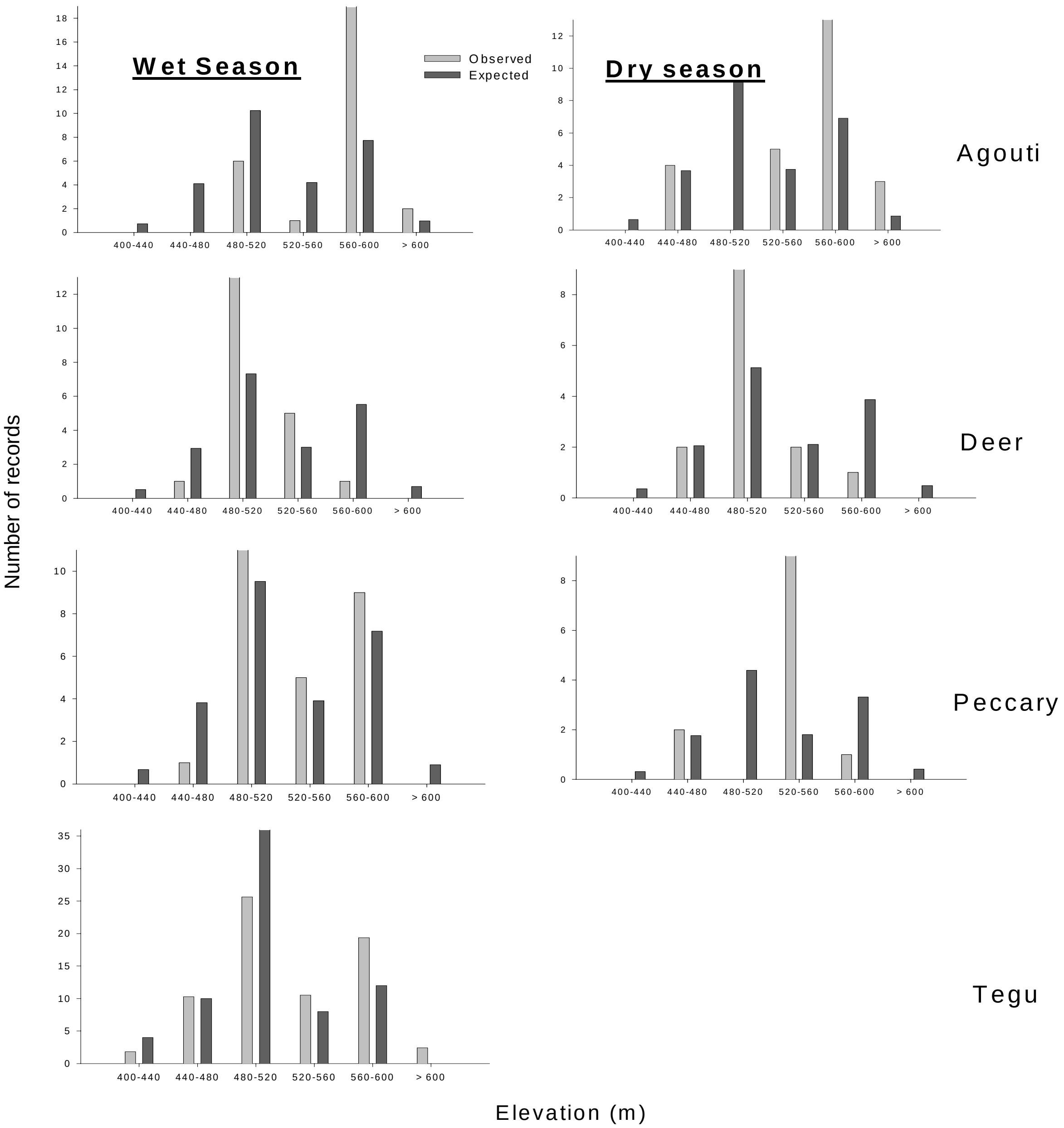

Figure 1.4. Seasonal elevational distribution of agoutis, deer, peccaries and tegu lizards in Serra da Capivara NP (October 1999-August 2000)

