ISSN 0097-4463

ANNALS
of CARNEGIE MUSEUM

CARNEGIE MUSEUM OF NATURAL HISTORY

4400 FORBES AVENUE • PITTSBURGH, PENNSYLVANIA 15213

VOLUME 51 6 MAY 1982 ARTICLE 5

ECOLOGY OF SMALL MAMMALS IN THE SEMIARID BRAZILIAN CAATINGA. I. CLIMATE AND FAUNAL COMPOSITION

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ABSTRACT

Environmental unpredictability has been the predominant characteristic of the Caatinga region of northeastern Brazil in both evolutionary and ecological time. The geographic center of the Caatinga harbors a relatively depauperate small mammal fauna, including nine species of rodents in four families and three species of marsupials in a single family. Basic ecological and behavioral information are presented for each species of this little-known fauna.

INTRODUCTION

The Caatinga region of northeastern Brazil is a unique tropical biome. Whereas most of the tropics is characteristically mesic and seasonally predictable, the Caatinga is semiarid and has an unpredictable rainfall regime. In essence, the Caatinga is a large xeric island of thorn scrub vegetation surrounded by predictable, relatively mesic biomes.

The uniqueness of the Caatinga with respect to the other major tropical biomes poses many interesting questions. Which species from the surrounding mesic-adapted tropical faunas have invaded this xeric zone? How have these species adapted to the unpredictable environment? Do differences exist in the relative degree of adaptation? How are the species distributed among the various habitats and what factors

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Submitted 10 May 1981.

are or were most influential in the development and maintenance of the distribution patterns?

Terrestrial small mammals are generally sedentary species, incapable either of the mobility of large mammals which can readily migrate from inhospitable areas or of bats and birds which can cover long distances in normal daily activities. These species must therefore adapt to prevailing localized conditions or fail to persist. Thus small mammals in the Caatinga should clearly exhibit adaptations to the constraints imposed by the unpredictable xeric environment.

A comprehensive analysis of a small mammal fauna must consider a wide variety of both proximate and ultimate factors which can influence species composition and patterns of distribution. The present report is primarily concerned with describing the environmental factors to which the fauna has had to adapt and with presenting baseline ecological information on each species. Subsequent reports will deal with (1) physiological adaptations (Streilein, 1982*a*), (2) reproduction and population ecology (Streilein, 1982*b*), (3) distribution patterns (Streilein, 1982*c*), and (4) agonistic behavior (Streilein, 1982*d*).

STUDY AREA

General Description of the Caatinga Physiography

Three distinct features typify the geological composition of the Caatinga (Ab'Saber, 1970). The dominant feature, in terms of area encompassed, is the basement level of Precambrian crystalline rock. In the extensive areas where this layer is exposed, surface relief is insignificant and flats or gradual slopes predominate. Numerous abrupt protrusions of granitic rock are widely distributed throughout the Caatinga in the form of low mountain ranges (serras), small mountain ridges (serrotes), and lowland outcroppings (lajeiros). These sharply delineated formations have been uncovered and shaped through the processes of erosion and denudation, frequently resulting in extremely rugged terrain. Finally, there are areas where the surface layer of sedimentary rock (primarily sandstone) has remained intact. Some of these areas are elevated above the surrounding countryside as steep-sided plateaus (chapadas).

The distinctive physiography of the Caatinga is largely attributed to the abundant, ubiquitous granitic formations. Overall spatial heterogeneity in the Caatinga is greatly enhanced by the distribution of serrotes, serras, and lajeiros of various sizes and shapes. Within these formations, the total degree of three-dimensional structural complexity is normally quite high. The sandstone and crystalline rock areas are, by comparison, relatively uniform and structurally very simple. Structural diversity in the Caatinga on both the geographic and local scales

is thus determined primarily by the number, types, and distributional patterns of the granitic formations.

Loss of the surface layer of porous sedimentary rock and the subsequent exposure of the underlying crystalline layer over much of the Caatinga has had a profound impact on the hydrological balance of the region. The compact structure of the crystalline rock and the great depth to which it extends prevent the formation of ground water. In addition, the soil layer is often sparse or totally lacking. Most of the water entering the system is thus lost via rapid runoff. The water retaining function of the sedimentary rock is dramatically demonstrated by the presence of the "oasis" of Cariri (centered at the base of the northern side of the Chapada do Araripe, approximately 60 km from the study site, near the southern edge of the Chapada) in an otherwise semiarid area. This mesic locale is situated in such a manner that it receives an abundant supply of water in the form of seepage from the sandstone of the Chapada (Markham, 1972). In general, the capacity for absorption and retention of water is negligible in the Caatinga. The geological composition of the Caatinga thus has a significant adverse effect on the hydrological balance and is instrumental in maintaining the semiarid nature of the region. If the rainfall was spread over a longer interval of time rather than the brief period typical of the Caatinga, this effect would be less pronounced.

Climate

The current geographic boundaries (Fig. 1) of the Caatinga extend from 3° to 16° south latitude and from 35° to 45° west longitude, encompassing an area of 650,000 km^2 (Reis, 1976; Frota-Pessoa et al., 1971). Evidence has begun to accumulate, however, which demonstrates that both the geographic limits and the degree of aridity experienced fluctuated substantially during the Quaternary.

Until recently, the climate of tropical South America was generally considered to have been relatively stable through time. This idea induced investigators to formulate the "evolutionary time" hypothesis of species diversity, which postulated that the great number of species of tropical organisms was the result of a long period of adaptation to a stable environment (Pianka, 1966). The concept of tropical zone stability was challenged by Haffer (1969) and Vanzolini and Williams (1970), who independently proposed the existence of faunistic refugia during periods of climatic change. Vuilleumier (1971) has since concluded, after reviewing the available zoological and geological data for the entire continent, that "a series of humid-arid cycles drastically and repeatedly altered vegetation patterns during the Quaternary" in tropical South America (see also Meggars, 1975, 1977; Brown, 1977*a*, 1977*b*; Simpson and Haffer, 1978). Vanzolini (1970) has also compiled

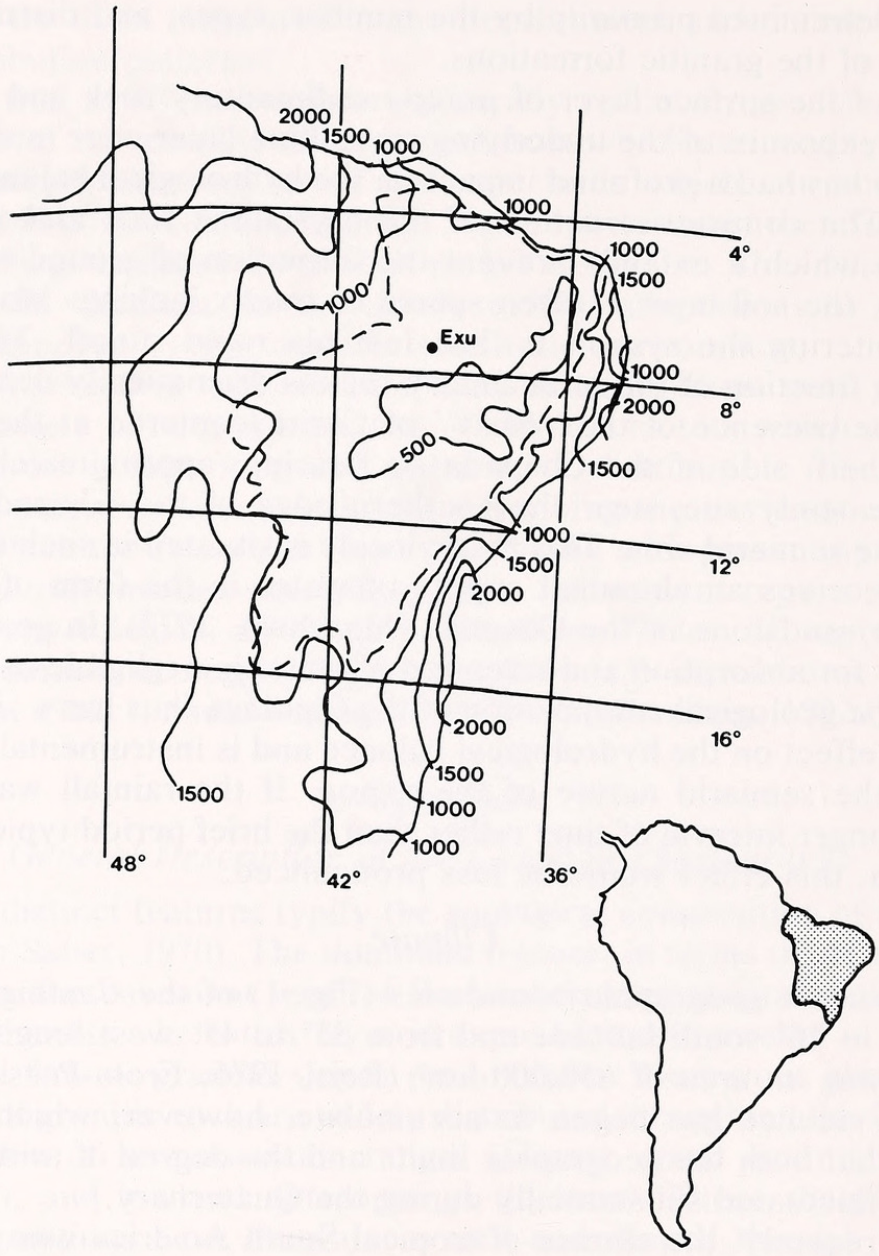

Fig. 1.—Annual rainfall in northeastern Brazil (in mm). The limits of the Caatinga are indicated by the dashed line, and approximately follow the 1000 mm isohet. Exu is the location of the study site. Modified from Reis (1976).

diverse botanical, zoological, and geological evidence which indicates that substantial climatic fluctuations altered the Amazon Basin and by extension, the neighboring Cerrado and Caatinga zones.

