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# THE ECOLOGY OF SMALL MAMMALS IN THE SEMIARID BRAZILIAN CAATINGA. IV. HABITAT SELECTION

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# Abstract

Distributional patterns in the small mammal fauna of the Caatinga were examined. Most of the caviomorph rodent and marsupial species preferentially utilize granitic outcroppings. Pronounced affinity for the stable, mesic granitic habitats evolved as an avoidance response to the unpredictable occurrence of extreme climatic conditions characteristic of the Caatinga. None of the murids exhibited this behavior.

#### INTRODUCTION

### Background

When a species first invades a new region, it most likely selects the habitats most similar to those in which it has been successful through evolutionary time, especially if the previous selective pressures mandated strict adherence to a particular type of habitat. On the other hand, species occupying an area in which a new habitat develops have the opportunity to slowly adapt to the changing set of conditions; for example, the fossorial habits of the geomyids apparently developed in response to the gradual appearance of xeric habitat in North America (Russell, 1968). Because reduction of water stress is a primary consideration for small mammals in xeric areas, habitats which reduce water stress should be strongly favored, with species eventually developing pronounced affinities for these habitats. The rate of development of

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habitat selectivity will, however, be related to predictability of the environment; in xeric areas, timing and extent of rainfall are the critical elements. If water stress is continual or occurs at regular intervals within the life span of the animals, the environment must be tracked by individuals and rigorous natural selection processes will operate on each generation. Natural selection pressures operating on each generation will vary if severe environmental fluctuations occur only at intervals greater than individual life spans while intervening conditions are more moderate. The variability in natural selection pressures will thus decrease the overall rate of development of habitat specificity. At the species level then, habitat specificity and other related adaptations will accumulate slowly because individuals that select suboptimal habitat are not necessarily penalized, through shorter lifespans and less reproductive success, during moderate intervals when habitat of lower quality suffices. Subsequently, when the intermittent severe conditions and accompanying intense natural selection pressures reappear, populations occupying suboptimal habitat will be decimated. Invading, short-lived species should therefore find it especially difficult to adapt to an area where severe conditions occur only at widespread, irregular intervals.

The climatic regime of the Caatinga poses special problems for small mammal species. Although the area is generally semiarid, it is subject to both extremes of the precipitation spectrum, experiencing extended droughts and prolonged periods of heavy rainfall. The unpredictable occurrence of these disparate phenomena is a further confounding factor. Accumulation of specializations for the mean, semiarid environmental state will be extremely difficult or perhaps impossible for species occupying unstable Caatinga habitats because they are irregularly subjected to widely divergent selective pressures; the water conservation capabilities, foraging strategies, and predator-escape tactics favored in a sparsely-vegetated, arid environment are probably detrimental or of dubious value during mesic, thickly vegetated intervals. Small mammal species with origins in the surrounding, predictably mesic biomes should therefore require an extended period of time to develop a high degree of adaptation to the unusual climatic conditions which prevail in the Caatinga. A critical, mitigating factor is, however, present in the region; a large number of "microrefugia" exist. The abundant granitic outcroppings scattered throughout the area are relatively stable and mesic compared to the bulk of the Caatinga. The availability of these microrefugia has been of paramount importance in the adaptation of many Caatinga species.

### The Caatinga

The current geographic boundaries of the Caatinga extend from  $3^{\circ}$  to  $16^{\circ}$  south latitude and from  $35^{\circ}$  to  $45^{\circ}$  west longitude, encompassing

