THE ECOLOGY OF SMALL MAMMALS IN THE SEMIARID BRAZILIAN CAATINGA. V. AGONISTIC BEHAVIOR AND OVERVIEW

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ABSTRACT

Basic agonistic behavior repertoires are described for Caatinga species. The results of interspecific encounters suggest that behavioral interactions contribute to the maintenance of observed distributional patterns; Galea spixii is actively excluded from granitic habitats by Kerodon rupestris.

Analyses of water conservation capabilities, reproductive and population parameters, and distribution patterns indicate that the caviomorph rodents and marsupials, in general, exhibit a higher level of adaptation to the Caatinga than do the murid rodents.

INTRODUCTION

A comprehensive study of a small mammal community must explore the possibility that interspecific behavioral interactions influence distributional patterns. Within a community, interspecific interactions may range from overt unidirectional aggression or mutual intolerance to unilateral, active avoidance or mutual avoidance. MacMillen (1964) and Bateman (1967) documented the existence of dominance hierarchies in two rodent faunas in xeric areas of North America. The hierarchies were generally correlated with body size of the constituent species and were maintained with a minimum of overt aggression. Heller (1971) and Terman (1974), on the other hand, examined situations in which overt aggression was commonplace. Although the mechanism may vary, a similar result is obtained; a species can be partially

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or completely excluded from a particular area or by another species. This process may be viewed as one of the many forms of competition.

In the Caatinga, as in any other xeric region, habitats with favorable water balance are limited and by logical extension, should be focal points for competitive interactions. MacMillen’s (1964) study of the rodent fauna of a semiarid area confirmed the impact of interspecific behavioral relationships under these conditions. Most of the species studied were dependent upon patches of cacti (Opuntia occidentalis) as a water source, but the socially dominant species (Neotoma lepida) excluded subordinate species from the water-rich patches. It was expected that a similar process might occur in the Caatinga, with living space in the granitic outcroppings being the limited resource. Granitic outcappings in the Caatinga serve as relatively mesic, stable micro-refugia that moderate both the mean, xeric environmental conditions and the unpredictable occurrence of intervals of extended drought.

Different degrees of agonistic interactions were anticipated in the interspecific encounters. Because Galea spixii and Kerodon rupestris were closely related, both phylogenetically and ecologically, they were expected to exhibit the most intense agonistic behavior. No overt aggression, but possibly some type of avoidance response, was anticipated between Thrichomys aperooides and Galea spixii or T. aperooides and K. rupestris because these pairs were quite different in activity patterns, and taxonomic affinities. Habitat selection by Bolomys lasiurus appeared to be determined by factors other than exclusion by another species, so few or no interactions were expected between T. aperooides and B. lasiurus.

**Materials and Methods**

The qualitative analysis of behavior commenced with an attempt to describe the basic behavioral repertoire of each species. Individuals were isolated in glass- or screen-fronted observation cages to study maintenance and exploratory behavior. Social interactions were then observed in male-male, male-female, and female-female pairs. Family units were also observed when possible. Agonistic, sexual, marking, and grooming displays and postures were the primary areas of interest.

These components were then quantified in intraspecific social interactions, within the context of staged encounters in neutral arenas. Varying sizes of arenas were used depending on average body size of each species: Bolomys lasiurus and Oryzomys subflavus, 0.4 m²; Monodelphis domestica, 0.8 m²; and Galea spixii and Thrichomys aperooides, 1.4 m². External reproductive condition of test animals was recorded in order to isolate possible effects of reproductive status. To reduce artifacts produced by prolonged confinement, trials were limited to five minutes; all individuals used were wild-caught adults maintained in the lab for several weeks before testing. The number of trials in each species ranged from 40 (Monodelphis) to 117 (Bolomys). Two individuals were simultaneously released and a record made of actions following the first encounter.

Finally, interspecific interactions among rodent species were studied; marsupial species were excluded from this phase as interactions were likely to be of a predator-prey nature. Only those species which occurred on the grid were used. The primary objective was
interactions between rock dwelling species, so trials were conducted as follows: *Thrichomys* versus *Galea*; *Thrichomys* versus *Kerodon*; and *Galea* versus *Kerodon*. *Thrichomys apereoides* was also tested against *Bolomys lasiurus*. Twenty 5-min trials were conducted in each category. Ten males of one species were matched with five males and five females of the other species and ten females were also matched with an equal number of males and females. This system was adopted to minimize possible sex-related differences in the interactions.

**Intraspecific Agonistic Behavior**

The basic components of the agonistic behavioral repertoire of each species are presented in Table 1. *Didelphis albiventris* and *Galea spixii* are the only species which lack upright postures. Relative differences rather than absolute differences in behavioral patterns must also be considered (Eisenberg, 1967). The frequency of utilization of various components was quite variable within species. Infrequently observed events were sometimes very important in the context in which they occurred. Because individual variation was large and the frequency with which events occurred was dependent upon the actions of both individuals in a trial, description of displays, movements, and postures and the context in which they generally occur are given only for species with a substantial number (>40) of trial encounters. The data presented in Tables 2–5 reflect both aggression and active defense. Typical sequences of behaviors and agonistic displays and postures are portrayed for *M. domestica* (Figs. 1–2), *B. lasiurus* (Figs. 3–4), *G. spixii* (Figs. 5–6), and *T. apereoides* (Figs. 7–8).

**Displays and Postures of Monodelphis domestica**

Open mouth threat.—The prominence of this display varies directly with the intensity of the situation. At a low level, the jaws are only slightly open and only the canines are obviously exhibited. At a high level of intensity, the jaws gape and the lips are drawn back, exposing all of the teeth. Open mouth threats are observed in all postures.