Contraction and subsequent expansion of the rain forest permitted the concomitant expansion and later contraction of the open formations. Various geomorphological formations, including stone lines and alluvial and lateritic deposits formed in arid climates, have been found far beyond the contemporary boundaries of the xeric zone; at one

time, an arid climate prevailed at least to Brasilia in the West and Belem and Sertanea in northwest Brazil (Vanzolini, 1970). Indirect evidence gleaned from biogeographic studies of plants and animals demonstrates a close correspondence in species composition between the now widely disjunct open formation enclaves within the Amazon Basin and the Cerrado and Caatinga. There is also faunistic evidence that the extent of the xeric zone was considerably reduced. Localized areas of orographic rainfall (brejos) within the Caatinga support humid forest habitat, and have many endemic forms peculiar to the region and radically different from those in the surrounding Caatinga, but also share numerous elements with the Amazon Forest (Vanzolini, 1970).

The occurrence of a series of wet and dry cycles in the Quaternary is now widely accepted, but the exact number of cycles and their approximate time periods have not been established. Vanzolini (1973) proposed that at least three cycles took place during the last 100,000 years, with the two latest episodes occurring approximately 11,000 (Damuth and Fairbridge, 1970) and 2600 (Vanzolini and Ab'Saber, 1968) years ago.

The Caatinga is also noted for radical short-term climatic fluctuations with regard to predictability and amount of precipitation. The extreme variability in rainfall patterns, frequently culminating in extended droughts or severe flooding, has led various authors to graphically describe this area as a "zone of calamity" (Freise, 1938), "the polygon of drought" (Eidt, 1968), and the "region of anomalous drought" (Markham, 1972). Relative to other areas of Brazil, the Caatinga also possesses some of the most extreme meteorological values recorded, including the highest insolation, lowest degree of cloudiness, highest mean temperatures, lowest relative humidity, and the most instances of scarce and irregular rainfall (Reis, 1976).

The rainfall pattern in northeastern Brazil is primarily influenced by the Southeast Trade Winds in conjunction with three large, mobile masses of air—the equatorial continental mass; the Intertropical Convergence Zone; and the South Atlantic Anticyclone (synonymous with the Atlantic Polar Front). While under the influence of the Southeast Trade Winds, the Caatinga receives no precipitation (Reis, 1976). This condition prevails during part of every year but often persists for a much longer period of time, producing the droughts characteristic of the region. No single causal mechanism has yet been discovered that can explain this phenomenon, which occurs at random intervals. Generally, the three moisture-laden air masses introduce some rain into the Caatinga in any "normal" year. The amount of rain attributable to each mass of air, however, often varies greatly from year to year. All three air masses are affected to a greater or lesser extent by the orographic features they encounter. Rainfall in any given area is also

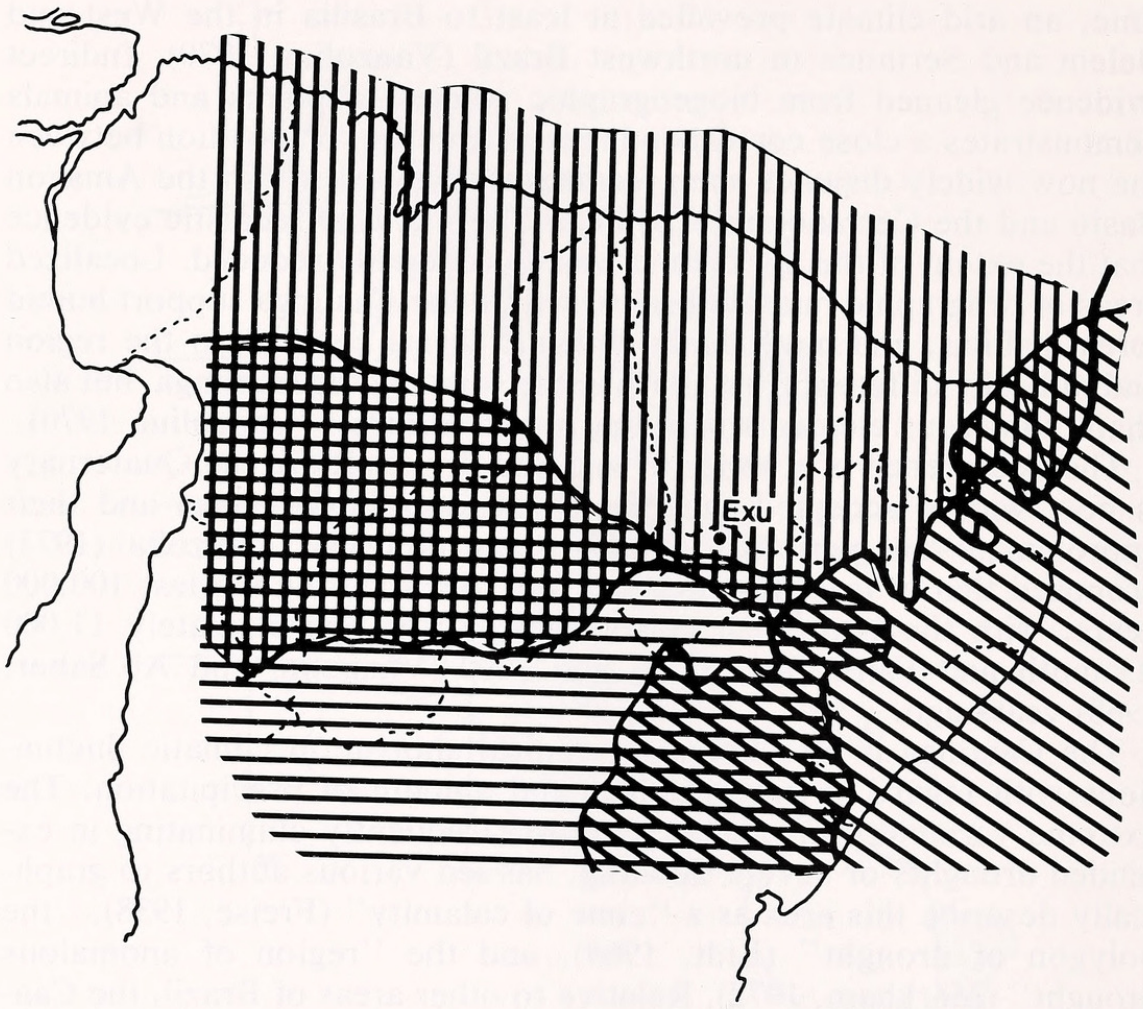

Fig. 2.—Normal extent of influence of the three major air masses affecting precipitation in northeastern Brazil. Vertical lines represent the Intertropical Convergence Zone (precipitation occurs mainly in January–April), horizontal lines represent the continental equatorial air mass (precipitation occurs mainly in November–January), diagonal lines represent the South Atlantic Anticyclone (precipitation occurs mainly in May–July). Modified from Reis (1976).

an inverse function of distance from each air mass, the exact positions of which may vary considerably between years. The normal spheres of influence for each air mass are shown in Fig. 2. Zones of overlap do not usually have significantly augmented rainfall because they occur where the influence of each air mass is reaching its limit of effectiveness. A more detailed account of the rainfall regimes and the patterns of atmospheric circulation can be found in Reis (1976) and Markham (1972).

The effectiveness of the orographic features is related to altitude, distance from the coast, and orientation with respect to the direction of advance of the three air masses. Locales which receive augmented rainfall, brejos, are capable of sustaining humid forest. Andrade and

Lins (1964) list 22 principal brejos in the state of Pernambuco alone, thus the number of mesic refugia is substantial. The orographic features responsible for the increased humidity of brejos also create rain shadows on the leeward side.

The climate of the Caatinga is thus distinguished by its unpredictability with respect to both evolutionary and ecological time.

Vegetation

The key characteristics of the xerophytic Caatinga vegetation are adaptations to the constraints imposed by the irregular and limited rainfall. Deciduousness during dry periods is the most common, conspicuous strategy of water conservation, while the succulents utilize the alternate strategy of long term water storage. The pronounced xerophytic adaptations of Caatinga plants, such as the many species of Cactaceae and Euphorbiaceae, strongly indicate that aridity has persisted for thousands of years in this region (Alvim, 1949).

Vegetation associations in the Caatinga range from relatively simple to extremely complex assemblages with regard to species abundance and composition, characteristic species, and foliage height profiles. In general, the boundaries of Caatinga vegetation closely parallel the 1000 mm rainfall isohet throughout northeastern Brazil (Fig. 1). A number of different types of vegetation are frequently found in a relatively small area, creating a vegetational mosaic. The terms Low Caatinga (=Caatinga Baixa) and High Caatinga (=Caatinga Alta), will be employed throughout this study as general classes of vegetation based upon foliage height profiles. Low Caatinga includes the various types of scrubby vegetation which have canopy elements generally attaining only 3 to 5 m, while High Caatinga refers to vegetation types where the dominant canopy elements are typically greater than 5 m.