an area of 650,000 km<sup>2</sup> (Reis, 1976; Frota-Pessoa et al., 1971). Although the Caatinga lies within the tropics, it is semiarid and experiences an unpredictable rainfall regime, thus deviating substantially from the bulk of tropical South America, which is relatively mesic and seasonally predictable. The rainfall regime is primarily influenced by the Southeast Trade Winds, in conjunction with three large, mobile masses of air. A general description of the climate can be found in Streilein (1982a), whereas a more detailed account of the patterns of rainfall and atmospheric circulation is available in Reis (1976) and Markham (1972). Each of the three moisture-laden air masses generally introduces some rain into the Caatinga in each year, but the amount of rain varies greatly from year to year, irregularly culminating in extended droughts and severe flooding. Three distinct geological features typify the Caatinga (Ab'Saber, 1970). A basement level of Precambrian crystalline rock, once covered by sedimentary rock, is now the dominant feature in the Caatinga, in terms of area encompassed. The surface layer of sedimentary rock has remained intact in certain areas, some of which are elevated above the surrounding countryside in the form of steepsided plateaus (chapadas). The distinctive physiography of the Caatinga is attributed to the abundant, ubiquitous granitic formations; the sedimentary rock plateaus and extensive crystalline rock flats are relatively uniform and structurally simple compared to the granitic areas. Granitic rock occurs in the form of low mountain ranges (serras), small mountain ridges (serrotes), and lowland outcroppings (lajeiros). Structural diversity in the Caatinga on both local and geographic scales is primarily determined by the number, types, and distributional patterns of the granitic formations. Vegetation in the Caatinga ranges from relatively simple to extremely complex assemblages with regard to species abundance and composition, characteristic species, and foliage height profiles. In general, however, Caatinga vegetation can be classified into two largely distinct categories on the basis of foliage height profiles, with Caatinga Baixa (low thorn scrub) consisting of the various types of scrubby vegetation where canopy elements normally attain only 3 to 5 m, whereas Caatinga Alta (high thorn scrub) refers to vegetation types where the dominant canopy elements are typically greater than 5 m. Some of the granitic formations and sedimentary rock plateaus are elevated enough to function as orographic barriers and thus receive augmented rainfall. These areas (brejos) are able to sustain humid forests; the botanical affinities of the humid forests lie with the Atlantic Rain Forest (Andrade and Lins, 1964). A more comprehensive account of Caatinga geology and vegetation is contained in Streilein (1982a).

Most of the fieldwork for this project was done in the municipality of Exu in the northwestern corner of Pernambuco, Brazil. All of the three major geological features representative of the Caatinga are found in close proximity in that area. The dominant element, however, is the

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Chapada do Araripe, an extensive sandstone plateau that stretches for hundreds of kilometers from east to west along the border of Pernambuco and Ceará. Numerous structurally complex granitic outcroppings, in the form of serrotes and lajeiros, are also present. The vegetation reflects the complexity of the area; the overall vegetation pattern may best be described as a mosaic of patches of variable size, some of which are clearly distinct while others gradually merge.

# MATERIALS AND METHODS Gross Habitat Utilization

Gross Habitat Utilization

Trapping and observations were conducted in each major habitat in the vicinity of Exu and on the Chapada do Araripe. Trapping records and field sites of AGGEU, a public health agency responsible for monitoring the small mammal species that harbor bubonic plague vectors, were examined for the municipality of Exu. Observations by AGGEU's professional collectors were also noted. Additional information was obtained during general mammal surveys in other parts of the Caatinga. A general treatment of distribution patterns for Caatinga mammals can also be found in Mares et al. (1980).

#### Microhabitat Utilization

A permanent, 12 by 12 (2.7 ha) live trapping grid was established at Fazenda Batente, 6 km SE of the town of Exu (7°31'S, 39°43'W), Pernambuco, Brazil. The grid encompassed portions of three distinct microhabitats. Sharply delineated microhabitats allowed each grid station to be classified in one of three categories—lajeiros (rock), Caatinga Baixa (low thorn scrub), or old field. Individual capture locations were recorded for the eight species captured between December 1976 and February 1978. Chi-square tests were performed to determine if the species were utilizing the microhabitats in proportion to their frequency of occurrence on the grid. In several instances, the low thorn scrub and old field categories were combined because the number of expected captures in the old field was too small to satisfy the requirements of the Chi-square tests.