Quadrupedal.—Defensive or aggressive lunges may originate while the animal is in the basic quadrupedal stance.

One forepaw raised.—A single forepaw is flexed and held roughly parallel to the ground but close to the chest. This is generally observed only in animals being approached. Animals which assume this posture are more likely to employ an active defense than to flee.

Semi-erect.—Both forepaws are flexed and held parallel to the ground. This posture is similar to the position adopted by most individuals during feeding bouts and is easily maintained for long periods. Approaching animals frequently enter this posture before attacking, while in individuals being approached, it signals an imminent defensive strike. The chief advantage of this upright posture to these otherwise largely quadrupedal animals appears to be a more favorable angle of
Table 1.—Basic agonistic behavioral repertoires of Caatinga species.

| Component                  | Species                  |
|---------------------------|--------------------------|
|                           | Monodelphis domesticus  | Didelphis aboventris | Oryzomys subflavus | Bolomys lasiurus | Callomys callosus | Wiedomys pyrrhorhinos | Kerodon rupestris | Galea spixii | Thrichomys apereoides |
| Postures                  |                          |                       |                    |                 |                  |                       |                 |             |                        |
| Quadrupedal               |                          |                       |                    |                 |                  |                       |                 |             |                        |
| Arch                      | X                        |                        |                    |                 |                  |                       |                 |             |                        |
| Tail up                   | X                        |                        |                    |                 |                  |                       |                 |             |                        |
| Intermediate              |                          | X                      | X                  | X                | X                 |                       |                 |             |                        |
| 1 forepaw up              | X                        | X                      | X                  | X                | X                 |                       |                 |             |                        |
| Upright                   |                          | X                      | X                  | X                | X                 | X                      | X                |             | X                        |
| Semi-erect                | X                        | X                      | X                  | X                | X                 | X                      | X                |             | X                        |
| Full erect                | X                        | X                      | X                  | X                | X                 | X                      | X                |             | X                        |
| Display and movements     |                          | X                      | X                  | X                | X                 | X                      | X                |             | X                        |
| Open mouth                | X                        | X                      | X                  | X                | X                 | X                      | X                |             | X                        |
| Piloerection              | X                        | X                      | X                  | X                | X                 | X                      | X                |             | X                        |
| Lunge                     | X                        | X                      | X                  | X                | X                 | X                      | X                |             | X                        |
| Strike with forepaws      | X                        | X                      | X                  | X                | X                 | X                      | X                |             | X                        |
| Spar                      | X                        | X                      | X                  | X                | X                 | X                      | X                |             | X                        |
| Kick with rear paw        |                          |                        |                    |                 |                  |                       |                 |             |                        |
| Chest kick                |                          |                        |                    |                 |                  |                       |                 |             |                        |
| Locked upright            |                          |                        |                    |                 |                  |                       |                 |             |                        |
| Alternate stretch         |                          |                        |                    |                 |                  |                       |                 |             |                        |
| Run at                    |                          |                        |                    |                 |                  |                       |                 |             |                        |
| Wrestle                   | X                        | X                      | X                  | X                | X                 | X                      | X                |             | X                        |
| Bite                      | X                        | X                      | X                  | X                | X                 | X                      | X                |             | X                        |
Table 2.—Frequency of agonistic behavior components for Monodelphis domestica.

Means based on total trials for each class. No. = number of trials in which each component occurred. MPT = mean per trial. Total number of trials in which agonism occurred/total number of trials.

| Classes              | $\delta\delta$ 13/16 | $\delta\delta/\varnothing$ 14/6 | $\varnothing\varnothing$ 8/8 | Total 35/40 |
|----------------------|-------------------------|----------------------------------|-------------------------------|-------------|
| Components           | No.  | MPT  | No.  | MPT  | No.  | MPT  | No.  | MPT  |
| Open mouth           | 12    | 2.6  | 14    | 3.8  | 8    | 5.0  | 34    | 4.0  |
| One forepaw up       | 2     | 0.1  | 1     | 0.1  | 1    | 0.1  | 4     | 0.1  |
| Semi-erect           | 3     | 0.3  | 6     | 0.5  | 2    | 0.4  | 11    | 0.4  |
| Full erect           |       |      | 3     | 0.3  | 2    | 0.4  | 5     | 0.2  |
| Chase                | 2     | 0.4  | 1     | 0.1  | 4    | 1.0  | 7     | 0.4  |
| Bite                 | 5     | 0.9  | 5     | 0.4  | 4    | 1.3  | 14    | 0.8  |
| Wrestle              | 2     | 0.2  | 2     | 0.1  | 4    | 1.1  | 8     | 0.4  |
| Lunge                | 6     | 0.5  | 4     | 0.4  | 5    | 1.5  | 15    | 0.7  |
| Strike with forepaws | 1     | 0.1  | 3     | 0.3  | 1    | 0.1  | 5     | 0.2  |
| Spar                 |       |      | 4     | 0.3  | 1    | 0.1  | 5     | 0.2  |

attack; the opponent is less likely to effectively use its canines in an upward direction.

Full erect.—This posture is of very brief duration and invariably precedes an extended lunge. The flexed forepaws are raised above the shoulders as the animal throws itself forward and down onto the opponent.

Lunge.—The body is hurled forward at the opponent. Forepaws function more in grabbing the opponent prior to administering a bite than as striking weapons.