Classification of vegetation with regard to foliage height arbitrarily groups a number of distinct vegetation types. Plant species characteristic of a certain type of Caatinga vegetation may include representatives of the cacti, euphorbs and/or legumes, depending upon the geographic location. The dominant species may also differ greatly between locales, while conforming to the Low Caatinga type. Within a given locale variation is also the result of microclimatic and edaphic factors, minor differences in topography, and the actions of domestic animals. The most frequently encountered form of vegetation is Caatinga Baixa; the preponderance of this form is due in part to the activities of man and various animals, especially goats.

Another general type of vegetation found within the Caatinga region is strictly associated with areas of orographic rainfall. These areas, "brejos," do not experience the intense hydrological deficits characteristic of the surrounding countryside and are thus able to sustain

humid forests which in turn differ radically from the true xerophytic Caatinga vegetation. The botanical affinities of the brejos lie with the Atlantic Rainforest (Andrade and Lins, 1964).

Study Site

Most of the field work was conducted in the municipality of Exu in the northwestern corner of the state of Pernambuco, Brazil. This is a complex area with respect to geology and vegetation. All of the three major geological features that typify the Caatinga region are found in close proximity there. The dominant element in this portion of the Caatinga is the Chapada do Araripe, an extensive sandstone plateau which stretches for hundreds of kilometers from east to west along the border of Pernambuco and Ceará. Numerous granitic outcroppings, in the form of lajeiros and serrotes, greatly enhance the structural diversity of the area in both the horizontal and vertical dimensions. The composition of the vegetation typically reflects the complexity of the area. Abrupt, drastic changes in plant species composition frequently occur over relatively small horizontal or vertical distances but gradual transitions are also common. The overall pattern may best be described as a mosaic of patches of variable size, some of which are clearly distinct while others are blurred around the edges. A few elements atypical of Caatinga vegetation are present in the flora, having invaded the area from the Chapada do Araripe. This chapada receives a substantial amount of orographic rainfall (Markham, 1972) which, in conjunction with soil conditions, permits the existence of Cerrado vegetation in the heart of the Caatinga.

The primary site studied within the municipality was at Fazenda Batente, located 6 km southeast of the town of Exu (7°31′S, 39°43′W) and approximately 10 km south of the base of the Chapada do Araripe. The fazenda contained a variety of habitat types—several lajeiros, extensive stands of low thorn scrub, pastures, agricultural fields, and abandoned fields in various stages of succession.

MATERIALS AND METHODS

Faunal Composition and Species Accounts

A permanent 12 × 12 live trapping grid (Fig. 3) was established at Fazenda Batente in January 1977 after preliminary trapping in December 1976 indicated the suitability of the site. Trap stations were placed at 15 m intervals (2.7 ha). The grid was positioned to include portions of three distinct, sharply delineated microhabitats—rocky areas (lajeiros), low thorn scrub, and old field. Trapping was conducted from January 1977 through February 1978. One large Sherman live trap and a larger, wire live trap manufactured in Brazil were set at alternate

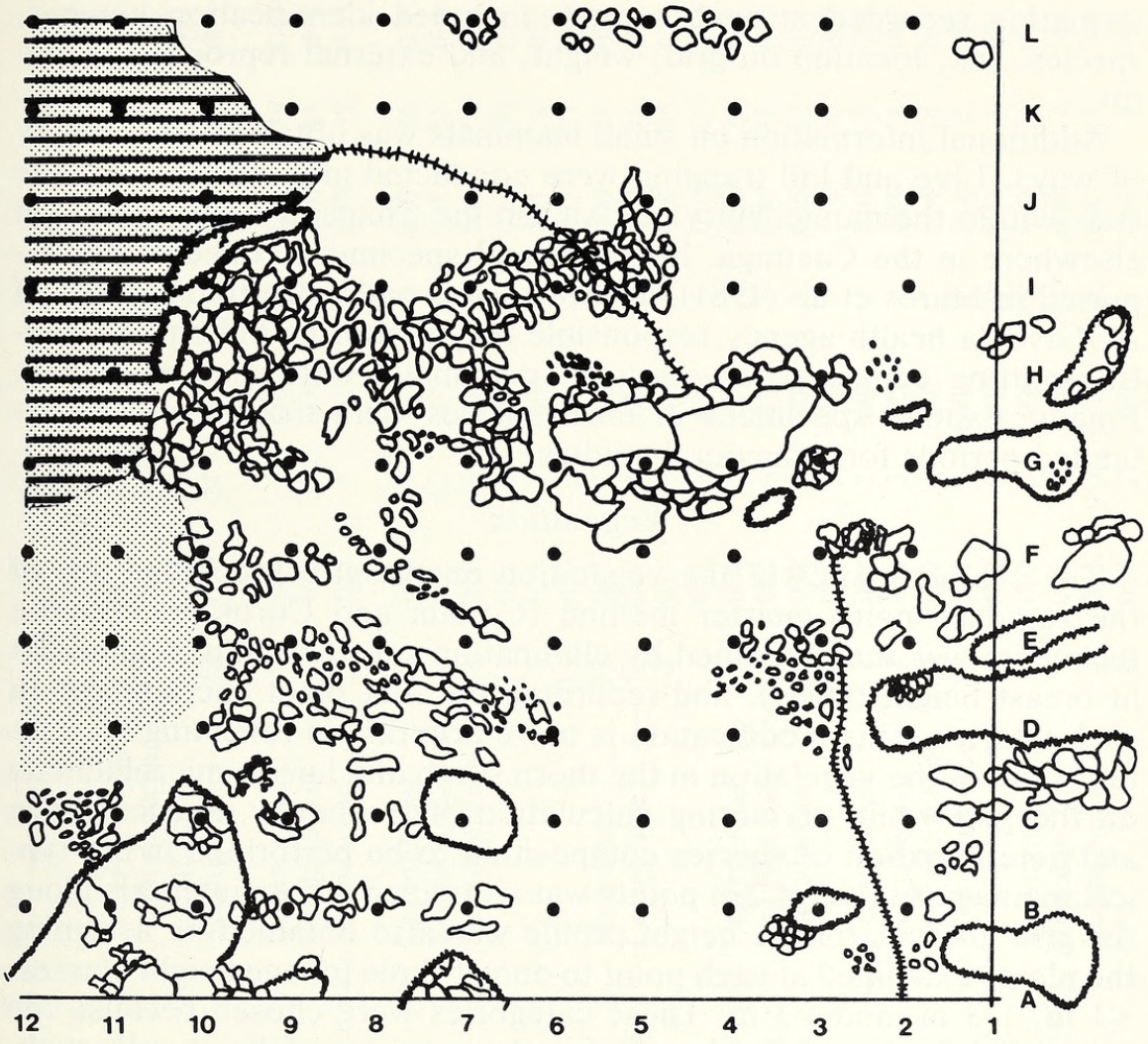

Fig. 3.—Map of the Fazenda Batente study area. Unshaded area represents thorn scrub, with exposed rock floors (zig-zagged lines) and major rock formations indicated. Shaded area denotes old field, and the superimposed horizontal lines represent the area covered by a temporary lake. Trap locations are indicated by numbers and letters. Hatched line represents a wooden fence.

stations. Traps were rotated after 3 to 14 days, depending on total number of days trapped each month, capture success, and weather conditions. Capture success was extremely low during the first months, so the planned trapping period of 7 days each month was slowly increased through July, after which traps were set every possible day. Traps were opened just before dusk and checked the following morning. A number of baits (Brazil nuts, peanuts, field corn, pineapple, and other fruits) were used because the availability varied. Total trapping effort during the 14-month study was approximately 25,000 trap nights.

Animals on the grid were toe-clipped when first captured. The in-

formation recorded at each capture included identification number, species, sex, location on grid, weight, and external reproductive status.

Additional information on small mammals was obtained in a variety of ways. Live and kill trapping were conducted at a number of other sites within the municipality of Exu, on the Chapada do Araripe, and elsewhere in the Caatinga; localities and specimens collected are reported in Mares et al. (1981). Trapping sites and collection records of AGGEU (a health agency responsible for monitoring bubonic plague-transmitting ectoparasites on small mammals) were also examined. Finally, captive specimens of most species were maintained for extended periods for behavioral studies.

Vegetation

The characteristics of the vegetation on the grid precluded use of the standard point quarter method (Cottam and Curtis, 1956). The technique was then modified by eliminating consideration of diameter at breast height (DBH), and recording the first plant encountered in each quarter. This modification is more accurate in reflecting the natural state of the vegetation in the thorn scrub and lajeiro microhabitats on the grid while permitting calculation of frequency of occurrence and determination of species composition to be performed in the typical manner. A total of 278 points was examined at 5-m intervals along the grid lines. A foliage height profile was also obtained by assigning the plants examined at each point to one of three foliage height classes: <1 m, 1–3 m, and >3 m. These categories were chosen because the height distribution of Caatinga Baixa plants tends to fall naturally within these divisions.

Climate

Weather records were not available for Exu. The closest station was in Ouricuri, located approximately 60 km to the south. Information on minimum and maximum daily temperatures and precipitation were provided by SUDENE, Divisão de Hidrologia. The area around Exu is somewhat more mesic than that around Ouricuri due to the proximity of Exu to the Chapada do Araripe.

