Revista de Etologia 2000, Vol.2, N°1, 3-15

Behavioral Repertoire of the Spiny Rat *Proechimys* (*Trinomys) yonenagae* (Rodentia: Echimyidae) in Captivity

PAULO MANAF E ELISABETH SPINELLI DE OLIVEIRA

Universidade de São Paulo

This is the first description of the behavioral repertoire of *Proechimys [Trinomys] yonenagae* (Rodentia: Echimyidae) in captivity. *P. [T.] yonenagae*, a fossorial dweller of sand dunes in the Caatinga, is a species which belongs to a genus associated to rainforests. It possesses morphological traits that favor anti-predator strategies such as an asymmetrical quadrupedal bound gait and the capacity for jumping, hopping, scratch digging and foot drumming. Sexually aroused males display foot tapping but otherwise the sexual repertoire is quite simple. Tactile and auditory communication mechanisms are commonly used. A complex set of interactions suggests the existence of a communal organization, tolerant parental and alloparental behaviors, which probably have ecological significance in a xeric dunes context. A rather simple pattern of agonistic behavior may also be related to the species habitat. Our results stand in contrast to the assumption that all *Proechimys* are solitary and territorial.

Index terms: Behavioral repertoire. Caatinga. Rodent. Caviomorpha. Proechimys (Trinomys) yonenagae.

Repertório comportamental do rabo de facho *Proechimys [Trinomys] yonenagae* (Rodentia: Echimyidae) em cativeiro. Esta é a primeira descrição do repertório comportamental de *Proechimys [Trinomys] yonenagae* (Rodentia: Echimyidae) em cativeiro. *P. [T.] yonenagae*, um roedor fossorial das dunas da Caatinga, é uma espécie pertencente a um gênero associado a florestas. O grupo apresenta características morfológicas que favorecem estratégias antipredatórias, tais como locomoção saltatorial e a capacidade de cavar, saltar, pular e tamborilar. Embora o repertório de comportamentos sexuais seja simples, os machos exibem uma seqüência rápida de movimentos das patas anteriores durante a corte. Tanto a comunicação tátil como a auditiva desempenham um papel importante. O conjunto complexo de interações exibido por grupos em cativeiro sugere a existência de uma organização comunal e de comportamentos parentais e aloparentais tolerantes, de provável significado ecológico num contexto de ambiente semi-árido. Nossos resultados contrastam com os da literatura que colocam *Proechimys* como um bom exemplo de um grupo solitário e territorial.

Descritores: Repertório comportamental. Caatinga. Roedor. Caviomorpha. Proechimys (Trinomys) yonenagae.

The Rodentia have far more species than any other order of mammals. Among them the South American hystricognath rodents are one of the most diversified and widespread groups (Nowak, 1991). The basic behavior of members of this sub-order is very uniform considering great differences in the size and life style of species. Several behavioral characteristics which are atypical of rodents have nevertheless evolved, particularly those related to reproduction and anti-predator devices (Kleiman, 1974).

Echimyidae is the largest and the most speciose family of caviomorph rodents with about 15 genera, all but four found in humid forests (Emmons, 1997). *Proechimys* is a genus of Echimyidae constituted of terrestrial, nocturnal and solitary animals which are often the most numerous non-flying mammals find

Elisabeth Spinelli de Oliveira, Departamento de Biologia, FFCLRP-USP. Av. Bandeirantes, 3900, CEP 14049-901, Ribeirão Preto, São Paulo, Brazil. E-mail: esolivei@usp.br. Paulo Manaf, Núcleo de Apoio à Pesquisa em Neurociências e Comportamento, USP.

We thank Prof. Dr. Pedro L. B. Rocha for providing most of the animals and for comments; Patricia F. Monticelli, Rosana Suemi Tokumaru, and Prof. C. Ades for the sonograms; FAPESP for the financial support (proc. 96/06205-6, 98/0141-1, 97/12656-3).

Figure 1. A specimen of *Proechimys [Trinomys] yonenagae*, *rabo de facho*, from the main sand dune field of Ibiraba, Bahia State, Brazil (weight: 156 g). Photo by PCARP-USP.

in neotropical rainforests (Emmons, 1997). Spiny rats have an extensive distribution, occurring in Central and South America (Eisenberg, 1989; Emmons, 1997; Nowak, 1991). Two subgenera are recognized: *Proechimys (Proechimys)* J. A. Allen 1899, and *Proechimys (Trinomys)* Thomas 1921, although Lara, Patton and Silva (1996) have recently suggested the elevation of the Atlantic Forest *Trinomys* to generic status. *Trinomys* includes seven species which are geographically restricted to eastern Brazil, from São Paulo to Bahia. All species but *Proechimys (Trinomys) yonenagae* inhabit forested areas and most of them can be found in the Atlantic rainforest.

The aim of the present study is to describe the behavioral repertoire of *Proechimys (Trinomys) yonenagae* kept in captivity in individual cages or in small colonies. The single exception among *Trinomys,* the spiny rat known locally as *rabo de facho* (Figure 1), is a semifossorial dwelling rodent from the Brazilian semiarid caatinga (Rocha, 1995). It was chosen because it has autapomorphic structures and is the only small mammal species known to inhabit successfully the main sand dune field (Rocha, 1992). The open environment of the caatinga is subjected to low relative humidity, high solar intensity, low degree of cloudiness, high average temperature, scarce and irregular rainfalls within and between years. In the caatinga the shallow rocky soil, and the presence of a non-porous crystalline basement greatly depress the water retention capacity of the soil. When rain does fall, it is lost through rapid runoff (Reis, 1976). Ecological data indicate that individuals of *P. (T.) yonenagae* are found in high density sites and that they build extensive burrows, up to 15 m, in the sand (Figure 2), to depths ranging from 0.5 to 1.5 m, where they spend the daylight hours (Rocha, 1992). Their most striking anatomical features may be related to life in the sand dunes: small body size, long hind feet, inflated tympanic bullae, and long pencilled tail (Figure 1). A knowledge of their behavior could prove very instructive when compared with the behavior of other species of the *Proechimys* genus.