Wrestle.—Biting is common. The nails on the hindfeet are used to rake the opponent.

Agonistic behavior was recorded in 35 of 40 trials (Table 2). Individuals were intolerant of other individuals in close proximity regardless of sex. Open mouth threats were frequently observed and were generally successful at inhibiting approaching animals. When physical contact did occur, it was usually of brief duration and rarely resulted in serious injury.

Displays and Postures of Bolomys lasiurus

Open mouth threat.—The jaws gape and the lips are drawn away from the teeth. This display denotes either an inclination to attack (when given by an approaching animal) or a willingness to engage in active defense (when given by an animal being approached). It is typically given in conjunction with all of the postural displays.

One forepaw raised.—This posture is an intermediate stage between
Table 3.—Frequency of agonistic behavior components for Bolomys lasiurus. Means based on total trials for each class. No. = number of trials in which each component occurred. MPT = mean per trial. VO = vagina open; VC = vagina closed; TD = testes descended; TND = testes not descended. 1Number of trials in which agonism occurred/total number of trials. 2Average based on two trials.

| Components             | VO × VO 2/2 | VO × VC 9/15 | VO × TND 5/7 | VO × TD 10/13 | VC × VC 13/17 | VC × TND 6/8 | VC × TD 5/13 | TND × TND 1/2 | TND × TD 14/15 | TD × TD 25/25 | Total 90/117 |
|------------------------|-------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|
|                        | No. | MPT | No. | MPT | No. | MPT | No. | MPT | No. | MPT | No. | MPT | No. | MPT |
| Open mouth             | 2   | 1.52| 9   | 2.1 | 4   | 2.3 | 8   | 3.0 | 11  | 2.2 | 6   | 3.0 | 5   | 1.8 |
| One forepaw up         | 2   | 0.1 | 5   | 0.5 | 3   | 0.5 | 1   | 0.4 | 1   | 0.4 | 2   | 0.2 | 4   | 0.5 |
| Semi-erect             | 2   | 4.52| 8   | 2.1 | 5   | 1.7 | 6   | 2.1 | 11  | 1.6 | 5   | 2.0 | 5   | 1.8 |
| Full erect             | 1   | 3.02| 4   | 0.4 | 1   | 0.1 | 2   | 0.2 | 4   | 0.4 | 2   | 0.4 | 3   | 0.7 |
| Alternate stretch       | 1   | 1.52| 2   | 0.2 | 1   | 0.1 | 1   | 0.1 | 1   | 0.2 | 1   | 1.02| 1   | 0.1 |
| Strike with forepaws   | 1   | 1.02| 7   | 0.9 | 4   | 1.0 | 4   | 0.5 | 5   | 0.7 | 4   | 0.8 | 1   | 0.1 |
| Kick with rear paws    | 1   | 0.52| 3   | 0.7 | 1   | 0.3 | 3   | 0.5 | 2   | 0.1 | 2   | 0.4 | 2   | 0.3 |
| Wrestle                | 2   | 0.2 | 3   | 0.2 | 1   | 0.2 | 4   | 0.3 | 7   | 0.4 | 17  | 0.2 |
| Chase                  | 3   | 3.0 | 4   | 2.4 | 3   | 0.2 | 1   | 0.5 | 3   | 0.9 | 1   | 0.52| 6   | 0.9 |
| Bite                   | 1   | 0.52| 3   | 0.5 | 3   | 0.9 | 7   | 2.5 | 4   | 0.7 | 3   | 1.3 | 4   | 0.8 |

Bite 1 0.52 3 0.5 3 0.9 7 2.5 4 0.7 3 1.3 4 0.8 1 2.02 6 1.7 12 1.8 44 1.3
Table 4.—Frequency of agonistic behavior components for Galea spixii. Means based on total trials for each class. No. = number of trials in which each component occurred. MPT = mean per trial. VO = vagina open; VC = vagina closed; TD = testes descended; TND = testes not descended. Number of trials in which agonism occurred/total number of trials. Average based on two trials.

| Components          | TD x TND 1/7 | TND x TND 0/1 | VO x VO 1/2 | TND x VC 3/7 | TD x VO 7/22 | VO x VC 12/14 | VC x VC 18/23 | TD x TD 16/28 | Total 59-108 |
|---------------------|--------------|---------------|-------------|--------------|--------------|---------------|---------------|---------------|--------------|
|                     | No. MPT      | No. MPT       | No. MPT     | No. MPT      | No. MPT      | No. MPT       | No. MPT       | No. MPT       | No. MPT      |
| Arch                | 1 0.6        | 1 3.0         | 3 1.1       | 3 0.8        | 4 0.8        | 9 1.4         | 15 3.9        | 36 1.8        |              |
| Open mouth          | 1 3.3        | 1 1.0         | 1 0.3       | 2 0.1        | 2 0.4        | 2 0.4         | 6 0.2         |               |              |
| Piloerection        | 1 0.3        | 1 0.1         | 1 0.1       | 3 0.1        | 3 0.1        | 4 0.2         | 9 0.1         |               |              |
| Stiff-legged hop    | 1 0.3        | 1 0.1         | 1 0.1       | 3 0.1        | 3 0.1        | 4 0.2         | 9 0.1         |               |              |
| Bite                | 1 0.7        | 1 2.5         | 2 2.1       | 6 1.5        | 4 0.9        | 9 2.9         | 10 2.7        | 33 2.0        |              |
| Lunge               | 1 0.3        | 1 0.1         | 3 0.2       | 1 0.1        | 1 0.1        | 8 0.7         | 15 0.3        |               |              |
| Run-at              | 1 0.6        | 1 0.3         | 2 2.0       | 6 2.0        | 3 1.0        | 11 3.1        | 11 2.9        | 35 2.0        |              |
| Tail up             | 1 0.5a       | 1 0.6         | 1 0.1       | 10 2.0       | 8 1.1        | 5 0.5         | 26 1.0        |               |              |
| Chase               | 1 0.3        | 2 0.4         | 1 0.2       | 4 0.5        | 7 1.7        | 8 1.9         | 23 1.0        |               |              |
Table 5.—Frequency of agonistic behavior components for *Thrichomys aperoides*. Means based on total trials for each class. No. = number of trials in which each component occurred. MPT = mean per trial. TND = testes not descended; VO = vagina open; VC = vagina closed. Total number of trials in which agonism occurred/total number of trials.