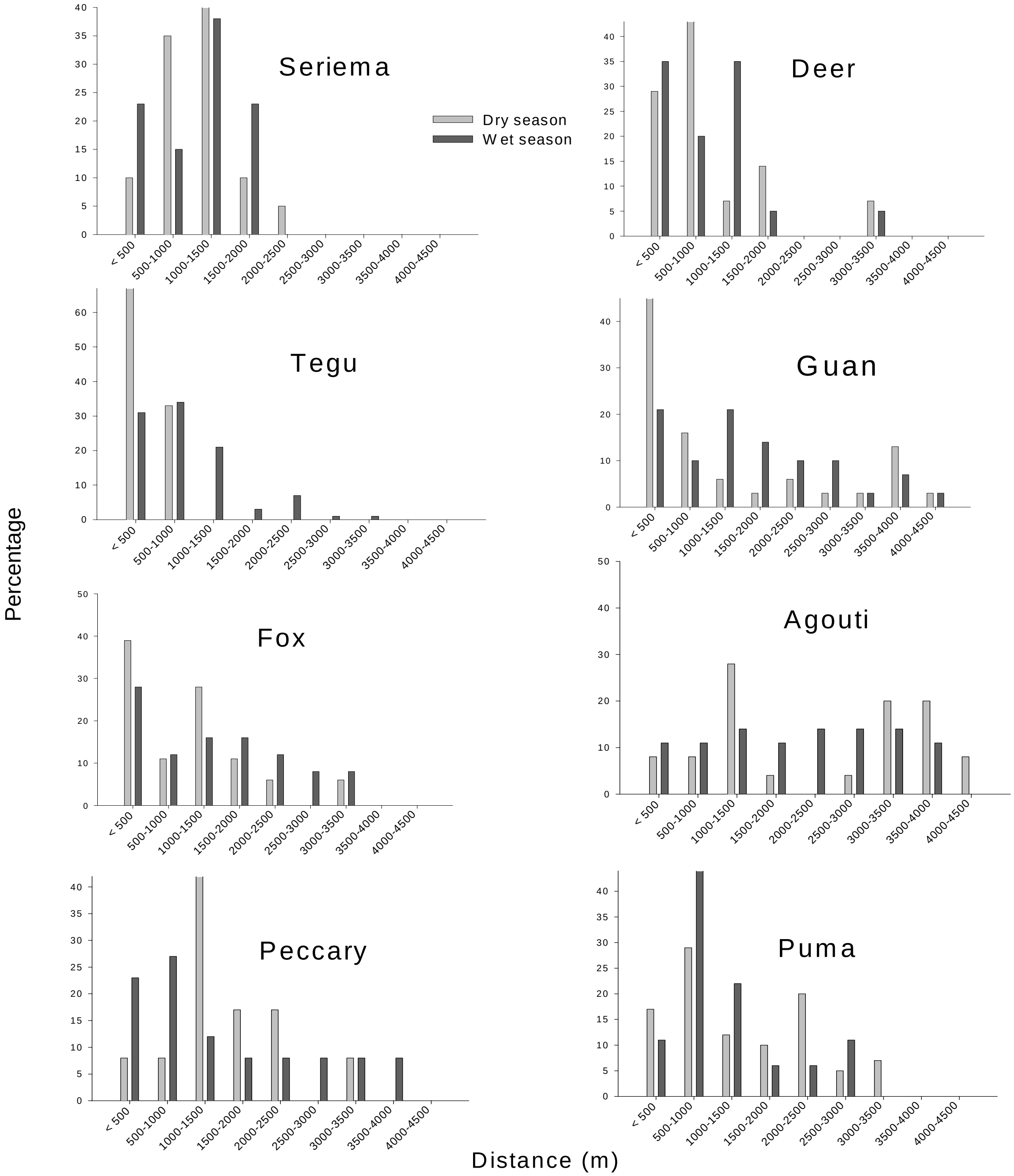

Figure 1.5. Percentage of animals sightings within 500 m intervals from the nearest water hole during the wet and dry season in Serra da Capivara NP (October 1999-August 2000)

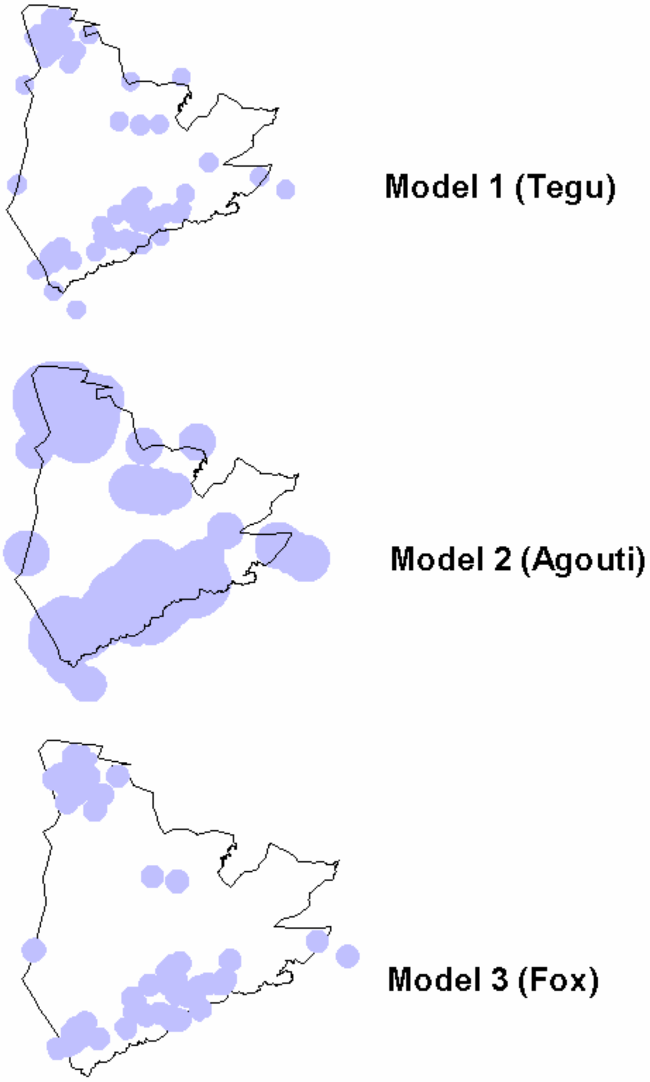

Figure 1.6. Comparative illustration of area of potential habitat identified according to the three water requirement models (one species per model is shown)

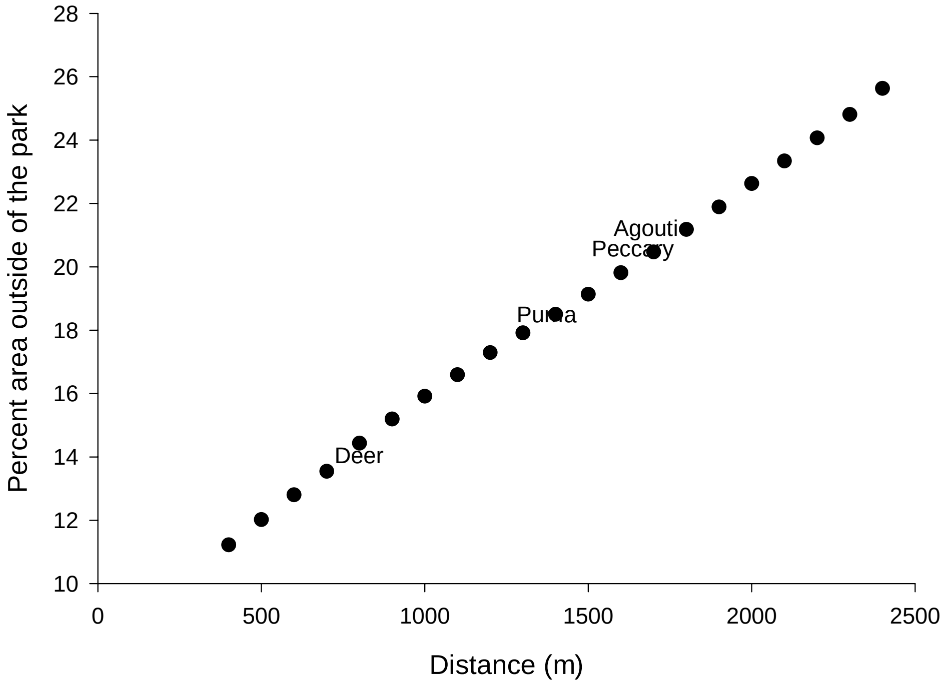

Figure 1.7. Relationship between distance to the nearest water hole (m) and the percentage of the area of occupancy found outside of the park's boundaries

CHAPTER II

FEEDING ECOLOGY OF PUMAS (*PUMA CONCOLOR*) IN CAATINGA AND THE IMPORTANCE OF PREY AVAILABILITY IN DETERMINING RELATIVE ABUNDANCE OF NEOTROPICAL CATS

INTRODUCTION

The puma (*Puma concolor*) is the most widely distributed mammal species (apart from humans) in the western hemisphere, ranging from southwest Canada to the southern tip of Argentina (IUCN, 1996). It occurs in habitats as diverse as arid deserts, tropical rainforests and cold coniferous forests, from sea level up to 5,800 m in the Andes (Eisenberg and Redford, 1999). The species composition and characteristics of prey (i.e., abundance, distribution, size, defenses), vegetation, climatic conditions and the presence and abundance of other large carnivores and potential competitors vary considerably across the puma's geographic range. Each of these factors and any combination thereof may represent ecological constraints that can directly and indirectly affect the feeding ecology and abundance of pumas (Sunquist and Sunquist, 1989).