RESULTS AND DISCUSSION

Vegetation

The species composition and frequency of occurrence within each foliage height class are listed in Table 1. A total of 62 species occurred on the grid. Leguminosae and Euphorbiaceae were well represented, with nine and four species, respectively. The 10 most frequently en-

Table 1.—*Species composition and frequency of occurrence by foliage height class for Caatinga vegetation.*

Common name	Scientific name	Family	<1 meter		1–3 meter		>3 meter		Total	
			N	Freq	N	Freq	N	Freq	N	Freq
Marmeleiro	*Croton jacobinensis*	Euphorbiaceae	49	.191	116	.334	219	.430	384	.345
Canela de nambu	*Jacobinia* sp.	Acanthaceae	32	.125	53	.153	18	.035	103	.093
Camara	*Ruellia paniculata* and *Ruellia bahiensis*	Acanthaceae	18	.070	24	.069	50	.098	92	.083
Feijao de rolinha	*Phaseolus peduncularis*	Leguminosae	1	.004	2	.006	47	.092	50	.045
Maria preta	*Cordia globosa*	Boraginaceae	9	.035	27	.078	8	.016	44	.040
Chucalhode vacquiero	*Cardiospermum halicacabum*	Sapindaceae	6	.023	5	.014	28	.055	39	.035
Mororo		Leguminosae	21	.082	9	.026	5	.010	35	.031
Vrido	*Erythroxylum* sp.	Erythroxylaceae	2	.008	12	.035	21	.041	35	.031
Cancasao	*Cnidoscolus wrens*	Euphorbiaceae	18	.070	15	.043	1	.002	34	.031
Lambe bes			11	.043	8	.023	11	.021	30	.027
Frejois			6	.023	1	.003	17	.033	24	.022
Malva	*Sida galheirensis*		15	.059	5	.014	1	.002	21	.019
Melosa	*Gaya* sp.	Malvaceae	12	.047	7	.020	0	.000	19	.017
Bamburra	*Blainvillea rhomboidea*	Compositae	12	.047	4	.012	0	.000	16	.014
Quichaba			4	.016	6	.017	5	.010	15	.013
Pao moco			1	.004	7	.020	5	.010	13	.012
Catingeira	*Caesalpinia pyramidalis*	Leguminosae	1	.004	1	.003	11	.021	13	.012
Camara do boi	*Ruellia* sp.	Acanthaceae	3	.012	6	.017	3	.006	12	.011
Folha de carne	*Serjania* sp.	Sapindaceae	2	.008	2	.006	8	.016	12	.011
Cipo de cruz			1	.004	2	.006	7	.014	10	.009
Espinheiro branco	*Mimosa* sp.	Leguminosae	2	.008	2	.006	5	.010	9	.008
Orelha de onca	*Cordia insignis*	Boraginaceae	1	.004	3	.009	4	.008	8	.007
Manicoba	*Manihot* sp.	Euphorbiaceae	0	.000	1	.003	7	.014	8	.007
Gitirana	*Ipomoea sobrevoluta*	Convolvulaceae	1	.004	0	.000	7	.014	8	.007
Rompe-gibao			0	.000	6	.017	0	.000	6	.005
Mucuna	*Erythrina velutina*	Leguminosae	0	.000	0	.000	5	.010	5	.004
Parreira	*Cissis simsiana*	Vitaceae	0	.000	0	.000	4	.008	4	.004
Angico marco		Leguminosae	4	.016	0	.000	0	.000	4	.004
Batata de tiu			0	.000	2	.006	2	.004	4	.004
Cipo	*Commelina* sp.	Commelinaceae	1	.004	2	.006	1	.002	4	.004

Table 1.—*Continued.*

Common name	Scientific name	Family	<1 meter		1–3 meter		>3 meter		Total	
			N	Freq	N	Freq	N	Freq	N	Freq
Bananinha			3	.012	0	.000	0	.000	3	.003
Juro beba	*Solanum paniculatum*	Solanaceae	3	.012	0	.000	0	.000	3	.003
Juazeiro	*Ziziphus joazeiro*	Rhamnaceae	2	.008	1	.003	0	.000	3	.003
Xique-xique	*Pilosocereus gounellei*	Cactaceae	1	.004	2	.006	0	.000	3	.003
Feijao braba	*Capparis* sp.	Capparaceae	2	.008	0	.000	0	.000	2	.002
Carrancuro			2	.008	0	.000	0	.000	2	.002
Capim			2	.008	0	.000	0	.000	2	.002
Cordao de Sao Francisco	*Leonotis nepetaefolia*	Labiatae	0	.000	2	.006	0	.000	2	.002
Canafistula	*Cassia excelsa*	Leguminosae	0	.000	2	.006	0	.000	2	.002
Chanana	*Centratherum punctatum*	Compositae	0	.000	2	.006	0	.000	2	.002
Amarra cachorro			1	.004	0	.000	1	.002	2	.002
Espinheiro de algulha			0	.000	2	.006	0	.000	2	.002
Bura leteira			0	.000	0	.000	2	.004	2	.002
Brao ulna			1	.004	0	.000	0	.000	1	.001
Gini papo			1	.004	0	.000	0	.000	1	.001
Falva			0	.000	0	.000	1	.002	1	.001
Yami			0	.000	1	.003	0	.000	1	.001
Anjico		Leguminosae	0	.000	0	.000	1	.002	1	.001
Velame	*Croton campestris*	Euphorbiaceae	0	.000	1	.003	0	.000	1	.001
Graviola			0	.000	0	.000	1	.002	1	.001
Pao piranha			0	.000	1	.003	0	.000	1	.001
Mamaozinho			0	.000	1	.003	0	.000	1	.001
Imbu	*Amburana cearensis*	Leguminosae	0	.000	0	.000	1	.002	1	.001
Pao pretinha			1	.004	0	.000	0	.000	1	.001
Malva preta	*Sida peniculata*	Malvaceae	1	.004	0	.000	0	.000	1	.001
Aroeira	*Astronium urundeuva*	Anacardiaceae	0	.000	1	.003	0	.000	1	.001
Ortiga			1	.004	0	.000	0	.000	1	.001
Violette			0	.000	1	.003	0	.000	1	.001
Manda caru	*Cereus jamacaru*	Cactaceae	0	.000	0	.000	1	.002	1	.001
Capim mimosa	*Aristida* sp.	Gramineae	0	.000	1	.003	0	.000	1	.001
Maracuja de estrela			1	.004	0	.000	0	.000	1	.001
		Totals	256	.230	347	.312	509	.458	1112	

countered plants comprised 76.1% of the vegetation sampled and included five trees, three vines, and two woody shrubs. Marmeleiro (*Croton jacobinensis*) was by far the most abundant plant in all three size classes. The >3 m class constituted 45.8% of the vegetation, the 1–3 m class contributed 31.2%, and the <1 m class comprised only 23.0% of the total. Inclusion of vines in the >3 m class inflated this subtotal but vines were often much longer than 3 meters and substantially increased the density of the canopy. Many produced large quantities of fruits and/or seeds. Of the 10 most abundant plants in the >3 m class, five were trees, four were vines, and one was a shrub; these 10 species constituted 84.2% of the total in that class. In the 1–3 m category, the 10 most abundant plants accounted for 80.1% of the total. The <1 m size class was least common and in part reflects the density of the canopy; the 10 most common species in the lowest layer comprised 76.9% of the total.

Climate

Climatograms (Walter, 1973) portray the relative water balance of an area by plotting mean, monthly maximal temperatures against mean monthly rainfall. When mean monthly rainfall in millimeters exceeds two times the mean monthly maximal temperature in °C, a surplus of water is indicated. As the difference between rainfall and temperature increases, so does the relative degree of surplus. Because the measure is a relative one, direct comparisons between areas on the basis of climatograms must be made with caution. Also, climatograms do not take into account any factors other than temperature and rainfall; in the Caatinga, the geological composition compounds the degree of water deficit.

Mean monthly rainfall and mean, maximum monthly temperature for the period of September 1964 through August 1978 are plotted in Fig. 4 in the form of a modified climatogram. Monthly averages are used to illustrate the relative abundance or paucity of water in a given region. Mean values alone, however, may be misleading when variability is high within the system. The enormous variability in rainfall is depicted in Fig. 5; the months of June, July, August, and September consistently experience substantial water deficits but the other months are more variable. A summary of the occurrence of water deficits and surpluses is presented in Table 2. The water surpluses which occur approximately 50% of the time in December and January, and less frequently in November, are produced by the erratic advances of the continental equatorial air mass which sometimes penetrates as far east as the middle of the São Francisco River basin (Reis, 1976). Sufficient precipitation to produce a water surplus is most likely to fall in March and April, but this failed to occur 20% and 35% of the time, respec-