| Components                  | Females 4/18 | TND × TND 7/14 | TND × VC 5/14 | TND × VO 5/13 | Total 21/59 |
|-----------------------------|--------------|----------------|---------------|--------------|-------------|
|                             | No. | MPT | No. | MPT | No. | MPT | No. | MPT | No. | MPT |
| Semi-erect                  | 3   | 0.8 | 3   | 0.4 | 2   | 0.5 | 4   | 0.4 | 12  | 0.5 |
| Full erect                  | 3   | 0.5 | 4   | 1.1 | 4   | 0.6 | 1   | 0.1 | 12  | 0.6 |
| Strike with forepaws        | 1   | 0.1 | 3   | 0.3 | 2   | 0.1 | 1   | 0.1 | 7   | 0.1 |
| Spar                        |     |     | 2   | 0.2 |     |     | 2   | 0.1 |     |     |
| Locked upright              | 3   | 0.2 | 3   | 0.4 | 4   | 0.3 |     |     | 10  | 0.2 |
| Chase                       |     |     | 2   | 0.2 |     |     | 1   | 0.1 | 3   | 0.1 |
| Lunge                       | 1   | 0.1 | 1   | 0.2 | 1   | 0.1 | 1   | 0.1 | 4   | 0.1 |
| Bite                        | 1   | 0.1 | 4   | 0.4 | 1   | 0.1 | 2   | 0.2 | 8   | 0.2 |
| Chest kick                  | 2   | 0.1 | 3   | 0.4 | 2   | 0.1 |     |     | 7   | 0.2 |

quadrupedal and upright postures and denotes slightly increased intensity. Animals may immediately progress into an upright posture without exhibiting this posture.

**Semi-erect.**—This posture has several functions. It signals a high probability of active defense to an intruder, typically a forward and downward lunge with a blow delivered by both forepaws; it often stops or delays the advancing animal. If the animal being approached is bluffing, as is often the case when subordinance had been determined by previous encounters, it takes advantage of the intruder’s hesitation to leap away. When the approaching animal assumes this posture, an attack is likely to occur.

**Full erect.**—When assumed in defense by an animal being approached, the probability of a defensive strike is close to 100% if the approach continues. Full erect by an approaching animal frequently provokes flight or is the immediate precursor to an aggressive strike. Alternatively, both individuals may opt for the alternate vertical stretches sequence and avoid physical contact.

**Alternate vertical stretches.**—First one individual stretches vertically into a more pronounced full erect, then the other does so, and so forth. The individual with the maximum stretch holds it and the other animal slowly drops in stages back to the quadrupedal stance and moves off. The stretching sequence is sometimes repeated one or more times before the outcome is determined. Because increasing body
length is directly related to increasing body weight, the opponents can gauge each other’s size (and presumably strength) and settle an encounter without engaging in physical contact.

**Circling.**—In extended aggressive bouts, mutual circling sometimes occurs when both individuals are in semi-erect or full erect postures. Circling is of variable duration but is apparently an attempt to maneuver into a position with a more advantageous angle for attacking.

**Strike with forepaws.**—Blows are typically directed at the head of the opponent with the forepaws raked over the eyes. This tactic is used from semi-erect and full erect postures. In a defensive context, the blow is given quickly and the animal maintains its position, often drawing back into the ready position. In the agonistic context, striking
with the forepaws is more often the culmination of an extended lunge at the opponent.

*Kick with one rear paw.*—The animal hops past the opponent’s side and kicks out laterally with a rear paw. This tactic was most frequently observed during extended, mutually aggressive encounters and is most often used from the circling mode.

*Wrestle.*—Animals are usually stomach to stomach and on their sides. Hind feet are used to rake the opponent’s abdomen.

*Chase.*—Active pursuit of a fleeing individual. Chases are generally terminated after the fleeing animal is caught and bitten.

Agonistic behavior was observed in 90 of 117 trials (Table 3). Open mouth threats and the semi-erect posture were the most frequently used components. Physical contact between opponents was common but serious injuries were rare. In the majority of trials, mutual intolerance was the rule.

**Displays and Postures of Galea spixii**

*Quadrupedal.*—Attacks may be precipitated from the basic quadrupedal stance.

*Arch.*—The back is arched somewhat as the entire body is held higher off the ground. The body may curl (on the lateral plane) during this display. This posture advertises an inclination toward active defense when given by an animal being approached. In also serves as an indicator than an attack is probable when exhibited by an approaching animal.

*Stiff-legged hop.*—This posture is essentially the same as the arch posture, but the animal bounces directly toward the opponent or parallel to it. Apparently, it conveys a high intensity message because in the relatively few times it was observed, a fleeing response was invoked in the opponent before any physical contact was made.