Whereas competition is often the ultimate force regulating relative abundance of sympatric predators (Seidensticker, 1976; Sunquist and Sunquist, 1989; Creel and Creel, 1996; Durant, 1998), it is strongly influenced by the availability of prey (Karanth and

Nichols, 1998; Karanth and Sunquist, 2000). Interspecific competition may be reduced by selection of different prey species (Karanth and Sunquist, 1995, 2000), selection of different prey size (Gittleman, 1985), selection of different habitats (Fedriani et al., 1999) or spatial avoidance (Durant 1998). Differences in prey selection among sympatric predators may occur because of differences in hunting strategies (Kruuk, 1972; Schaller, 1972) or because of differences in body size of predators that have similar morphologies and hunting strategies (Rosenzweig, 1966).

In temperate systems, pumas co-occur with wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), and coyotes (*C. latrans*), with which they share a common prey base primarily composed of ungulates. Differences in hunting strategies suggest that prey selection should differ among these species (Kruuk, 1972; Schaller, 1972), but empirical evidence of such differences is still lacking (Kunkel et al., 1999). In the Neotropics, pumas, ocelots (*Leopardus pardalis*) and jaguars (*Panthera onca*) are sympatric over the most of the jaguar's range. In general, jaguars (49.0 – 99.5 kg) are larger than pumas (26.0 – 52.8 kg), although male pumas reach the same body weight as female jaguars. Ocelots are less than one-third the weight of a puma (8.9- 11.2 kg)[1]. Several small felids co-occur with these three larger cats throughout their common distributional range. Differences in body size among species suggest that their coexistence may be mediated by prey-size segregation. Indeed, although dietary overlap between jaguars and pumas is high, pumas tend to take relatively smaller prey than jaguars, at least in most places (Schaller and Crawshaw, 1980; Emmons, 1987; Taber et al., 1997). Ocelots prey mainly

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[1] (weight ranges represent the maximum and minimum mean weight recorded from different localities in the neotropics, see de Oliveira, 1994)

on species weighing less than 1 kg and show little dietary overlap with both large cats (Emmons, 1987; Crawshaw, 1995).

Studies of tigers (*Panthera tigris*) and leopards (*P. pardus*) have shown that their coexistence and relative abundance is governed primarily by the availability and relative abundance of prey of different size classes (Karanth and Nichols, 1998; Karanth and Sunquist, 2000). Based on these studies, the following predictions were developed to explain the relative abundance of two different-sized felids in forested areas (Karanth and Nichols, 1998; Karanth and Sunquist, 2000): 1.) High densities of both cats are expected in areas with abundant large and medium-sized prey because diet segregation by prey size is possible. 2.) The density of the smaller species is expected to decline in areas with low densities of large prey because the larger cats switch to medium-sized prey, resulting in increased competition between species. 3.) The density of the larger species is expected to decline and that of the smaller one to increase in areas where both large- and medium-sized prey are scarce because smaller cats are able to better survive on smaller prey.

Differences in taxonomic composition and body-weight distribution of mammal assemblages throughout the Neotropics (Fonseca et al., 1999) suggest that substantial geographic variation in competitive interactions and relative abundance among neotropical felids should be expected. Considerable geographic variation in diet of jaguars and pumas substantiate this suggestion (see Rabinowitz and Nottinham, 1986; Taber et al, 1997; Nunez at. al, 2000; Crawshaw and Quigley, 2001 in press). When competition with jaguars is low (i.e., because of low density of large- and medium-sized prey; prediction 3), pumas are expected to be more abundant. In return, this may increase interspecific competition between pumas and ocelots, leading to lower densities of the latter. Low densities of ocelots, on the other hand, may lead to high densities of small cats, suggesting that relative abundance of pumas and jaguars may indirectly control the relative abundance of smaller cats (see Terborgh, 1988).

In the absence of competition with jaguars (i.e., low density of medium- and large-sized prey) prey selection by pumas is expected to be influenced mainly by the relative size distribution and abundance of prey. Theory predicts that when prey density is low, pumas are expected to select prey in accordance with their relative abundance in the environment (i.e., number maximizer) and not show a preference for larger, more energetically profitable prey (i.e., energy maximizers) (Griffith, 1975).

In this paper, I describe the diet of pumas in relation to prey availability in caatinga, a dry forest in northeastern Brazil that is characterized by low abundances of small mammals and the absence of several large mammals found in other systems (Streihlein, 1982, Sampaio, 1995; Fonseca et al., 1999). I then estimate the relative abundance of pumas, jaguars, ocelots and small felids in this particular system and discuss how prey availability may influence the relative abundance of felids in the neotropics. The importance of abundance of water and relative differences in body size among neotropical ecosystems is also discussed. This study is among the first to provide simultaneous data on relative abundance of neotropical felids and their major prey species from a single site. My predictions are that pumas should be more abundant than jaguars because of low species richness and abundance of prey and that ocelots should be rare because of low densities of small mammals and increased competition with pumas for medium prey. Small cats are expected to be more abundant than ocelots because of reduced competition by the latter and the greater ability of small cats to rely on small lizards as an alternative prey to small mammals. Pumas are expected to act as number maximizers, taking their prey in accordance to relative abundance in the environment, rather than their relative biomass.

STUDY SITE

This study was conducted at Serra da Capivara National Park (SCNP), which covers approximately 130,000 ha in the southeast of the state of Piaui, Brazil (approx. 8°30' - 8°50' S and 42° 20' - 42°50' W) (FUMDHAM, 1998). It is the largest caatinga preserve and likely represents the last area in the entire caatinga ecosystem where jaguars, giant anteaters (*Myrmecophaga tridactyla*), and white-lipped peccaries (*Tayassu pecari*) co-occur (Olmos, 1992; FUMDHAM, 1998). Caatinga is characterized by a semi-arid climate. Annual rainfall in SCNP is extremely variable and unpredictable both in total amount of rain as well as timing throughout the year (de Andrade Lima, 1981; Emperaire, 1984; Sampaio, 1995). In SCNP, most rain falls between September and March. Average annual rainfall is 644 mm, with a 50-year maximum of 1,131 mm and minimum of 250 mm (Emperaire, 1984). Mean annual temperature is 27.6° C.