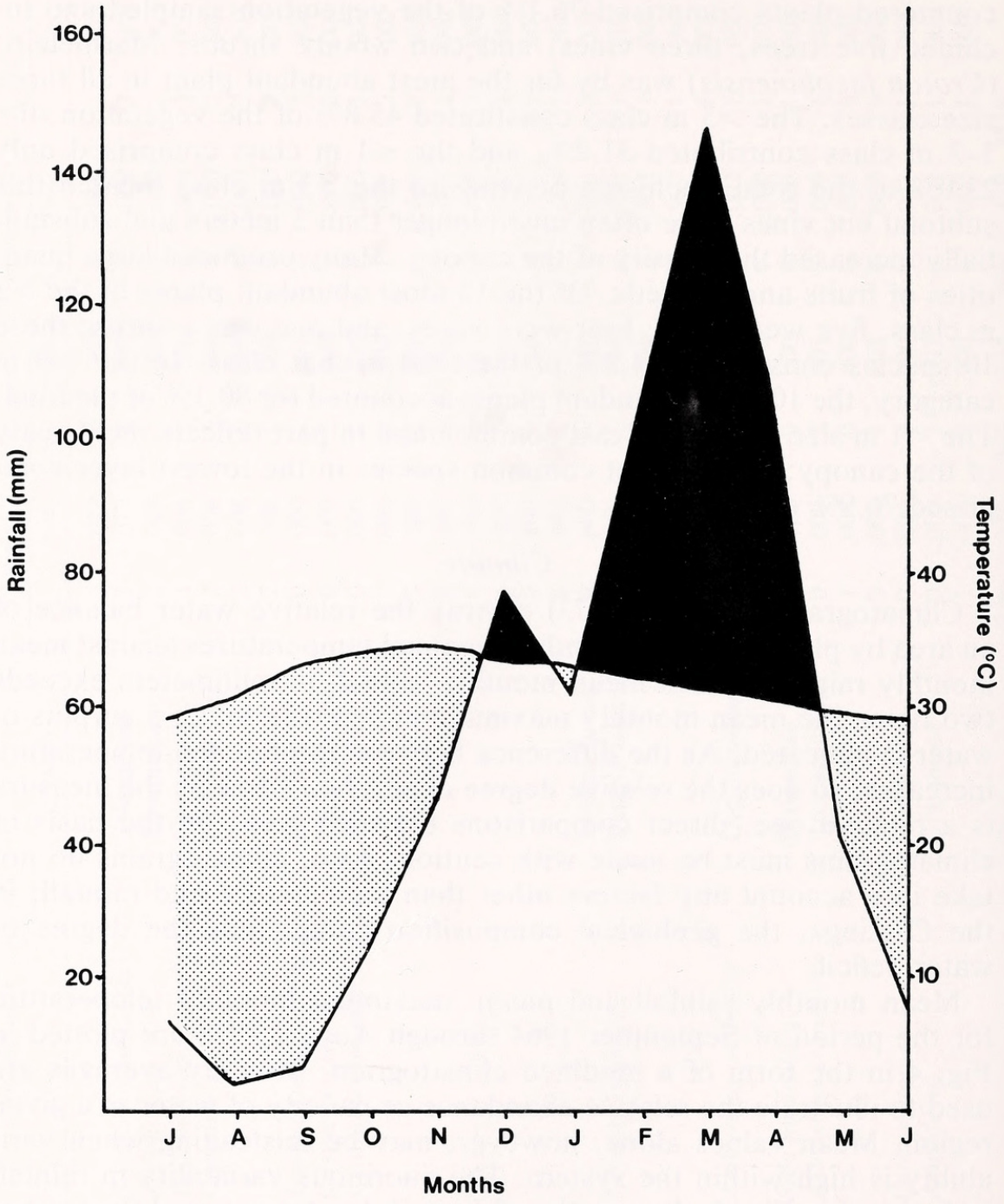

Fig. 4.—Modified temperature (mean of average maximum monthly temperature in °C)-rainfall (mean total monthly rainfall in mm) climatogram for the 14-year period, September 1964–July 1978. Light shading indicates periods of relative water deficit; dark shading represents relative water surplus.

tively, between 1964 and 1978. Water surpluses also occurred approximately one-half (57%) of the time in February and approximately one-third (36%) of the time in May. Precipitation in these months is generated by the Intertropical Convergence Zone and generally constitutes the bulk of the annual rainfall, although quantities vary greatly

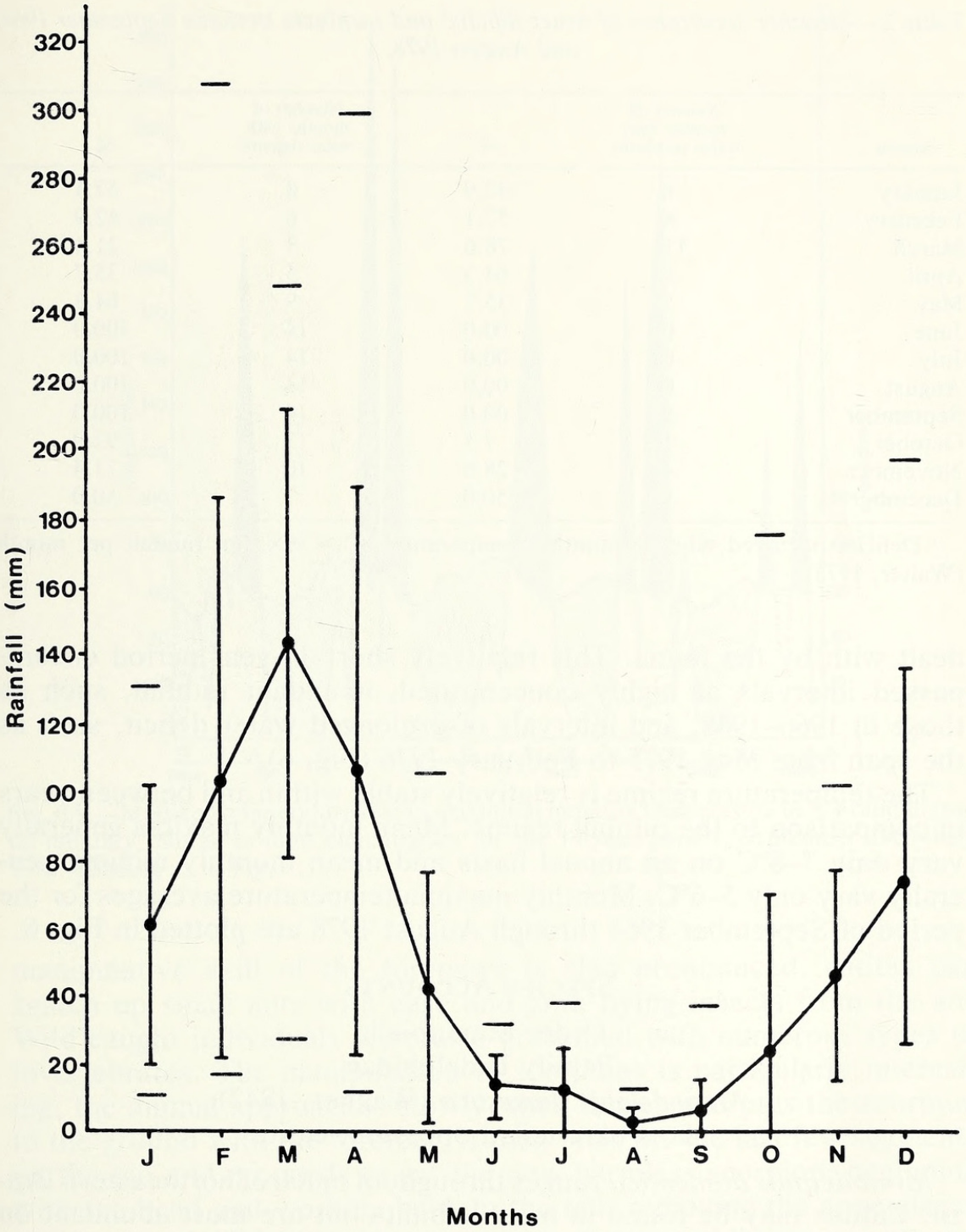

Fig. 5.—Mean monthly rainfall (mm) recorded at the SUDENE weather station in Ouricuri, Pernambuco. Vertical bar indicates ± standard station in Ouricuri, Pernambuco. Vertical bar indicates ± standard deviation; horizontal lines show the range.

among months and between years. The wide range of conditions produced by the unpredictable rainfall in the Caatinga is obscured when mean values only are used. Therefore, modified climatograms were constructed for each year to illustrate the conditions which must be

Table 2.—*Monthly occurrence of water dificits*[1] *and surpluses between September 1964 and August 1978.*

Month	Number of months with water surpluses	%	Number of months with water deficits	%
January	6	42.9	8	57.1
February	8	57.1	6	42.9
March	11	78.6	3	21.4
April	9	64.3	5	35.7
May	5	35.7	9	64.3
June	0	00.0	14	100.0
July	0	00.0	14	100.0
August	0	00.0	14	100.0
September	0	00.0	14	100.0
October	1	7.1	13	92.9
November	4	28.6	10	71.4
December	7	50.0	7	50.0

[1] Deficits occurred when $\bar{x}$ monthly temperature °C > ½× mm rainfall per month (Walter, 1973).

dealt with by the fauna. This relatively short 14-year period encompassed intervals of highly concentrated, abundant rainfall, such as those in 1966–1968, and intervals of prolonged water deficit, such as the span from May 1975 to February 1976 (Fig. 6).

The temperature regime is relatively stable within and between years in comparison to the rainfall regime. Mean monthly maxima generally vary only 7–8°C on an annual basis and mean monthly minima generally vary only 5–6°C. Monthly maxima temperature averages for the period of September 1964 through August 1978 are plotted in Fig. 6.

Species Accounts

Order Marsupialia
Family Didelphidae
Monodelphis domestica (Wagner, 1842)
short bare-tailed opossum; catita

Monodelphis domestica ranges throughout much of northeastern Brazil. Catitas may be found in most habitats but are most abundant on the various types of granitic outcroppings. These small marsupials are basically nocturnal, with peak activity occurring just after dusk. Catitas are primarily terrestrial but are also adept climbers.