*Piloerection.*—This display may accompany any of the postures. The pelage along the mid-dorsal line is usually raised but the phenomenon may extend over much of the dorsal surface.

*Open mouth threat.*—The mouth is held open to varying degrees and the lips are drawn away, further exposing the teeth. This display is frequently observed in all postures.

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Fig. 2.—Agonistic displays and postures for *Monodelphis domestica* depicting defensive actions by the animal on the right when approached by a conspecific: open mouth display (A), raising one forepaw (B), and assuming the semi-erect posture (C). In (D), the defensive response escalates into a lunge from the full erect posture when the intruder approaches too closely, followed by biting the intruder (E). A wrestling bout ensues (F).
Fig. 3.—Agonistic behavior sequences for *Bolomys lasiurus*. Open mouth displays are common in all postures. Striking and kicking occur intermittently while the animals circle one another.

Lunge.—This tactic is most frequently used when the animals are in close proximity. The entire body is hurled at the side or hindquarters of the opponent. It may be used in longer range situations to signify agonistic intent and often provokes immediate flight in a subordinate animal.

Run at.—This tactic is used only in active aggressive attacks. An animal runs at full speed toward its opponent, ramming into its side if the opponent does not flee.

Wrestle.—Bouts are usually of brief duration. Biting is common and the rear legs are used extensively.

Chase.—Pursuit is often prolonged, with continuous biting of the rump. Agonistic chases are similar in form to mating chases but the bites directed at the rump are much more intense.

Agonistic behavior was observed in 59 of 108 trials (Table 4). Female-female encounters accounted for more than one-half of the aggressive behavior. Most of the agonistic behavior in male-male trials was initiated because one male reacted aggressively after the other initiated sexual activity.

Display and Postures of *Thrichomys apereoides*

Semi-erect.—The forepaws are drawn up to shoulder height and flexed. A defensive strike is probable if an approaching animal contin-
jumps and kicks at the opponent with one rear paw (C). The alternate vertical stretch sequence is initiated in (D) as the animal on the right stretches higher, followed by the opponent’s stretch in response (E). The sequence is completed in (F) when the animal on the right attains a greater height with its stretch, thus winning the encounter without physical contact; its opponent begins to twist down and away.
Fig. 5.—Agonistic behavior sequences for *Galea spixii*. Open mouth displays occur in all postures.

ues to move closer. It also denotes a high probability of an aggressive attack when presented by an approaching animal. The hindlegs and thick muscular tail constitute the three points of a triangle, thus maintaining a stable base for balancing in the upright postures.

*Full erect.*—This posture conveys the same information as semi-erect but at an increased level of intensity. Forepaws are generally raised higher and extended forward slightly.

*Locked upright.*—Numerous attempts to grasp the opponent’s shoulders may be made before both individuals secure a firm grip. Immediately after the grips are secured, the animals begin a vigorous shoving match in which each attempts to push the other onto its side or back. These bouts may go on continuously for several minutes before one animal gains the advantage. As in the simpler semi-erect and full erect postures, no attempt is made to bite the opponent when both are upright, even though their heads are in close proximity during the locked interval. Biting is typically directed at the back or hindquarters as soon as one animal succeeds in throwing its opponent to the ground.

*Strike with forepaws.*— Strikes are delivered from both semi-erect and full-erect postures in two general styles. The first is of a limited extent; the animal maintains balance and position and immediately returns to an upright posture. The second is the final movement of a forward lunge in which the animal launches its entire body at the opponent.

*Chest kick.*—This tactic is typically observed only in conjunction with a locked upright. One individual upsets the balance of the other,
Fig. 6.—Agonistic displays and postures for Galea spixii. When being approached, the animal on the right exhibits a defensive open mouth display and piloerection (A). Continued approach evokes the arched posture (B). The intruder turns away, assuming the defensive tail up posture (C).

jumps off the ground, swings its hind legs back, and then kicks them forward and up into the chest of the opponent. Several individuals caught by chest kicks suffered serious damage, such as broken forelegs or ribs.

Wrestle.—Bouts are usually of brief duration. Each individual attempts to obtain a position on the back of the other. Biting is common while wrestling.

Chase.—Active pursuit of a fleeing animal. Biting is generally directed at the hindquarters.

Agonistic behavior was observed in only 21 of 59 trials (Table 5). Upright postures and displays were the predominant components of aggressive behavior.
INTERSPECIFIC AGONISTIC BEHAVIOR

Thrichomys apereoides versus Bolomys lasiurus.—Initiation of first approach was similar in both species (Table 6). *Thrichomys apereoides* never engaged in prolonged aggressive behavior toward *B. lasiurus* and essentially ignored the smaller species. Some *Bolomys* actively avoided *Thrichomys*, but mutual interactions were minimal. Agonistic postures in *Bolomys* (Table 7) did not elicit responses from *Thrico-
Fig. 8.—Agonistic displays and postures for *Trichomys apereoides*. Animals mutually assume the semi-erect posture (A), then stretch into the full erect posture. Brief preliminary sparring may occur before the animals enter the locked upright position (C). A vigorous pushing contest ensues.

*Trichomys*, but persistent approaches sometimes did provoke defensive actions by *Trichomys*.

*Trichomys apereoides* versus *Galea spixii*.—*Galea* initiated the first approach twice as often as *Trichomys* (Table 6). *Galea* postures and displays did not invoke agonistic responses in *Trichomys* unless the *Galea* were in close proximity. *Trichomys* typically reacted with a semi-erect defensive posture and sometimes struck at the face of the *Galea* with their forepaws (Table 7). Dominance was clearly established in only two of the 20 trials; 12 of the trials had no agonistic interactions.