## RESULTS

## Gross Habitat Utilization

The occurrence of species in each major Caatinga habitat is summarized in Table 1; however, some of the relationships between species and habitats require further clarification. Both *Monodelphis domestica* and *Didelphis albiventris* are ubiquitous, but population densities are greatest in the granitic outcroppings. The other marsupial, *Marmosa karimii*, was extremely rare. It is known to occur only in thorn scrub and the latter seral stages of old field succession, but may occasionally utilize other habitats. *Wiedomys pyrrhorhinos* is the only widespread murid species. *Oryzomys eliurus* and *O. subflavus* occupy the habitats listed in Table 1 only in the immediate vicinity of the Chapada do Araripe; *Calomys callosus* also has a very restricted distribution. *Bolomys lasiurus* extends somewhat further into the Caatinga proper but populations are very localized. *Galea spixii* does occur in Caatinga Baixa, but individuals are concentrated at the interfaces with agricul-

Species	Naturally occurring				Agriculture	
	Granitic outcroppings		Caatinga		— Cultivated	Abandoned fields (in suc-
	Lajeiros	Serrotes	Baixa	Alta	fields	cession)
Marsupialia					ing.	inguese M
Didelphidae						
Monodelphis domestica	Х	Х	Х	Х	Х	Х
Marmosa karimii	?	?	X	?	?	Х
Didelphis albiventris	Х	Х	Х	Х	Х	Х
Rodentia						
Muridae						
Oryzomys eliurus					Х	
Oryzomys subflavus					Х	
Bolomys lasiurus					Х	Х
Calomys callosus			Х			X
Wiedomys pyrrhorhinos			X			
Caviidae						
Kerodon rupestris	Х	Х				
Galea spixii	Х		Х		Х	Х
Echimyidae						
Thrichomys aperoides	Х	Х				

#### Table 1.—Habitat types utilized by Caatinga small mammals.

turally derived habitats; extensive stands of low thorn scrub are virtually devoid of G. spixii.

Examination of Table 1 reveals three significant trends. First, murids are totally lacking in the relatively mesic, granitic outcroppings. Second, three of the five murid species (*B. lasiurus* and both species of *Oryzomys*) are found only in habitats created by agricultural practices. Third, the only species restricted to the granitic outcroppings are both caviomorph rodents, one caviid (*Kerodon rupestris*) and one echimyid (*Thrichomys apereoides*).

# Microhabitat Utilization

None of the six species examined, on the basis of total captures, utilized the microhabitats with respect to proportion of occurrence on the grid (Table 2). While *K. rupestris* did not readily enter traps, visual observations followed a similar pattern, with sightings concentrated in structurally-complex boulder strewn areas (Lacher, 1981; personal observation). Three species, *M. domestica*, *D. albiventris*, and *T. aperoeoides*, disproportionally frequented the traps in rocky areas. The largest percentage of the variance in *G. spixii* microhabitat usage re-

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Species	Rock	Thorn Scrub	Old Field	Total	
Marsupialia		where pend	well's meet	Merry milantine and	
Didelphidae					
Monodelphis domestica					
Observed	112	17	6	135	
Expected	67.8	59.3	8.0		
$\chi^2$	28.8	30.2	0.5	59.5***	
% Variance	48.4 (+)	50.8 (-)	0.8 (-)	$P \ll .001$	
Didelphis albiventris					
Observed	151	85	15	251	
Expected	126.0	110.2	14.8		
$\chi^2$	5.0	5.8	0.0	10.8**	
% Variance	46.3 (+)	53.7 (-)	0.0	P < .01	
Rodentia					
Muridae					
Bolomys lasiurus					
Observed	0	12		12	
Expected	6.0	6.0			
$\chi^2$	6.0	6.0		12.0***	
% Variance	50.0 (-)	50.0 (+)		P < .001	
Calomys callosus					
Observed	1	16		17	
Expected	8.5	8.5			
$\chi^2$	4.8	4.8		9.6**	
% Variance	50.0 (-)	50.0 (+)		.01 < P < .001	
Caviidae					
Galea spixii					
Observed	66	32	16	114	
Expected	57.2	50.0	6.7		
$\chi^2$	1.4	9.7	10.3	21.4***	
% Variance	6.5 (+)	45.3 (-)	48.1 (+)	P < .001	
Echimyidae					
Thrichomys apereoides					
Observed	731	77	14	822	
Expected	412.6	360.9	48.5		
$\chi^2$	245.7	223.9	24.5	493.5***	
% Variance	49.8 (+)	45.2 (-)	5.0 (-)	$P \ll .001$	

Table 2.—Results of Chi-square tests on microhabitat utilization on the grid based on total captures. The (+) denotes a substantial portion of the variance which is due to greater-than-expected utilization. (-) denotes the converse relationship.