Eight vegetation types have been described in SCNP (Emperaire, 1984). Most of the park is covered by a species-rich, arboreal-arbustive (i.e., shrubby) vegetation (6-10 m tall). Other vegetation types range from mesic 30 m tall semi-deciduous forests located in canyons to bushy formations, rich in cacti and bromeliads that occupy rocky areas (Olmos, 1992).

METHODS

Scat collection and analysis

The diet of pumas was described following analysis of scats collected in SCNP between October 1999 and July 2000. All signs (e.g., tracks, scrapes, odor) useful for subsequent identification of the species producing the scat were recorded for each collection. Scats were collected opportunistically throughout the park but most sampling effort was allocated to trails and roads used for prey censuses (see chapter 1). Because I frequented these trails on a regular basis, scats were collected 'as they were produced', which increased the likelihood of finding associated tracks or other sign that allowed *in situ* identification of the species depositing the scats in most cases. When *in situ* identification was impossible, scats were searched for carnivore hair, which are ingested during autogrooming. Hairs were compared to a reference collection of hair samples of all carnivores that occur in the park. Scats which could not be identified to species were not included in analyses.

Scats were air-dried following collection. Dry scats were broken up under running water and remains were separated by thorough washing through a sieve with a mesh size of 0.5 mm. Macroscopic remains retained by the sieve were separated, dried in the sun and examined under a stereoscope. Remains of vertebrates were identified to species if possible. Identification of macroscopic remains was done using a reference collection of vertebrate hair, teeth, bones, dermal scutes (armadillos), claws, and scales (reptiles).

The mean weight of vertebrate prey (MWVP) was calculated by summing the products of the number of individual prey found in scats by their natural-log-transformed weight, divided by the total number of prey (Iriarte et al., 1990). The standardized food niche-breadth (B_{sta}) was calculated following Colwell and Futuyma (1971): $B_{sta} = (B_{obs} - B_{min})/(B_{max} – B_{min})$, where B_{obs} is the observed niche breadth (i.e., $B_{obs} = 1/\Sigma p^2_i$, where p_i is the relative occurrence of prey taxon i in the diet), B_{min} is the minimum niche breadth (= 1), and B_{max} is the maximum possible niche breadth (the number of prey taxa taken). This standardized measure (B_{sta}) has been used in other studies of puma diets (Iriarte et al., 1990; Taber et al., 1997).

Dietary composition was described as the frequency of occurrence of different food items, expressed as the percentage of the total number of scats (FO_i) and the percentage of occurrence, expressed as the percentage of the total number of occurrences of all food items (PO_i) in the diet. Percent biomass or prey consumed (PBC_i) was calculated using a correction factor ($Y = 1.98 + 0.035 X$) developed by (Ackerman et al., 1984), which accounts for prey size and differences in the amount of prey remains found in scats due to differences in prey body size, where Y is the weight of food consumed per scat and X is the weight of the live prey. This correction factor reduces the likelihood of overestimating the relative importance of small prey in a predator’s diet.

Pumas need, on average, 2 to 2.5 kg of meat each day (Nunez 2000) and references therein), which converts to 730 – 913 kg of meat annually. To convert data on biomass consumed into estimates of numbers of individuals killed, I multiplied minimum and maximum estimates of meat consumed each year by the percentage of biomass consumed for each prey species. This amount was then divided by the body weight of the prey item, except for large prey, such as deer and peccaries, which are rarely consumed in their entirety. For large prey, I followed Nunez et al., (2000) and assumed that large cats eat an average of 8.5 kg of meat from a large kill.

Relative abundance of felids and their prey

The relative abundance of jaguars, pumas, ocelots and medium to large prey of puma was evaluated based on remote camera data. I used CamTrakker^{TM} remote cameras, triggered by an infrared motion and heat detector. All cameras where fitted with an AGC (Automatic Gain Control) unit, maintaining detector sensitivity at high ambient temperatures (Camtrak South, Inc., Watkinsville, GA). Six cameras were placed along six permanent transects and remained continuously activated for the whole study period. Cameras were fixed to trees at a height of approximately 40 cm from the ground and with a minimal distance from the trail center of 1.5 m. The position of cameras was changed along each transect weekly, to reduce repeated recordings of single individuals that frequently use a particular area. Camera locations along transects were chosen based on the presence of suitable trees on which to fix cameras. Date and time were automatically recorded for each photograph. An additional three cameras were used only part of the time and were frequently moved among strategic points (i.e., areas where cat sign was observed, water holes) within the park. In total, cameras were placed at 10 different sites (counting each transects as one site). Camera stations were not baited, with the intention to limit detection biases due to species-specific preferences of bait and to reduce behavioral changes of animals. Remote cameras remained activated for a total of 2,064 camera nights.

Availability of mammalian prey found in puma diets is expressed both in terms of relative abundance (RA) and percent biomass of prey in the environment ($PBPE = RA_i * W_i / \Sigma (RA_i * W_i)$, where W_i is the weight of prey species i). Relative abundance was expressed as the percentage of photographs per species of the total number of photographs of all species combined. Relative abundance of prey and felids were calculated separately.

I also calculated minimum and maximum values of relative abundance estimates of felids based on estimates of different individuals per species detected. Spotted cats were identified by coat patterns, which are highly variable among individuals. Pumas were distinguished based on size, sex, natural earmarks, black coloration on fore- and hind legs, and scars. Maximum values of individuals were calculated by adding the number of identifiable individuals and those not identified across all transects. Minimum number of individuals was calculated by considering all non-identifiable individuals per transect as one and adding this number to the number of identified individuals.

Prey selectivity

I used a Chi-square test (Zar 1999) to compare sample counts of scats containing each prey to expected numbers of scats containing that prey in the environment. Expected numbers of scats containing each prey were calculated based both on observed relative abundance and relative biomass of prey in the environment. Significant differences indicate non-random, selective predation; Bonferroni confidence intervals were used to evaluate selection for or against prey species (Byers et al. 1984).