*Trichomys apereoides* versus *Kerodon rupestris*.—The much larger species, *K. rupestris*, initiated the first approach in 19 of the trials and the first aggressive approach in seven trials (Table 6). Approaches
or upright postures by *Kerodon* typically prompted *Thrichomys* into assuming an upright posture (15 trials), often accompanied by a fore-paws strike (nine trials). Most of the encounters were stand-offs (13 of 20). *Kerodon* never fled from *Thrichomys*.

*Kerodon rupestris* versus *Galea* spixii.—Even though *Galea* initiated the first aggressive approach in four trials, *Galea* were never judged to be dominant (Table 6). *Kerodon* established dominance in 13 of the trials. *Kerodon* made physical contact with *Galea* in 14 trials, generally from a semi- or full erect posture. Approximately one-half of the *Galea* received serious injuries or died as a result of the agonistic encounters with *Kerodon*. Arched postures by *Galea* did not effectively stop approaches by the opponent as they often did in intraspecific encounters.

**Discussion**

*Monodelphis domestica* and *Bolomys lasiurus* were very intolerant of conspecifics of either sex. Open mouth threats by *Monodelphis* were generally effective at preventing approaches. *Bolomys*, on the other hand, were more likely to engage in physical contact. Adoption of upright postures was characteristic of the *Bolomys* encounters. Both species react agonistically if the minimum “individual distance” (Hediger, 1941 as cited by Wilson, 1975) is broached. In periods of high density population, the probability of chance encounters between *Bolomys* individuals is escalated but the results of the encounter experiments in neutral arenas indicate the adoption of upright defensive postures frequently fails to inhibit approaching animals. Do *Bolomys* typically engage in physical contests in high density situations? If they do, a great deal of time and energy are expended and the risk of serious injury climbs. One particular behavioral sequence probably assumes

| Genera tested | Initiate first approach | Initiate first aggressive approach | Physical contact with opponent | Flee from opponent one or more times | Clearly dominant | Dominance not established | No aggression |
|---------------|------------------------|-----------------------------------|--------------------------------|-------------------------------------|-----------------|--------------------------|--------------|
| *Thrichomys*  | 1                      | 1                                 | 10                             | 7                                   | 0               | 13                       | 5            |
| *Kerodon*     | 19                     | 7                                 | 5                              | 0                                   | 2               | 6                        | 12           |
| *Thrichomys*  | 7                      | 1                                 | 6                              | 2                                   | 1               | 6                        | 12           |
| *Galea*       | 13                     | 5                                 | 2                              | 4                                   | 1               | 2                        | 5            |
| *Kerodon*     | 15                     | 11                                | 12                             | 0                                   | 13              | 2                        | 5            |
| *Galea*       | 5                      | 4                                 | 1                              | 14                                  | 0               | 4                        | 9            |
| *Thrichomys*  | 9                      | 1                                 | 5                              | 0                                   | 7               | 4                        | 9            |
| *Bolomys*     | 12                     | 5                                 | 2                              | 9                                   | 0               | 0                        |              |
Table 7.—Frequency of agonistic behavior components during interspecific trials. Means based on total number of trials for each class. 
No. = number of trials in which each component occurred. MPT = Mean per trial. B = Bolomys; T = Thrichomys; G = Galea; K = Kerodon. ^1Total number of trials in which agonism occurred/total number of trials.

| Components       | Classes          | No. | MPT  | No. | MPT  | No. | MPT  | No. | MPT  | No. | MPT  | No. | MPT  |
|------------------|------------------|-----|------|-----|------|-----|------|-----|------|-----|------|-----|------|
|                  | B (×T) 19/20     | 10  | 1.6  | 8   | 1.5  | 9   | 0.7  | 2   | 0.1  | 2   | 0.2  |
|                  | T (×B) 19/20     | 1   | 0.1  | 3   | 0.2  | 13  | 3.9  | 6   | 0.4  | 1   | 0.2  | 2   | 0.3  |
|                  | G (×K) 14/20     | 1   | 0.1  | 1   | 0.1  | 2   | 0.3  | 2   | 0.2  | 2   | 0.3  |
|                  | K (×T) 18/20     | 6   | 0.7  | 1   | 0.1  | 2   | 0.3  | 1   | 0.3  | 2   | 0.3  |
|                  | T (×K) 10/20     | 7   | 0.9  | 5   | 0.9  | 15  | 1.9  | 9   | 1.8  | 5   | 0.4  |
|                  | G (×T) 12/20     | 3   | 0.2  | 2   | 0.2  | 4   | 0.2  | 9   | 0.9  | 5   | 0.4  |
|                  | T (×G) 12/20     | 5   | 0.3  | 6   | 0.7  | 7   | 0.6  | 4   | 0.7  | 4   | 0.8  |
|                  | Ploerection      | 7   | 0.9  | 11  | 1.4  | 8   | 0.5  |
|                  | Arch             | 9   | 1.2  | 1   | 0.1  | 5   | 1.1  |
|                  | Drum             | 3   | 0.2  | 3   | 0.4  | 1   | 0.1  |
|                  | Wrestle          | 2   | 0.6  | 1   | 0.1  | 2   | 0.2  | 1   | 0.2  |
|                  | Chase            | 2   | 0.3  | 1   | 0.1  | 2   | 0.2  |
|                  | Kick with rear paw | 2   | 0.3  |  |  |  |  |  |  |
greater importance when populations are dense. Alternate stretching was observed in only 15 of 117 trials in the neutral arenas, but effectively eliminated physical contact; when both individuals have attained maximum stretches, their relative sizes are displayed. An attack pressed upon a larger individual is not likely to succeed as a general rule. Indeed, the smaller individual usually dropped out of the full erect posture and moved away from its opponent.