Catitas are very efficient predators, concentrating on invertebrates in the field. Small vertebrates, including frogs, lizards, snakes, and mice were readily accepted as food items by laboratory specimens. A 20-g subadult is capable of subduing and killing a 15-g lizard. The

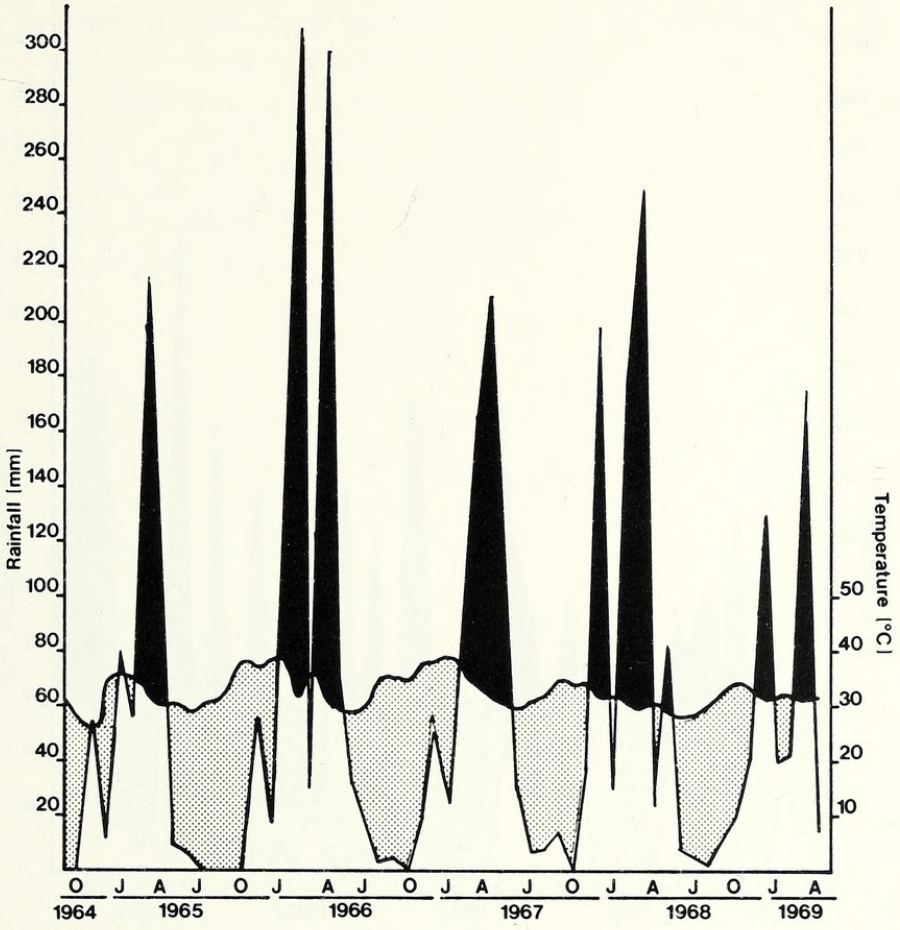

Fig. 6A.—Modified temperature (mean maximum monthly temperature in °C)-rainfall (total monthly rainfall in mm) climatogram for the 14-year period, September 1965–July 1978. Shading as in Fig. 4.

manipulative skill of the forepaws is also pronounced; catitas can snatch up small ants with ease and grab flying insects from the air. Wild caught individuals were also presented with numerous types of invertebrates. The manipulation of scorpions is particularly interesting; the animal approaches slowly, then lunges and pins the scorpion to the ground with the forefeet. It then bites off the last few segments on the tail and proceeds to eat the now harmless scorpion, beginning with the head and working back to the tail, removing the appendages in the process. When catitas are eating, they are oblivious to external disturbances, including agonistic threats by other individuals.

Reproduction occurs throughout much of the year in the field. Litter size ranges from one to 11 altricial young which are not protected by a marsupium. Single family groups were often maintained in captivity for extended periods of time with minimal fighting between individuals.

Monodelphis domestica is generally difficult to trap. They are rela-

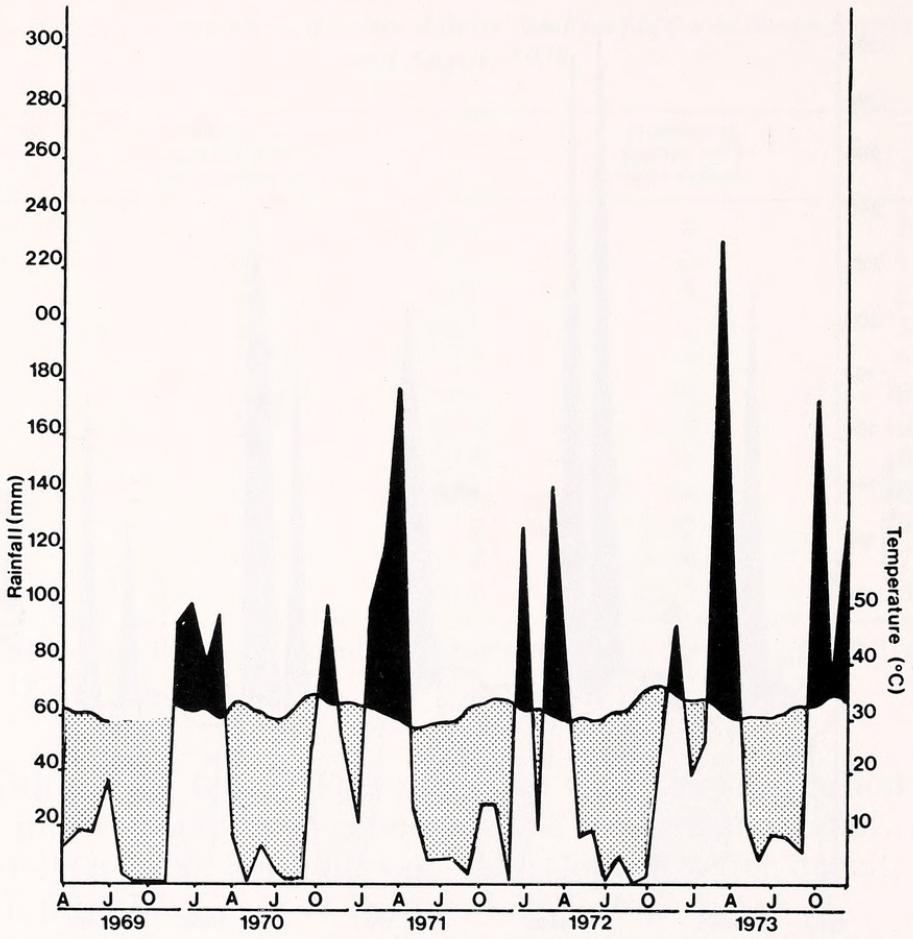

Fig. 6B.

tively docile and seldom attempt to bite. Upon release from traps or after handling, many individuals foraged as they moved away from the trap station. Much of their behavior is similar to that observed for *D. albiventris*.

Marmosa karimii Petter, 1968

Very little is known about this species. No information is available on macrodistribution or patterns of reproduction. It appears to be very rare; part-time collectors were offered a reward equal to the minimum daily wage for a farm hand for each animal caught, so the incentive was high, but only two specimens were captured. These were maintained in the laboratory on a diet of insects, beef, and fruit. Captive specimens were extremely timid and difficult to observe without disrupting their activity. The amount of time spent climbing or perched above the cage floor indicated a high degree of arboreal activity in this species. Flying insects were snatched in mid-flight and manipulated by the forefeet while the prehensile tail and hind limbs supported the body.

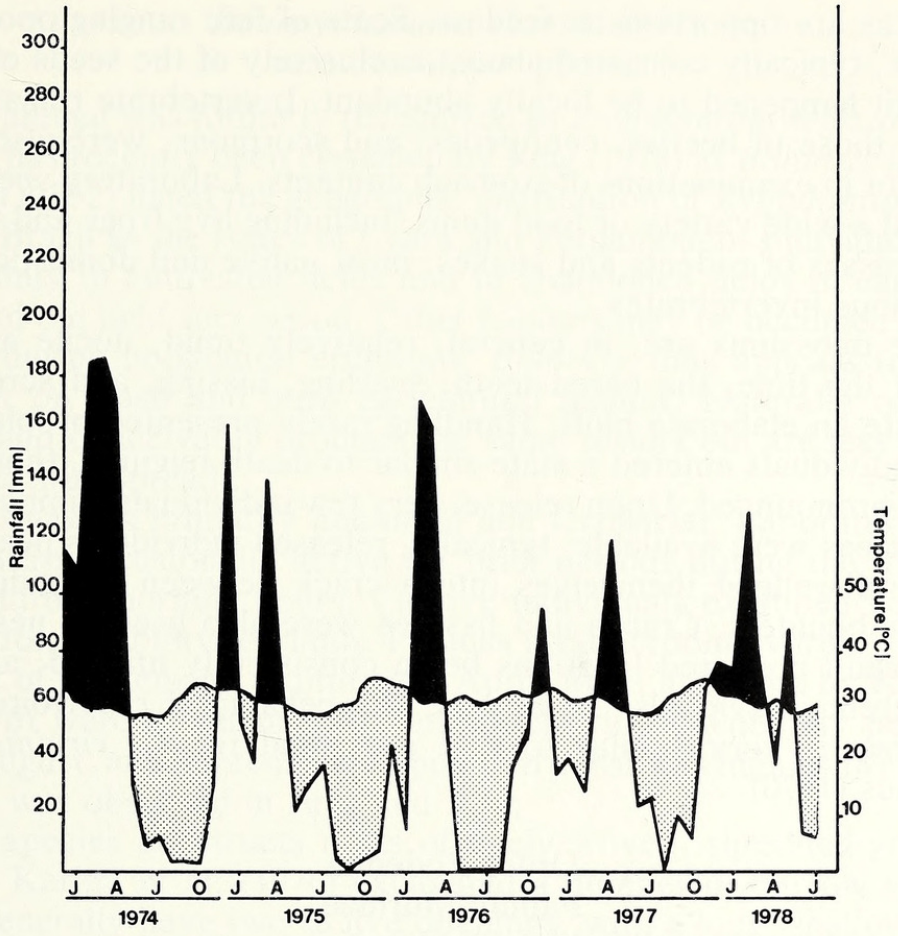

Fig. 6C.