Expected numbers of scats containing each prey were calculated following Karanth and Sunquist (1995): If r_i is the number of individuals killed of species i, λ_i the number of scats produced from one kill of species i ($\lambda_i = X / Y$, see formula given in Ackerman et al. 1984), and r_t is the total number of prey killed, then $p_i = r_i / r_t$ is the proportion of the i^{th} species in all kills and $s_i = r_t * p_i * \lambda_i$ is the number of scats containing the i^{th} prey species in the environment. The proportion of scats containing species i is $f = s_i / \Sigma\, s_i = (r_t * p_i * \lambda i) / \Sigma\, (r_t * p_i * \lambda_i) = (p_i * \lambda_i / \Sigma\, p_i * \lambda_i)$.

If a predator takes available prey in proportion to their relative abundance, $p_i = RA_i$ (where RA_i is the relative abundance of species i). If predation occurs in accordance with relative biomass of prey, $p_i = RBPE_i$ (where $RBPE_i$ is the relative biomass of species i). Thus, the expected proportion of scats containing species i can be obtained by $f_i = (RA_i * \lambda_i) / (\Sigma RA_i * \lambda_i)$ or $f_i = (RBPE_i * \lambda_i) / (\Sigma\, RBPE_i * \lambda_i)$.

RESULTS

Puma diet

Most scats disappeared rapidly during the rainy season as a result of runoff and the abundance of beetles (Scarabidae) and termites, which either carry off, or establish colonies around, fresh scats. Thus, my sample size for the wet season was low, which precluded seasonal comparison of puma diets. Of 88 felid scats collected, 65 scats were identified as originating from pumas. A total of 11 different types of food items were identified in puma scats (Table 2.1.). The average number of food items per scat was 1.32. Mammals accounted for 78.9 % of all food items, followed by grass (13.3 %) and reptiles (7.8 %). The standardized food niche breadth of pumas was 0.03 and the MWVP was 5.08 kg. Overall, 90.1 % of mammalian prey and 88.0 % of mammal biomass consumed by pumas were of medium-sized species (body weight 1 to 15 kg); large mammals (body weight >15 kg) represented 9.9 % of all prey items and 12.0 % of biomass consumed (Table 2.2.). Armadillos (*Dasypus* sp.) represented 70.4 % of all mammalian prey and 68.6 % of mammal biomass consumed. *Dasypus novemcinctus*, the nine-banded armadillo, represented 96 % of armadillo remains detected in puma scats. Armadillo remains could not be determined to the species level in two scats.

When converting relative biomass consumed per prey to numbers of individuals killed per year, a puma may kill 139 – 174 armadillos, 16 – 20 anteaters, 15 – 19 agoutis, 7 – 9 peccaries, 3 – 4 deer, and 3 – 4 skunks.

Relative abundance of prey and prey selectivity

Armadillos and peccaries accounted for 58.9 % of photographs of mammalian prey found in puma scats, followed by anteaters (15.1%). Peccaries represented 50 % of total biomass, followed by armadillos (17.2 %), and deer (15.3 %) (Table 2.3.).

Pumas took prey non-randomly, both in terms of their relative abundance ($\chi^2 = 59.62$, df = 5, $p < 0.001$) and relative biomass in the environment ($\chi^2 = 117.26$, df = 5, $p < 0.001$). Pumas preyed selectively on armadillos in terms of relative abundance and their relative biomass. Anteaters were taken more than expected based on their biomass but were taken in accordance with their relative abundance (see Table 2.4.). Deer and peccaries were taken less than expected both in terms of their relative abundance and biomass. Agoutis and skunks were killed in proportion to their relative abundance and biomass.

Relative abundance of felids

Pumas accounted for approximately 59 % of all cats photographed. Oncillas (*Leopardus tigrina*) accounted for 30 % of photographs, whereas jaguars and ocelots represented approximately 8 % and 3 %, respectively. Ranking in relative abundance of felids did not change when minimum estimates of individuals were compared (Table 2.5.). However, oncillas were more abundant than pumas based on maximum estimated number of individuals detected. Pumas were detected at 8 out 10 camera sites, followed by oncillas, jaguars and ocelots (Table 2.5.). Pumas were detected at 3 out of4 sites where jaguars were recorded. At 80 % of sites where oncillas were detected, large cats were also present. Ocelots were detected in an area frequented by all species. Pumas and oncillas were the only species detected at 2 sites. Jaguars were the only felid detected at one site.

DISCUSSION

Puma diet vs. prey availability. The nine-banded armadillo represented nearly 70 % of the mammalian biomass consumed by pumas and accounted for the fact that medium-sized prey made up nearly 90 % of its diet (biomass). High predation on armadillos also explains why diet breadth of pumas in Serra da Capivara NP was much smaller than in other sites in the neotropics (Table 2.6.). Similar reliance by pumas on medium-sized prey has been observed only in southern Chile, where pumas fed to a large extent on introduced hare (*Lepus capensis*) (Iriarte et al., 1990). Large mammals, accounted for less than 15 % of the biomass consumed by pumas in Serra da Capivara NP. This is in stark contrast with results from chaco (Taber at al. 1997), Jalisco (Nunez et al., 2000) and the llanos (Scogamillo, 2001) where large mammals accounted for more than half the biomass in puma diets. No small mammals were detected in puma scats from Serra da Capivara NP. In Jalisco and the llanos, small mammals contributed only marginally to the overall biomass in puma diets but were important in chaco (Table 2.6.).

Relative abundance and size distribution of prey likely explain the overall dietary habits of pumas in Serra da Capivara NP. There are only five species of large mammals reported from Serra da Capivara NP, and although there are no data on density, direct observations, track records and remote camera data suggest that their abundance is low. White-lipped peccaries and red brocket deer (*Mazama americana*) are extremely rare or absent from the study site. No observations of Giant anteaters had been made since 1994 (N. Guidon, FUMDHAM, personal communication) and they were detected only twice during this study. Gray brocket deer are restricted year round to areas with permanent water sources, which are rare and distributed very unevenly throughout the park. Thus, deer may be locally abundant but total population size in the park is probably small (Chapter 1). The most abundant large mammal in this site is the collared peccary. Capybaras, a common prey species of pumas in other ecosystems (Scognamillo, 2001), are absent from Serra da Capivara NP, although they are found along major rivers throughout caatinga. The absence of small mammals from puma scats likely reflects their particularly low overall abundance in caatinga (Streilein, 1982; pers. obs.). Rock cavies (*Kerodon rupestris*), a small mammal that reaches relatively high densities in mesic canyons, largely escape puma predation by using rock shelters in steep cliffs and by foraging in trees. Thus, overall, both small and large mammals are rare in Serra da Capivara NP, which by itself could explain the high predation by pumas on medium-sized prey.