The importance of the stretching sequence was further clarified by a fortuitous incident. Six Bolomys (three males and three females) were transferred to a vacant glass-fronted holding cage as a temporary measure. The individual B. lasiurus immediately reacted to movements by other animals with upright postures and defensive strikes. After a flurry of physical contact, the animals began to exclusively utilize the alternate stretching sequence. Several hundred encounters were observed in the first hour; in almost every instance, physical contact was circumvented and the smaller animal was the first to abandon the upright posture. The smallest individual frequently "won" encounters with much larger individuals, however, when it was standing on the ledge around the base of the cage. The additional height of the ledge permitted it to stretch higher than individuals which actually had much larger body sizes. If this behavioral sequence functions in the same fashion in natural situations, it would allow high density populations to exist with a minimum of physical aggression.

Agonistic behavior was observed in 59 of 108 Galea trials. Male Galea, especially individuals with descended testes, reacted to other Galea (including other testes descended males) with sexual interest. Females tended to interact aggressively with other females. Female Galea may maintain a core area exclusive of other female core areas, whereas males move about in search of sexually receptive females, interacting aggressively with other males only in the vicinity of estrous females. More field data are needed to substantiate this hypothesis.

The incidence of agonistic behavior was lowest in Thrichomys, occurring in only 21 of 59 trials. This was unexpected in view of the fact that female home ranges overlapped very little with other female home ranges, whereas male home ranges overlapped those of the females, but are relatively exclusive of other male home ranges. Avoidance rather than active defense was the general rule. Two pregnant females with neighboring home ranges were removed from the grid after the population study was terminated and subsequently paired in the neutral arena. A mutual approach and nose-to-nose contact immediately progressed into a "ritualistic" locked-upright encounter. Perhaps under natural conditions, violent encounters only occur at initial meetings, whereas subsequent avoidance results in exclusive home ranges.

In the Kerodon rupestris versus Galea spixii interspecific encoun-
ters, Kerodon was clearly dominant. Galea’s displays and postures were all of a quadrupedal nature. Kerodon used upright postures to strike down at the Galea, often dropping from the full erect onto the back of the Galea, pinning them to the ground with the forelegs; biting was then directed at the base of the skull and neck. This posture was essentially the same as the Kerodon mating posture. The upright postures which were successful tactics when Kerodon was paired with Galea were largely ineffectual against Thrichomys. Individual Thrichomys would typically give way before the much larger Kerodon, but if backed into a corner they would maintain an upright posture for extended periods and readily resorted to defensive strikes. The upright postures of Thrichomys gave them an advantage over Galea similar to that possessed by Kerodon, but the Thrichomys were not actively aggressive, reacting only when Galea individuals approached too closely. Both Thrichomys and Bolomys extensively used upright postures in intraspecific encounters, but Thrichomys generally ignored the much smaller Bolomys.

Some of the expected results were observed. Thrichomys interacted very little with Bolomys and Galea unless approached too closely, in which case they assumed upright postures and were likely to strike at the intruder. Kerodon was aggressive toward and dominant over Galea but was unexpectedly aggressive toward Thrichomys. The existence of active aggression by Kerodon toward Galea and Thrichomys further clarifies the distributional patterns observed on the grid. Kerodon and Thrichomys occupy the same habitat but they have opposite activity patterns; Kerodon is largely diurnal and Thrichomys is nocturnal with crepuscular peaks. Coexistence through temporal separation is thus possible. Galea, however, are diurnal and likely to encounter Kerodon. The complex three-dimensional structural diversity of the rock habitats prevents Kerodon from totally excluding Galea, but the level of interaction is sufficient to reduce the density of individuals. Partial exclusion of Galea by Kerodon explains why Galea is the only non-murid not concentrated in the more favorable rock habitats during the dry months. The presence of Kerodon in a particular site may serve as a continuous, passive deterrent to future encroachment by individual Galea that have experienced agonistic responses from the much larger Kerodon. Hypothetically then, Galea would be expected to exhibit a greater degree of utilization of rock habitats when Kerodon is absent. Lacher (1981) mixed various combinations of Kerodon and Galea colonies under semi-natural conditions and consistently found that Kerodon were dominant over Galea and forcibly excluded them from the simulated rocky microhabitat. The aggressive nature of Kerodon might be related to the distribution of free water in the rocks. Restricting the access of other species to
the temporary, limited sources of water through a behavioral response might be of great significance because *Kerodon* has weakly-developed water conservation capabilities (Streilein, 1982b).

**Overview**

Environmental unpredictability has been the predominant characteristic of the Caatinga in both evolutionary and ecological time (Streilein, 1982a). Wet-dry climatic cycles in the Quaternary induced concomitant, large-scale contractions and expansions of the Caatinga. Extended periods of extreme drought continue to punctuate the “normal” semiarid state at irregular intervals. The adaptation of the small mammal fauna to the fluctuating Caatinga environment has been dependent upon the presence of a large number of granitic outcroppings; the outcroppings apparently served as relatively stable, mesic “micro-refugia” during the dry phases of the climatic cycle and moderate the generally xeric ambient conditions and intermittent occurrence of severe environmental stress over ecological time.