Didelphis albiventris Lund, 1841
white-eared opossum; casaca

Didelphis albiventris ranges throughout the upper subtropical and temperate zones of the Andes, southern and southeastern Brazil, and bordering parts of the Patagonian subregion (Hershkovitz, 1972) and can be found in a wide variety of habitats. In a similar fashion, its northern relative, *D. virginiana,* is often cited as the classic example of an ecological generalist with regard to number and types of habitats occupied, morphology, and food resources utilized. Casacas are ubiquitous in the Caatinga, but differentially utilize microhabitats in response to rainfall patterns, granitic outcroppings being preferred only in months with water deficits.

Reproduction is relatively synchronized in this species. Females produce a single litter per year ranging in size from one to nine young. A reasonably well-developed marsupium is present and serves to protect the extremely altricial young. One female which lost her entire litter was able to reproduce again within a month.

Casacas are opportunistic feeders. Scats of free ranging opossums, however, typically consisted almost exclusively of the seeds of whatever fruit happened to be locally abundant. Invertebrate remains, especially those of beetles, centipedes, and scorpions, were also found in scats or in examinations of stomach contents. Laboratory specimens accepted a wide variety of food items, including live frogs and lizards, the carcasses of rodents and snakes, most native and domestic fruits, and various invertebrates.

These opossums are, in general, relatively timid, docile animals. Most of the time, the bared teeth, snarling, hissing, and screeching constitute an elaborate bluff. Handling rarely presented problems, as many individuals entered a state similar to death feigning, though not quite as pronounced. Upon release, very few individuals climbed, even though trees were available; typically, released individuals headed for rocks and wedged themselves into a crack between or under large rocks or boulders. Cracks and fissures were also used as nest sites, with certain preferred locations being consistently utilized, although by different individuals. In general, the behavioral repertoire of *D. albiventris* is very similar to that described for *D. virginiana* by McManus (1970).

Order Rodentia
Family Muridae
Subfamily Cricetinae
Oryzomys eliurus Wagner, 1845
rice rats; ratinha da cana

Vieira (1955) reported the distribution of *O. eliurus* as ranging from southern Mato Grosso, Minas Gerais, and Bahía, to the state of Paraná. In the area around Exu, this mouse is only found relatively close to the base of the Chapada do Araripe. The Cerrado vegetation on the top of this plateau has apparently served as an invasion corridor; *O. eliurus* is more common on the more mesic northern slope and top of the chapada. The only microhabitats occupied by this species near Exu are cultivated fields and recently abandoned fields.

Oryzomys subflavus Wagner, 1842
rice rats; rato da cana

The distribution includes northern and northeastern Brazil to the state of Minas Gerais (Vieira, 1955). This species is essentially commensal in the area around Exu and is restricted to sugar cane fields and occasionally other cultivated fields near the base of the Chapada do Araripe. *Oryzomys subflavus* is another species common in the Cerrado which is a marginal inhabitant of the Caatinga and can only exist in the more mesic locales near the chapada.

Bolomys lasiurus (Lund, 1841)
rato do campo; pixuna

This animal was formerly recognized as *Zygodontomys pixuna* Moojen but has recently been classified by Reig (1978) as *Bolomys lasiurus*. Moojen (1952) listed the geographic distribution of *Zygodontomys pixuna* in Brazil as the states of Ceará and Pernambuco. Individuals were found only in cultivated fields and in abandoned fields in early seral stages of old field succession. Other habitats may be occupied to some extent during population eruptions. *Bolomys* thus appears to be dependent on slash and burn agricultural habitat. Naturally occurring fires could conceivably produce the same results but are less predictable and widespread.

B. lasiurus is primarily nocturnal and terrestrial. Laboratory specimens were occasionally active for brief periods during the day, generally during morning hours. Captive individuals exhibited very little inclination or ability to climb. Pixunas are microomnivores.

Most of the females captured in April, May, and June by Karimi et al. (1976) were pregnant; population density subsequently peaked in July, August, and September. Population density as high as 187 individuals/ha was observed in June and July.

This species constructs nests of finely woven, shredded grass and leaves. Karimi et al. (1976) excavated a number of burrow systems; these generally have two to five openings, with a long, shallow tunnel leading down into a chamber lined with finely shredded material. More elaborate systems have two branching tunnels leading into a spherical chamber 15 to 20 cm in diameter and approximately 40 cm below the surface. If soil conditions were suitable, Karimi et al. (1976) found that animals placed in terrariums immediately dug out nests; with poor soil conditions, surface nests were constructed but hidden under grass.

Individuals were often relatively docile when handled. When released from traps, their escape behavior usually consisted of rapid, weaving movements into progressively thicker vegetation.

Calomys callosus Rengger, 1830
vesper mouse; rato pequeno

Calomys has a broad geographic distribution, including eastern Brazil; forest fringes and scrublands in southern Brazil, Paraguay, and the Bolivian Chaco; the plains of northern Argentina; and the eastern Andean slopes between La Paz, Bolivia, and Córdoba in Argentina (Hershkovitz, 1962). In the Caatinga, *C. callosus* was found only in the latter seral stages of old field succession and Caatinga Baixa habitats.

Calomys callosus is an active, agile climber. The long tail is used as a climbing aid. A pronounced inclination toward arboreal activity was

observed in the laboratory. In the field, this species probably spends as much or more time foraging in trees and shrubs as it does on the ground. Adults are capable of sheer vertical leaps of approximately 0.7 to 0.8 m.

These animals were strictly nocturnal in the laboratory and quite easily maintained. They accepted most native seeds offered to them, but appeared to prefer the seeds of an unidentified legume common in open thorn scrub formations and the seeds of various grasses. Moths and beetles were also highly preferred food items. Nests constructed in the laboratory were essentially spherical in shape and consisted of finely shredded, interwoven plant material. This sort of material also lined the nests found in the field, but these were simple depressions hollowed into the ground, approximately 10 to 15 cm in depth and width and camouflaged with twigs and leaves. A few nests were found under thin, flat rocks or roofing tiles. These systems were a bit more complex and had two or more openings; occasionally, small stores of seeds would be located a short distance from the central nest.

Calomys were never found in large numbers and were generally uncommon. Karimi et al. (1976) reported a similar conclusion.

Mello (1977*a*, 1978*b*) presented information on their general biology and reproduction in the laboratory. The mean litter size was reported to be 4.5 (Mello, 1977*b*) and the range was from two to nine (Mello, 1978). This species has a postpartum estrous and a mean gestation period of 21.8 days (Mello, 1977*b*). The short gestation period, relatively large litter size, and postpartum estrous create a high reproductive potential.

Calomys are typically docile animals. The basic response to being startled or handled is to "freeze" in position and remain motionless. This behavior also functions in predator avoidance; when motionless, *Calomys* are essentially indistinguishable from the ground litter.

Wiedomys pyrrhorhinos (Wied, 1821)
red-nosed mouse; rato vermelho

The distribution of *Wiedomys pyrrhorhinos* in Brazil includes the states of Ceará, Pernambuco, Paraíba, Bahía, Minas Gerais, northern Mato Grosso, Paraná, and Rio Grande do Sul (Moojen, 1952). In the Caatinga, *W. pyrrhorhinos* was trapped only in Caatinga Baixa formations.

These nocturnal rodents are deft climbers and make extensive use of their long tails for balance. Laboratory animals spent a great deal of time climbing about the cages. Nests are typically placed above ground in trees or shrubs. One pregnant female was observed in an abandoned bird nest situated in a cansacão (*Cnidoscolus wrens*); these

plants are protected by spines covered with compounds exceedingly irritating to humans and presumably other animals. Moojen (1952) listed a number of objects used as nest sites, including holes in trees, parakeet-excavated termite mounds, and abandoned bird nests.

Litter size ranges from one to six altricial young. Lactating females readily adopt other young; one female successively nursed her own litter, a litter of *Calomys,* and a *Bolomys* litter. One pregnant female that was collected still had a subadult pelage.

This species was never abundant at any locale. Food items accepted by laboratory specimens included most native seeds. They avidly chased and ate beetles and moths in the laboratory, but were relatively inefficient predators. No evidence of food storage was observed. In general, these animals are timid and difficult to handle.

Family Caviidae
Kerodon rupestris (Wied, 1820)
rock cavy; mocó

The distribution in Brazil includes the northeastern states and portions of Bahía and Minas Gerais (Moojen, 1952). Mocós are generally restricted to structurally diverse rocky areas, especially serrotes and serras, but often occupy lowland lajeiros. *Kerodon* are subject to intense hunting pressure because they are large rodents with high quality flesh (Lacher, 1979), the stomach is prized as a starter for cheese, and certain behavioral traits make them easy prey for hunters. This species' practice of defecating on the same elevated locations, and characteristic alarm call (the call itself bounces off the rocks, making it difficult to locate the source) confirms its presence.