Prey selection. Despite this general concordance of puma food habits with prey availability, the prediction that pumas should take their prey in relation to their availability, i.e., act as number maximizers, was not supported. Pumas preyed more than expected on armadillos and anteaters and less than expected on large prey. Armadillos and anteaters may be particularly vulnerable to predation by pumas because of slow speed and, for armadillos, because of their noisy foraging behavior, which may increase their detectability (see Maehr et al., 1990). Other medium-sized prey that are less vulnerable (i.e., agoutis and skunks) were taken in proportion to their availability in the environment. Pumas preyed on large prey species such as deer and peccaries less than expected, which suggests that pumas do not act as energy maximizers. This was expected in an area of low density and low species richness of large, energetically profitable species. However, low representation of large prey in the diet of pumas may also be due to interspecific dominance by jaguars (Iriarte et al, 1990), despite their apparent low abundance, by lowering encounter rates of pumas with large prey and forcing pumas to rely mainly on smaller prey. Clearly, data on jaguar feeding habits in this site are needed to evaluate this hypothesis. Conversely, pumas may be hunting in a number-maximizing fashion, attacking prey on encounter, but differential vulnerability may lead to higher representation of some species. Differences in vulnerability to puma predation may be related to habitat structure, as hypothesized by Iriarte et al. (1990), who stated that closed habitat structure makes large prey less vulnerable to predation by large cats. However, vulnerability of prey may also be due to intrinsic characteristics of prey, such as defensive bahavior, aggressiveness (Maxit 2001) or their capacity to detect predators.

Influence of prey base on relative abundance of felids in the neotropics. Caatinga has the poorest assemblage of terrestrial mammals (> 1 kg) among major South American ecosystems (Figure 2.2.). Caatinga, and Serra da Capivara NP in particular, is poor in large mammals (5 species), half the number of species found in cerrado (10) or chaco (11). Caatinga has the fewest Artiodactyla (4) and lagomorphs, important food items of large cats in the chaco (Taber et al., 1997) are absent from Serra da Capivara NP. Tapirs (*Tapirus terrestris*), the largest native prey of large cats in the Neotropics, are also absent from caatinga. Overall, Amazonia, with 43 species, has the most species-rich assemblage of terrestrial mammals, followed by Atlantic forests (41), cerrado (40), chaco (37), pantanal (34), and caatinga (22) (Fonseca et al., 1996; Miserendino et al., 1998).

Although lowland evergreen forests have the most terrestrial mammals, they have fewer large mammals than do more open deciduous systems such as cerrado, pantanal or chaco. In addition, overall density of large mammals is generally higher in the latter ecosystems, particularly when large rodents (i.e., capybaras) and livestock are included (Robinson and Bennett, 2000; Leeuwenberg and Robinson, 2000). Domestic stock occurs at densities 10 times higher than native ungulates and represent a major food source of large cats in the pantanal and llanos (Eisenberg, 1980; Schaller, 1983; Hoogesteijn et al., 1993). Based on the high densities of both native and domestic ungulates, open savannas and seasonally flooded plains provide a greater opportunity for prey size segregation between both large cats. Thus, one may expect to find little difference in relative abundance of pumas and jaguars in these systems (prediction 1), assuming that human predation on both species is equal or absent (see Crawshaw and Quigley, in press). High habitat heterogeneity of floodplains further promotes the coexistence of large cats, by allowing different patch use and fine-scale habitat selection by pumas (Scognamillo 2001). In wet lowland forests, where large prey species are found at lower densities, jaguars are expected to be more abundant than pumas.

Evidence for changes in relative abundance of pumas and jaguars with changes in the availability of prey has recently been provided from Central American lowland forests (Carrillo et al., 2000), where a 4-year decline in abundance of white-lipped and collared peccaries was accompanied by a reversal in relative abundance of jaguars and pumas, with pumas becoming relatively more abundant as peccary numbers declined. Thus, a decline in large mammals alone, without a concurrent decline in medium prey is sufficient to negatively affect the abundance of jaguars. This is because natural prey density is lower and the size range of natural prey is smaller in the neotropics than in African savannas or deciduous forests in India (Robinson and Bennett, 2000; Karanth and Sunquist, 1992), providing fewer opportunities for prey-size segregation among jaguars and pumas. In fact, large prey of jaguars and pumas would be considered medium-sized prey of leopards and tigers. Thus, because available prey are relatively less abundant and smaller in the neotropics than in other systems, jaguars may be more vulnerable than other large cats to hunting or natural declines of prey.

As expected, caatinga, with low species richness and low abundance of both large and small prey favors higher abundance of pumas and small cats and lower abundance of jaguars and ocelots. Pumas are smaller than jaguars, have lower energetic needs, and wean their young earlier (Nowak, 1999), which are all factors that are likely to make pumas more successful than jaguars under the conditions such as those presented in Serra da Capivara NP. To what extend the relative abundance of ocelots is affected by pumas remains unclear however. Similarly, it is not known to what extend the relative abundance of small cats is affected by the abundance of ocelots. Interspecific competition among ocelots and small cats is likely to be less intense than among the larger cats because they feed on a larger variety of taxa, including birds, reptiles, small mammals, and invertebrates, which are less likely to be limiting. Thus, overall relative abundance of small cats will depend on the availability of alternative prey to small mammals if these are found at low abundance or if competition for small mammals with ocelots is high. In Serra da Capivara NP, oncillas feed extensively on small lizards (*Cnemidophorus* sp. *Tropidurus* sp.) (Olmos, 1993) and because of their smaller body size they may be better able to subsist on these small prey than ocelots.

Other factors influencing felid abundance. Relative abundance of jaguars in wet environments may depend to some extent on aquatic, allochthonous food subsidies (Rose and Polis, 1998), such as caiman and chelonians (Troeng, 2000) or even cetaceans (Defler, 1994). These prey are thought to be available mainly to jaguars, whose massive head structure allows them to feed on these prey (Hoogesteijn and Mondolfi, 1996). Elevated densities due to allochthonous input from aquatic systems have been observed for other large carnivores, such as polar bears (*Ursus maririmus*), lions (*Panthera leo*) or brown hyenas (*Hyaena brunnea*) (Rose and Polis, 1998 and references therein). The availability of aquatic food subsidies may indeed be important for jaguars and may contribute to their lower relative abundance in dry forests (see this study, Nunez et al., 2000). Spatial segregation related to water availability on a local scale, with jaguars using more mesic habitats along rivers and pumas being found in drier areas provides further evidence for this hypothesis (Schaller and Crawshaw, 1980; Emmons, 1987; Crawshaw and Quigley, 1991). Finally, pumas may be more abundant than jaguars because they are better adapted to dry environments (de Oliveira, 1994), although there is no direct evidence to support this.