Species	Rock	Thorn Scrub	Old Field	Total
Caviidae			Bart Designation	and Independent
Galea spixii				
Wet				
Observed	21	11		32
Expected	16.0	16.	.0	
$\chi^2$	1.6	1.6		3.2 ns
% Variance				.1 < P < .05
Dry				
Observed	45	24	13	82
Expected	41.6	35.3	5.2	
$\chi^2$	0.3	3.6	11.7	15.6***
% Variance	1.9 (+)	23.1 (-)	75.0 (+)	P < .001
Echimyidae				
Thrichomys apere	oides			
Wet				
Observed	189	27	1	217
Expected	108.5	96.1	12.4	
$\chi^2$	59.7	49.7	10.5	119.9***
% Variance	49.8 (+)	41.5 (-)	8.8 (-)	$P \ll .001$
Dry				
Observed	542	50	13	605
Expected	306.7	260.2	38.1	
$\chi^2$	180.5	169.8	16.5	366.8***
% Variance	49.2 (+)	46.3 (-)	4.5 (-)	$P \ll .001$

Table 3.—Microhabitat utilization by the caviomorph rodents, Galea spixii and Thrichomys apereoides, during wet and dry months on the grid. Months were classified as wet if mean monthly temperature in  $^{\circ}C < \frac{1}{2} \times mm$  rainfall/month.

sulted from the concentration of captures in the old field trap stations, and the underrepresentation in thorn scrub stations. Old field and thorn scrub categories were combined for B. *lasiurus* and C. *callosus* because the total number of captures was small; all of the B. *lasiurus* captures in the combined category were actually in the old field and those of C. *callosus* were all in the thorn scrub. The mixed category was much preferred over the rocky microhabitat.

Comparison of microhabitat utilization in wet versus dry months, based on months with relative water surpluses or deficits (Streilein, 1982a), revealed trends (Tables 3-4) obscured in the analysis of total captures. *Monodelphis domestica* and *T. apereoides* captures remained concentrated in the rocky areas in both wet and dry months. *Bolomys lasiurus* and *C. callosus* could not be compared in this man-

		Microhabitats			
Species	Rock	Thorn Scrub Old Field		Total	
Monodelphis domestic	ra			a subject	
Wet					
Observed	44	10		54	
Expected	27.0	27.0			
$\chi^2$	10.7	10.7		21.4***	
% Variance	50.0 (+)	50.0 (-)		P < .001	
Dry					
Observed	68	8	5	81	
Expected	41.1	34.8	5.1		
$\chi^2$	17.6	20.6	0.0	38.2***	
% Variance	46.1 (+)	53.9 (-)	0.0	$P \ll .001$	
Didelphis albiventris					
Wet					
Observed	33	25		58	
Expected	29.0	29.0			
$\chi^2$	0.6	0.6		1.2 ns	
% Variance				.3 < P < .2	
Dry					
Observed	118	62	13	193	
Expected	97.2	83.0	12.2		
$\chi^2$	4.2	5.3	0.0	9.5**	
% Variance	44.2 (+)	55.8 (-)	0.0	P < .01	

Table 4.—Microhabitat utilization by the marsupials, Monodelphis domestica and Didelphis albiventris, during wet and dry months on the grid. Months were classified as wet if mean monthly temperatures in  $^{\circ}C < \frac{1}{2} \times mm$  rainfall/month.

ner because the number of captures in each category did not provide an adequate sample size. Both *G. spixii* and *D. albiventris* exhibited distributions of captures proportional to the frequency of occurrence of microhabitats during the months with relative water surpluses. Captures in dry months, however, were not proportionally distributed; *D. albiventris* favored rocky areas and avoided thorn scrub while *G. spixii* was trapped much more often in the old field than was expected (75% of the variance).