Mocós are extremely agile animals. The leathery pads on the feet are used to great advantage as they maneuver in the rocks, often bounding or ricocheting from boulder to boulder. They are also deft climbers and obtain most of their sustenance by foraging in tree tops. They frequently leap straight to the ground if startled while foraging.

Mocós use rock fissures or the cracks beneath boulders as nest sites and refugia from predation, wedging their bodies into narrow cracks when pursued. Females reproduced year-round under laboratory conditions, with a litter size of one or two young (Lacher, 1980); the young are very precocial.

At times, as many as four or five individuals could be observed moving about the rocks during the day on a small but complex section of the grid, but only five individuals were captured in 25,000 trap nights on the grid. These animals were relatively docile, easily handled animals and never attempted to bite.

There is some potential for domestication (Lacher, 1979).

Galea spixii (Wagler, 1831)
cavy; preá

Galea spixii has a wide distribution in Brazil, ranging throughout the Northeast, in the states of Bahía, Goias, Mato Grosso, and Minas Gerais (Moojen, 1952). In the Caatinga, preás were found in most lowland habitats, especially in recently abandoned and cultivated fields. This cavy is tailless, terrestrial, and primarily diurnal, but is also active for short intervals during the night.

Reproduction occurred throughout the year and females were capable of producing several litters annually. Litter size ranged from one to five. The young are precocial but to a lesser degree than either *K. rupestris* or *T. apereoides*.

Galea spixii is the only Caatinga rodent which develops and consistently utilizes a network of runways. Areas frequented by preás were readily distinguished by the presence of runways and numerous small cleared patches used for sandbathing. Nest sites appeared to be temporary and are typically located under rocks or low, overhanging vegetation. Acceptable food items included most types of vegetation; *G. spixii* is strictly herbivorous.

Preás were often relatively difficult to capture unless traps were placed squarely in runways. The adherence to these familiar pathways is best illustrated by several incidents where *G. spixii* was spotted running under a boulder or into thick vegetation; an open live trap was then placed on the just-used runway and the hiding place approached from the other side. Each individual ran back along the entry route and into the trap, sometimes banging repeatedly against the back of the trap until it closed. This occurred even though the traps were plainly visible for 4 or 5 m at ground level and were easily avoidable.

Behavior in traps was quite variable, but a large portion of first-capture animals completely wore the fur off their snouts by constantly butting the sides of the trap. Some individuals continued to exhibit this behavior upon subsequent recaptures. Many preás struggled and kicked extensively when first handled, but during hundreds of handling bouts of live-trapped and laboratory animals, none attempted to bite. Preás frequently displayed a behavior similar to death feigning by opossums; when handled, the body became limp until deposited on the ground. This state sometimes persisted for several minutes beyond the completion of handling procedures.

Family Dasyproctidae
Dasyprocta prymnolopha (Wagler, 1831)
agouti; cotia

Cotias range in Brazil from the state of Pará to southern Brazil (Moojen, 1952). They were apparently quite abundant in the past on

the granitic outcroppings, but widespread habitat destruction and intense hunting pressure have extirpated them from most locales. Currently, cotias are restricted to patches of High Caatinga vegetation and isolated serrotes in much of the Caatinga. These animals apparently feed primarily on fruits and larger seeds.

Family Echimyidae
Thrichomys apereoides (Lund, 1841)
spineless spiny rat; punaré

The two species in the genus range throughout eastern and central Brazil and Paraguay (Walker, 1975). In the Caatinga punarés are found only in the granitic formations, including lowland lajeiros and elevated serrotes and serras. This strict association with rocky habitat is also characteristic of populations in the very mesic, remnant Atlantic Forest. Populations in the Cerrado are also restricted to isolated rocky areas (T. E. Lacher, Jr., personal communication). Echimyids typically occupy relatively mesic habitats, and most die when exposed to heat and dryness (Walker, 1975); thus *T. apereoides* is somewhat of an exception within the family.

This species is very agile and quite adept at maneuvering in structurally diverse, boulder strewn locales. Nests are typically situated under large boulders when available. The numerous cracks and crevices produced by the splitting and exfoliation of the granitic rock serve as temporary refuges. Individuals are difficult to dislodge when wedged into narrow cracks. Animals which escaped from cages were generally found jammed behind an object leaning against a wall.

Punarés tended to be active for short periods both day and night but exhibited definite crepuscular peaks in activity. They may perhaps be best classified as semiarboreal. Individuals were capable of traversing branches less than one-half centimeter in diameter with ease. The long, heavy tail was used extensively as a pendulum-like counterbalance while climbing and also served as the third leg of a tripod during the stereotyped, upright postures characteristic of agonistic behavior. Paradoxically, for such an important appendage the tail is easily fractured and portions are readily lost, as is the case with most other echimyid species (Walker, 1975). Adults grabbed by the tail leap forward and up into the air, executing a 360° side-to-side twisting of the body which autotomizes the tail at the point of contact or near the base; juveniles less than 12 hrs old have also been observed to attempt this maneuver.

Litter size ranged from one to six. The young are very precocial and often begin to eat solid foods on the day of birth. Grooming behavior is also initiated shortly after birth. Nursing frequently continued until the young weighed 50 to 60 g, but young as light as 15 to 20 g survived in the laboratory without nursing.

Table 3.—*General distribution patterns of small mammals in the Caatinga and adjacent biomes. W = widespread, L = limited distribution, A = absent, ? = unknown or uncertain.*

Species	Cerrado	Caatinga	Atlantic Rainforest
Marsupialia			
Didelphidae			
Monodelphis domestica	W	W	W
Marmosa karimii[1]	L?	W?	?
Didelphis albiventris	W	W	W
Rodentia			
Muridae			
Oryzomys eliurus	W	L	A
Oryzomys subflavus	W	L	A
Bolomys lasiurus	W	L	?
Calomys callosus	W	L	A
Wiedomys pyrrhorhinos	L	W	A
Dasyproctidae			
Dasyprocta prymnolopha[1]	A?	W?	A?
Caviidae			
Kerodon rupestris[2]	L	W	A
Galea spixii	W	W	W?
Echimyidae			
Thrichomys apereoides[2]	L	W	L

[1] Distributional patterns not well established.
[2] Limited to rocky habitats in areas of occurrence.

Laboratory specimens accepted essentially every type of native seed offered, including many from legumes. Insects, particularly beetles and moths, were quickly ingested. In general, food items less than 2 mm in length were not manipulated with the forepaws.

Punarés, especially subadults, are relatively easy to capture during dry periods. Adults tended to avoid traps in wet periods, but subadults remained very susceptible. Individuals caught for the first time were generally quite vocal and prone to struggle extensively when handled, but rarely attempted to bite. Most individuals became increasingly docile with subsequent recaptures.

DISCUSSION

The terrestrial small mammal fauna in this portion of the Caatinga consisted of 12 species. Rodents were represented by nine species in four families and marsupials by three species in a single family. Two other rodents, *Mus musculus* and *Rattus rattus,* were also present but

occur only in buildings. Additional information on the mammal fauna of the Caatinga can be found in Mares et al. (1981).

Most of the small mammal species have relatively broad geographic distributions in South America, extending far beyond the boundaries of the Caatinga. Hershkovitz (1972) has previously noted the low degree of endemism in the Caatinga. Approximately 50% of the species found in the Caatinga also occur in the Atlantic Rainforest (Table 3). The degree of overlap with the Cerrado is even greater; approximately 90% of the species are present in both biomes, however, eight of the 11 shared species have very limited distributions in one or the other biome. The fauna of the Caatinga is, in general, mainly composed of species that occur throughout the open formations (Vanzolini, 1973) that dominate central South America.

ACKNOWLEDGMENTS

A large number of people provided valuable assistance throughout the course of this project. I extend special thanks to my colleagues in Brazil, Drs. Thomas E. Lacher, Jr., and Michael R. Willig, and to my major advisor, Dr. Michael A. Mares. I also wish to thank Drs. Aristides Leão, Paulo Vanzolini, and Celio de Almeida, and the staff of the Brazilian Academy of Sciences. Antonio Lemos da Silva and Raimundo Lopes da Silva assisted with the field work, Drs. Marcelo de Ataide Silva and Dardano de Andrade Lima identified Caatinga plant specimens, Joyce Kotzuk prepared the figures, and Ruth Ann Schulte typed the manuscript. This manuscript was improved by the suggestions made by Drs. Peter L. Dalby and Margaret O'Connell; Martin Berg, William Downer, Joyce Kotzuk, and Anthony Nastase commented on portions of an earlier version of the manuscript. I am also very grateful to Dr. Richard T. Hartman of the Pymatuning Laboratory of Ecology and to Drs. Hugh Genoways and Duane Schlitter of the Carnegie Museum of Natural History for permitting me to use their facilities.

My study was supported by the Brazilian Academy of Sciences, project number 85, "Ecology, evolution, and zoogeography of Caatinga mammals" as part of the larger program, "Ecological studies of the semiarid region of northeastern Brazil." Additional funds were provided by the Carnegie Museum of Natural History.

This report is a portion of a dissertation submitted in partial fulfillment of the requirements for the Ph.D. degree from the University of Pittsburgh.

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