Relative abundance of felids may also be affected by changes in relative differences in body size. Throughout their geographic range, pumas tend to be smaller where they co-occur with jaguars (Iriarte et al., 1990; Gay and Best, 1996), although adult male pumas weigh as much as a small female jaguar. Within the Neotropics, pumas tend to be larger in dry biomes (Gay and Best, 1996), whereas jaguars reach their largest size in open floodplains (Hoogesteijn and Mondolfi, 1996). Thus one may expect relative size differences between jaguars and pumas to be lowest in dry biomes, alleviating the competitive inferiority of pumas.

Despite differences in prey availability and climatic conditions among different ecosystems, one should be cautious about making interferences about observed relative abundance of felids without taking into consideration current or past hunting of cats. Jaguars, and spotted cats in general tend to suffer from greater mortality rates through hunting than pumas (Crawshaw and Quigley, 2001 in press), which by itself may explain their low abundance in many places. Today hunting of cats is either very rare or has completely stopped in Serra da Capivara NP and interviews with former hunters revealed that pumas were always more common than jaguars in the area. Thus, despite past exploitation of cats it seems reasonable to believe that current relative abundance of felids is due to prey availability, which in return may be influenced by hunting pressure. Recent improvements in anti-poaching patrols in Serra da Capivara NP have allowed several game species, including armadillos and peccaries, to increase. The high reproductive rate of armadillos may have allowed this species to bounce back more quickly than others, but if this trend continues, other large prey species may also increase in abundance and prey size-distribution and relative abundance of prey may change in the future. Thus, current relative abundance of jaguars and pumas may change as prey populations build up to natural levels.

Conclusion. This study has shown that pumas are more abundant than jaguars in a dry environment that has no rivers and a low abundance of small and large mammals. Pumas relied nearly exclusively on medium-sized prey that are characterized by relatively poor escape capabilities. Small cats were more abundant than ocelots and relied on locally abundant small lizards as their staple prey. Lower density, lower species richness and smaller size range of mammalian prey in the Neotropics suggest that over-harvesting of prey may be particularly detrimental to both jaguars and ocelots and that pumas and smaller cats could be expected to be more resilient to hunting pressure. If hunting levels are maintained at low levels in Serra da capivara NP, continuous monitoring of felids and their prey will certainly provide new and exiting insights into the ecology of neotropical felid assemblages.

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Table 2.1.: List of prey taxa identified in puma scats, number of each prey type found in total (N_i), frequency of occurrence of prey expressed as a percentage of the total number of scats (FO_i), and percent of occurrence of prey as expressed as a percentage of the total number of food items identified (PO_i). (Grass is excluded in the calculation of PO)

Species	N_i	FO_i	PO_i
D. novemcinctus	48	73.8	61.5
Grass	12	18.5	
T. tetradactyla	8	12.3	10.3
D. prymnolpha	5	7.7	6.4
T. tajacu	5	7.7	6.4
Lizard	3	4.6	3.8
M. gouazoubira	2	3.1	2.6
Dasypus sp.	2	3.1	2.6
Snake	2	3.1	2.6
T. hispidus	2	3.1	2.6
C. semistriatus	1	1.5	1.3
TOTAL	89	100	100

Table 3.2.: Mean weight of mammalian prey (W_i), percentage of occurrence of prey (PO_i), frequency of occurence of prey (FO_i), correction factor (CF_i) developed by Ackerman et al. (1984), and relative biomass of prey consumed (RBC_i) by pumas in Serra da Capivara NP.

Taxon	W_i	PO_i	FO_i	CF_i[a]	RBC_i[b]
Total Large Prey		**9.9**			**12.0**
M. gouazoubira	16.3	2.8	3.1	2.53	3.3
T. tajacu	19.6	7.0	7.7	2.65	8.7
Total Medium Prey		**90.1**			**88.0**
D. novemcinctus	3.6	70.4	76.9	2.09	68.6
D. prymnolopha	3.2	7.0	7.7	2.07	6.8
T. tetradactyla	5.1	11.3	12.3	2.14	11.2
C. semistriatus	3.5	1.4	1.5	2.08	1.4

[a] $CF_i = 1.98 + 0.035\ W_i$

[b] $RBCi = (FO_i * CF_i) / \Sigma\ (FO_i * CF_i)$

Table 2.3.: Relative abundance of mammalian prey of puma in Serra da Capivara NP. Total number of photographs (N_i), relative abundance expressed as the percentage of the total number of photographs (RA_i), body weight (W_i), Total Estimated Weight (TEW_i), and Relative Biomass of Prey in the Environment ($RBPE_i$) are given.

Species	N_i	RA_i	W_i	TEW_i	$RBPE_i$
D. novemcinctus	56	38.4	3.6	201.6	17.2
*T. tajacu**	30	20.5	19.6	588.0	50.2
T. tetradactyla	22	15.1	5.1	112.6	9.6
D. prymnolopha	14	9.6	3.2	44.8	3.8
C. semistriatus	13	8.9	3.5	45.5	3.9
M. gouazoubira	11	7.5	16.3	179.3	15.3
Total				1,171.8	

* The number of photographs of peccaries was adjusted by the mean group size (3.03) obtained from direct observation.

Table 2.4.: Observed (FO_{iobs})and expected (FO_{iexp}) frequencies of occurence of prey and Bonferroni confidence intervals (95%). FO_{iexp} are given based on relative biomass and relative abundance of prey in the environment.

	FO_{iexp} (relative abundance)	FO_{iexp} (relative biomass)	FO_{iobs}	Lower limit	Upper limit
M. gouazoubira	0.146 **(-)**	0.205 **(-)**	0.031	-0.023	0.085
T. tajacu	0.457 **(-)**	0.688 **(-)**	0.077	-0.006	0.160
D. novemcinctus	0.199 **(+)**	0.031 **(+)**	0.077	0.637	0.901
D. prymnolopha	0.045 **(0)**	0.011 **(0)**	0.077	-0.006	0.160
T. tetradactyla	0.108 **(0)**	0.017 **(+)**	0.123	0.020	0.226
C. semistriatus	0.045 **(0)**	0.048 **(0)**	0.015	-0.023	0.054

(+) = species is selected for, (-) = species is selected against, (0) = species taken in proportion with availability

Table 2.5.: Minimum (N_{max}) and maximum (N_{min}) numbers of individual cats detected per species, minimum (RA_{min}) and maximum (RA_{max}) estimates of relative abundance and number of sites where species were detected.