#### DISCUSSION

The major types of habitats which naturally occur in the Caatinga are serrotes and lajeiros, Caatinga Alta, and Caatinga Baixa. A large area is currently covered by abandoned fields in various stages of succession (the result of slash and burn agriculture) and a smaller area is claimed each year from Caatinga Alta and Baixa habitats for agricultural purposes. These habitats encompass a rough moisture gradient, with serrotes and lajeiros being the most mesic, followed by Caatinga Alta, and finally Caatinga Baixa. The small mammals which inhabit the granitic outcroppings acquire two important advantages. First, even a light rain forms temporary pools in depressions in the rock as a result of runoff from more elevated surfaces; these ephemeral sources of free water are of paramount importance because the Caatinga is devoid of permanent streams. Second, some of the runoff percolates into cracks and fissures; this water is slowly lost to the atmosphere, thus maintaining higher relative humidity in the outcroppings.

The zoogeographic theories advanced by Patterson and Pascual (1968, 1972), Hershkovitz (1966, 1969, 1972), and Marshall (1979) basically agree that marsupials and caviomorph rodents were in South America long before the murids arrived. It is conceivable then that representatives of these groups could have already been occupying the area in which the Caatinga eventually arose, affording them the opportunity to adapt as environmental conditions gradually changed. Alternatively most of the species may still have invaded the Caatinga much earlier than the murids. In either case, they have generally had a longer period of time to adjust to the area and should thus exhibit a higher degree of adaptation.

Small mammals in xeric areas should theoretically select habitats which reduce water stress unless they are particularly well adapted to an arid environment. In the Caatinga, then, most species might be expected to inhabit serrotes and lajeiros. The observed distributional patterns for marsupials and caviomorph rodents generally followed this pattern; all of the common caviomorphs and marsupials utilized the granitic outcroppings to a large degree. Kerodon rupestris and T. apereoides were virtually limited to the immediate vicinity of the outcroppings, M. domestica populations were primarily concentrated in the rock-dominated habitats, and D. albiventris rapidly responded to the occurrence of relative water deficits by preferentially utilizing the outcroppings. The caviomorph, G. spixii, was the only species that did not exhibit highly preferential usage of the granitic outcroppings, even in intervals of severe water stress. Galea spixii did use the rocky habitats, so it was not a situation where the habitat was inaccessible or hostile. The observed pattern of distribution apparently resulted from K. rupestris actively excluding any G. spixii individuals encountered. Kerodon reacted aggressively and clearly established dominance over the much smaller Galea in behavioral trials in neutral arenas (Streilein, 1982d) and in three mixed-colony situations (Lacher, 1981). The most significant aspect of the situation is that none of the common species of the two groups that should have had the greatest amount of time to adapt to the Caatinga preferentially utilized Caatinga Baixa, the most extensive habitat-type available. All of them did, however, utilize the most stable, mesic habitat-type available, the granitic outcroppings.

Examination of two of the caviomorph species suggests that they may antedate the Caatinga or at least have invaded it at a very early date. Kerodon rupestris is the only representative of the ecologically and behaviorally diverse rodent family, Caviidae, with a distribution limited to rocky areas. This species also has morphological, rockdwelling adaptations, leathery pads on the feet and subcutaneous nails on all digits but the innermost digit of the pes, unique to the subfamily Caviinae (Lacher, 1981). Fifteen genera are currently recognized in the Echimyidae (Walker, 1975), but of the approximately 70 species in this family, only T. apereoides is known to exist in a xeric area. Thrichomys apereoides is also distributed solely in areas dominated by rock outcroppings. This affinity for rocks is pronounced; populations in the Cerrado biome are also found only in the limited number of rocky areas (T. E. Lacher, Jr., personal communication) as are the populations in the Chaco in Paraguay (P. Myers, personal communication). These disjunct populations were probably established when the Caatinga expanded during the dry phases of the Quaternary climatic cycles. The uniqueness of Kerodon and Thrichomys with regard to their respective congeners, considered in conjunction with the special attributes of the Caatinga biome, suggests a very ancient relationship.