The small mammal fauna of the Caatinga did not exhibit an advanced degree of physiological adaptation for aridity. Two species, *Thrichomys apereoides* and *Monodelphis domestica*, had moderate water conservation capabilities, but the other species examined had very poorly developed capabilities in comparison to small mammal species in other xeric regions (Streilein, 1982b). Some species of caviomorphs and marsupials—*Thrichomys apereoides*, *Kerodon rupestris*, *Monodelphis domestica*, and *Didelphis albiventris*—have compensated for the deficiency in physiological mechanisms with a behavioral response, selecting the relatively mesic granitic habitat types (Streilein, 1982d). None of the murid rodents exhibited this behavior.

In a fluctuating environment, the timing of reproduction is critical. The large amount of energy expended in the production of young will be lost unless individuals can accurately track environmental conditions, reproducing only during intervals of favorable conditions. Two general strategies that could have evolved in the Caatinga to minimize energy loss in reproduction are: 1) consistently concentrate reproductive effort in the interval when favorable conditions are most probable; 2) retain reproductive flexibility in order to rapidly respond to ephemeral, favorable conditions (Streilein, 1982c). *Didelphis albiventris* was the only Caatinga species that exhibited synchronized reproduction; timing the breeding season such that the young are weaned in the months when water surpluses are most probable. Reproductive patterns in the five murid species and *Galea spixii* did not parallel either strategy. Parturition occurred year round, even during periods of pronounced water stress, and essentially all of the mature females in the populations were reproductively active. A third strategy is also feasible
in the Caatinga because microrefugia are readily available. Three species, *K. rupestris*, *T. apereoides*, and *M. domestica*, were thus able to circumvent the general environmental constraints by preferentially utilizing the granitic outcroppings; reproduction occurred throughout the year, but generally at a lower rate and with a smaller gross output of young.

Intense reproductive effort in the murid rodents was not reflected in increased population size or in age structure (Streilein, 1982c). None of the murids were able to consistently maintain elevated population levels in the Caatinga even though the same species were the most abundant small mammals in the Cerrado biome. Populations were mainly composed of adults, indicating a very high level of mortality in young individuals. The marsupials and caviomorph rodents that inhibited the granitic outcroppings were able to maintain higher population levels than the murids. The only caviomorph that did not preferentially utilize the rocky habitats, *Galea spixii*, exhibited a reproductive effort that was more similar to the murid characteristics than to those of the other caviomorphs.

Several factors illustrate the generally low level of adaptation to the Caatinga in the murid rodents. First, four of the five murid species—*Bolomys lasiurus*, *Calomys callosus*, *Oryzomys eliurus*, and *O. subflavus*—were found only in the immediate vicinity of the Chapada do Araripe, an extension of the Cerrado biome that stretches unbroken through nearly three-fourths of the width of the Caatinga; most of the caviomorphs and marsupials had widespread geographic distributions within the Caatinga. Second, the habitats occupied in the Caatinga were likely to experience severe water stress, but the murids were not physiologically well-adapted for aridity. Third, low population levels were typical in the few habitats occupied; however, the Caatinga habitats closely corresponded with habitats that supported dense populations in the Cerrado. Fourth, none of the murids utilized the granitic outcroppings, the most mesic, stable habitats available in the Caatinga. The murids probably invaded the Caatinga through the Cerrado, and thus did not possess suitable preadaptations for the xeric, unpredictable environment of the Caatinga. Granitic outcroppings are extremely rare in the Cerrado, so these species could not develop an affinity for the most advantageous habitat available in the Caatinga. The Cerrado is also much more predictable and mesic (due in part to a more favorable geological composition) compared to the Caatinga. Most of the murids are caught in a situation wherein the habitat types in which they were previously successful are irregularly subjected to prolonged drought. Alternately, they also experience extended intervals of heavy precipitation. The widely divergent selection pressures that accompany these disparate climatic phenomena may effectively prevent ac-
cumulation of specialization for the “mean” semiarid state. *Wiedomys pyrrhorhinos*, however, has a broad geographic distribution in the Caatinga and is also the only small mammal species that is found solely in the most extensive habitat type available, the low thorn scrub formations. This preference for thorn scrub suggests that *Wiedomys* is evolving into a “true” thorn scrub specialist, at least within the limits imposed by the climatic vagaries. The other murid species may simply not have had an adequate period of time for adaptation.

The primary feature of the well-adapted species is the pronounced affinity for the microrefugia that exist within the Caatinga, at least during intervals of water stress. The evolution of this behavioral response resulted in a decreased emphasis on physiological adaptations to aridity. None of the common caviomorphs or marsupials exhibited preference for the thorn scrub habitats. *Galea spixii* utilized the outcroppings to a lesser extent than the other species, but was subordinate to *Kerodon rupestris* in agonistic interactions and was apparently partially excluded from the outcroppings.

**Acknowledgments**

I wish to thank my fellow researchers in Brazil, Drs. Michael R. Willig and Thomas E. Lacher, Jr., and my major advisor, Dr. Michael A. Mares, for their efforts on my behalf. This manuscript was reviewed by Drs. Peter L. Dalby and Margaret O’Connell and typed by Ruth Ann Schulte. Joyce Kotzuk prepared the figures that enhance this manuscript.

This report represents a portion of a dissertation submitted in partial fulfillment of the requirements for the Ph.D. degree from the University of Pittsburgh. Fieldwork was supported by the Brazilian Academy of Sciences, project number 85, “Ecology, evolution, and zoogeography of Caatinga mammals.” Additional funds were provided by the Carnegie Museum of Natural History.

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