Species	N_{min}	N_{max}	RA_{min} (%)	RA_{max} (%)	Sites
Puma	14	9	39	44	8
Jaguar	3	5	13	16	4
Ocelot	1	2	4	6	1
Oncilla	11	10	44	34	5

Table 2.6.: Percentage of occurrence PO_i) and relative biomass of small, medium and large prey consumed by pumas (RBC_i) in Jalisco, Mexico (Nunez et al 2000), chaco, Paraguay (Taber et al. 1997), the llanos, Venezuela (Maxit 2001) and caatinga, Brazil (this study). Standardized niche breadth (B_{sta}) and mean weight of vertebrate prey (MWVP) are also given.

	Jalisco		Chaco		Llanos		Caatinga	
	PO_i	RBC_i	PO_i	RBC	PO_i	RBC_i	PO_i	RBC_i
Small	22	2	44	13	17	1		
Medium	14	17	25	34	33	28	90	88
Large	42	75	24	51	50	70	10	12
B_{sta}	0.38		0.68		0.6		0.03	
MWVP	12.70		0.78		8.36		5.08	

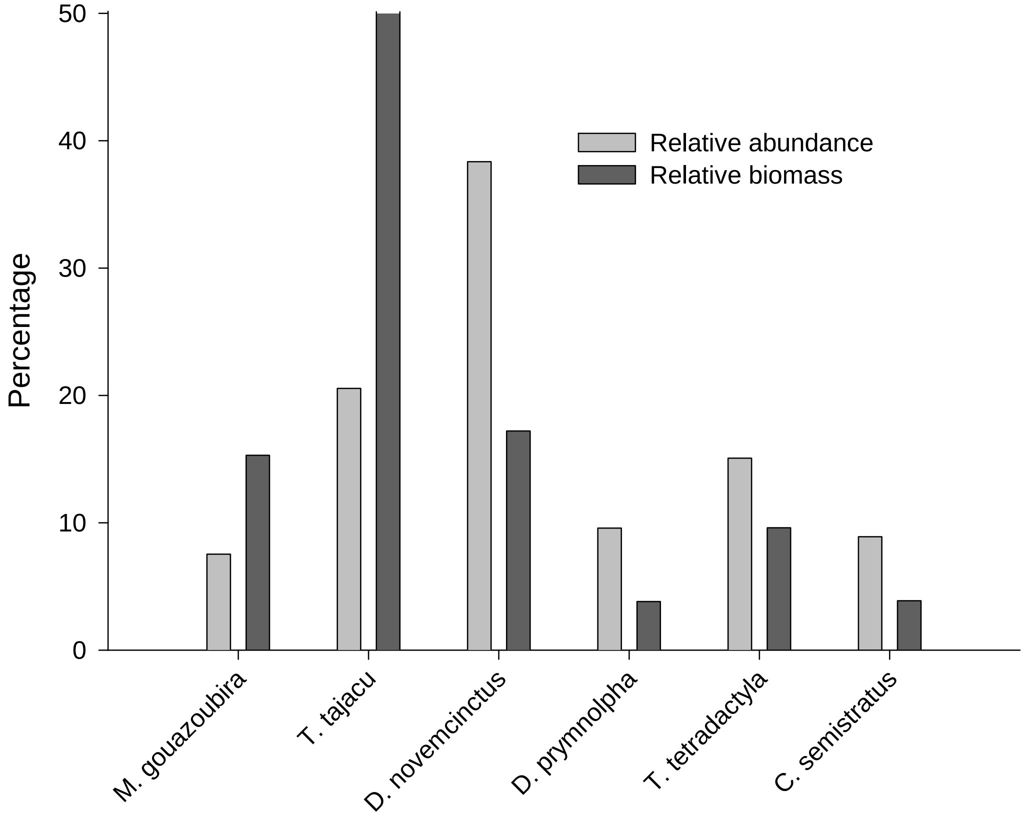

Figure 2.1. Relative abundance and relative biomass of puma prey in Serra da Capivara NP, based on remote camera data.

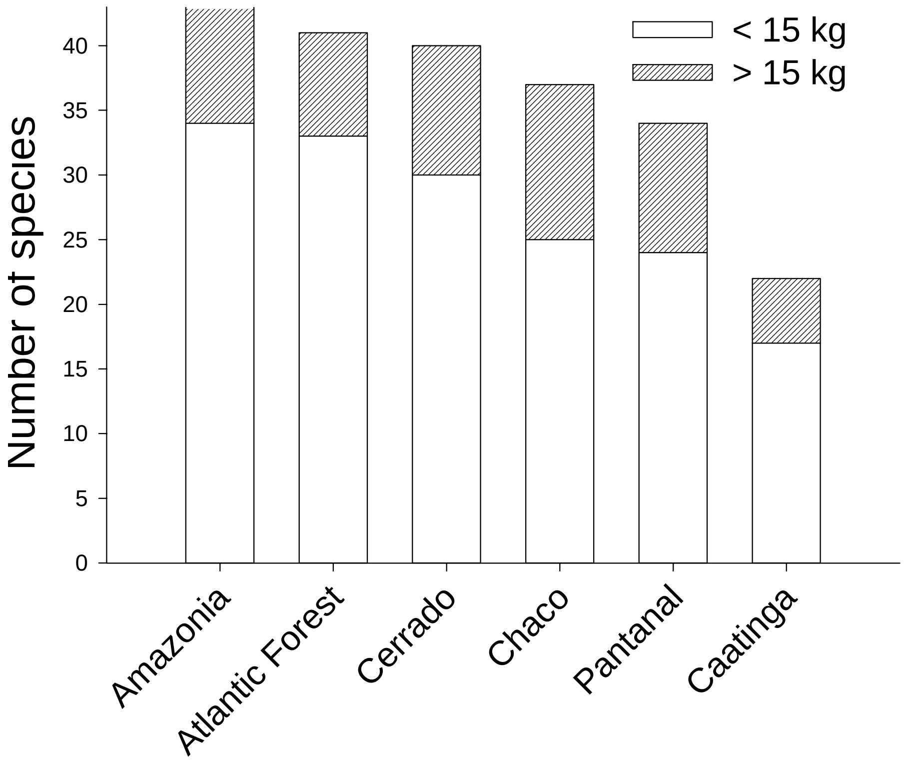

Figure 2.2. Prey size distribution of terrestrial mammals (> 1 kg) from the Amazon, caatinga, cerrado, pantanal, and chaco. Data were obtained from Fonseca et al (1996), and Miserendino et al. (1998). Mammal assemblages were divided into two categories: < 15 kg and >15 kg. Jaguars, pumas, and maned wolves (*Chrysocyon brachyurus*) were not included.