The absence of the murid rodents from the granitic outcroppings in the Caatinga is in stark contrast with the distribution patterns of the common caviomorph rodents and marsupials. Hershkovitz (1972) and Marshall (1979) contend that the immigration of murids commenced in the Miocene, whereas Patterson and Pascual (1972) propose arrival at the Pliocene-Pleistocene junction. If the murids did arrive in the Miocene, they have had ample time to disperse to the Caatinga; expansions of the Caatinga biome far into the Amazon valley during the Quaternary climatic cycles should have increased the probability of contact. The area currently occupied by neighboring biomes, primarily the Cerrado in the west and southwest and to a lesser extent, the Palm Forest in the northwest, does not, however, possess the numerous granitic outcroppings characteristic of the Caatinga. The narrow strip of Atlantic Rain Forest to the east does contain outcroppings, but the fauna of the Caatinga contains more elements in common with that of the Cerrado (Streilein, 1982a). Invading murid species are much more likely to have approached the Caatinga through an area lacking rocky habitats and thus did not have the opportunity to develop a habitat affinity that would have preadapted them for existence in the unpredictable environment of the Caatinga. The principal habitats occupied

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by C. callosus, B. lasiurus, and O. eliurus in the Cerrado included fields of felled trees with pastures, open scrub with herbs and grass, and early successional fields, whereas O. subflavus is found in all types of natural habitats but is rare in the open grassland (Mello, 1977). The limited number of habitats occuped by murids in the Caatinga are all strikingly similar to some of the primary habitats occupied by these species in the Cerrado.

The particular problems imposed by the climatic regime of the Caatinga may be invoked to explain why the murids continue to occupy habitats in the Caatinga similar to those occupied in the Cerrado, but which are much more unstable. Irregular subjection to widely divergent selection pressures in the thorn scrub habitats, operating in conjunction with the lack of a previously established affinity for rocky habitats, may effectively preclude both possible solutions-shifting habitat preference in favor of the granitic outcroppings or accumulation of specializations for existence in the thorn scrub. The absence of the murids from the granitic outcroppings does not appear to be related to morphological limitations as most of the murids are as capable of climbing as the morphologically general marsupials. An alternative hypothesis is that the murids may simply not have had a sufficient amount of time to adapt. The retention of affinity for habitats similar to those occupied in the Cerrado, the absence from the most stable, mesic habitats available, the inability to maintain the high population levels characteristic in the Cerrado (Streilein, 1982c), and the poorly developed water conservation capabilities of some of the species (Streilein, 1982b) indicate that the murids, in general, have not achieved a high degree of adaptation, but this situation can be attributed to either hypothesis. Two additional factors must also be considered. First, Galea spixii utilizes the granitic outcroppings in the Caatinga to some extent and has a broad distribution in open formations throughout South America, including broad expanses that lack rock outcroppings. Second, Wiedomys pyrrhorhinos is the only murid rodent that has a broad geographic distribution in the Caatinga and is the only small mammal species found only in Caatinga Baixa habitats. The preference for thorn scrub habitats suggests that Wiedomys is evolving into a true thorn scrub specialist, at least within the realm of constraints imposed by the climatic vagaries. Development of a high degree of specialization for the "mean" semiarid state may, in fact, be precluded by the disparate selection pressures. These two factors suggest that the alternative hypothesis is correct, with the major effect of the conditions incorporated into the first hypothesis being to prolong the transition.

The occurrence of most of the murid species in this portion of the Caatinga can be attributed to the presence of the Chapada do Araripe,

Cerrado biome that stretches unbroken through nearly three-fourths of the width of the Caatinga. Extant populations may be relicts of the most recent expansion of the Cerrado into the area currently occupied by the Caatinga, or the Chapada do Araripe may have served as an invasion corridor into the Caatinga. In either case, current distributions might be expected to be limited to the Chapada and immediate vicinity because microclimatic and vegetation differences rapidly become more pronounced with increased distance into the Caatinga proper. The observed distributional patterns of Calomys callosus and both species of Oryzomys were, in fact, restricted; individual C. callosus were encountered less frequently with increasing distance from the base of the Chapada, disappearing entirely after 15 to 20 km, whereas both Oryzomys species extended no more than 5 to 10 km into the Caatinga. Bolomys lasiurus was most abundant in sites next to the Chapada, but may be found at suitable localities more distant than 20 km from the Chapada. The outlying populations of Bolomys lasiurus were probably founded by emigrants from temporarily dense populations.

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