To the best of our knowledge this is the first description of the behavioral repertoire of a member of the genus *Proechimys (Trinomys)* and we assume that *P.(T.) yonenagae* has acquired

Figure 2. The entrance of a burrow (arrow) built by *Proechimys [Trinomys] yonenagae* in the main sand dune field of Ibiraba, Bahia State, Brazil. Photo by Martim de França S. Ribeiro.

behavioral responses that are of ecological significance in a xeric region such as the dunes.

Material and methods

Subjects

We observed 26 adult specimens of *Proechimys (Trinomys) yonenagae* (13 males: 122±17 g and 13 females: 138±17 g) collected in the sand dunes fields in Ibiraba (10°48'S, 42 °50'W), Bahia State, Brazil, in March 1996 and July 1998, and housed under controlled conditions (23±1 °C; 12:12h LD schedule, LD: 120-3 Lux; lights on at 6 PM), in the Biology Department of the FFCLRP-USP.

Observations were carried out from September to October 98 (colony 1), from October 98 to March 99 (colony 2), and from November 98 to March 99 (colony 3). The animals kept in cages were observed from January to August 98 and from the 28th to the 31st of May 98.

Maintenance conditions and equipment

Adult animals were housed individually and in pairs, either in standard laboratory cages (sizes 40 x 34 x 16 cm and 40 x 65 x 30 cm) or in groups up to six in three colonies. The colonies were 2.88 m^2 arenas with wooden walls 0.9 m high, reinforced at the intersection of partitions and sides with light gauge aluminium sheeting to prevent gnawing. The floor was covered with sand (colony 1) or wooden shavings (colonies 2 and 3), six artificial shelters either of U-shaped ceramic (60x10x5 cm) or L-shaped aluminium (50x8x10 cm) were put on the ground. Each colony had an equal number of adult animals of both sexes. Cages and colonies were cleaned once a week, when the animals were weighed. They were fed lab chow (NUVILAB) supplemented once a week with a variety of seeds, fruits, and insects (spiny rats feed avidly on peanuts, sunflower seeds, bananas and *Tenebrium* larvae). Water was available *ad libitum*.

The sessions were recorded by a JVC GR-DV1u high resolution digital camera, and two LG model GAC-PT1 colour Pan-Tilter cameras, the images were transferred to a PC Pentium 200 (JVC JILP digital system) and analysed (VCR Samsung VM-K87 and Toshiba TV-2066 SU 20") (Picture Works Photo Enhancer 3.2). Some sessions were directly registered by an observer utilising a portable computer (Palmtop, Psion model Workabout RS 232 1 MB).

Vocalisations and sounds were recorded by a portable Sony TCM-S64V tape recorder. The sound recordings were analysed with a AVISOFT SASLab Program 3.4.

Procedure

A 10-min habituation period with the observer in the room preceded each session with colony animals. Sessions begun during the dark phase after at least three days of habituation, they lasted one hour each and added up to 42 hours of observations in 6 months. *Focal animal* and *ad libitum* methods were used (Altmann, 1974). During eight sessions each animal was observed for 10 min, and during the remaining sessions the group was observed as a whole. Behavioral categories were defined according to Grant and Mackintosh, and Draper (1963, 1967, respectively, as cited by Silverman, 1978), Lacher (1981), Rood (1972), and the recommendations of Altmann (1974), Martin and Bateson (1988), and Lehner (1996). Walking, running, leaping up and digging were defined according to Hildebrand (1985a, 1985b).

The animals kept individually in cages were observed (1) using an *ad libitum* method (Altmann, 1974) throughout 6 months, and (2) using a *scan* sampling method (Altmann, 1974) during three nights, with one scan every two hours, adding up to 36 hours of observations. Observations were supplemented by photography; drawings were made from the pictures and reproduced in a computer by Paulo Manaf .

Sound samples were registered *Ad Libitum* (Altmann, 1974) both at the colonies or from

the animals kept in cages. We considered a syllable as an uninterrupted tracing on the horizontal axis of the sonograph, a phrase as a set of syllables not separated by time intervals greater than that separating two phrases. A click is a non-harmonic sound less than 20 ms in duration, short syllables are between 50 to 600 ms in duration, and long syllables over 600 ms.

Results

General behavior in captivity

Spiny rats are easily maintained in captivity. They are docile, healthy, ease to handle and they rapidly adapt to the conditions of the cage and habituate to the presence of an observer during experimental sessions. In colonies, they are prone to cache food outside the shelters and need a supply of water whether in food items or in bottles. In our laboratory, they remain fertile at more than four years of age, longevity is high and mortality rate is low.

The animals are nocturnal. During the light period they generally remain in their shelter resting or sleeping, and are hardly disturbed by the presence of the care-keeper or by noises in the environment. Spiny rats become very active and leave the shelter at dark. They can be observed busily moving, feeding and drinking, exploring all the available space and displaying a wide range of spontaneous behaviors. It is however possible to observe them resting and huddling at night, for intervals of 20 to 30 min. In animals kept individually in cages, no sleeping episodes are observed at night but some time (6.5 % of categories observed) is dedicated to eating.

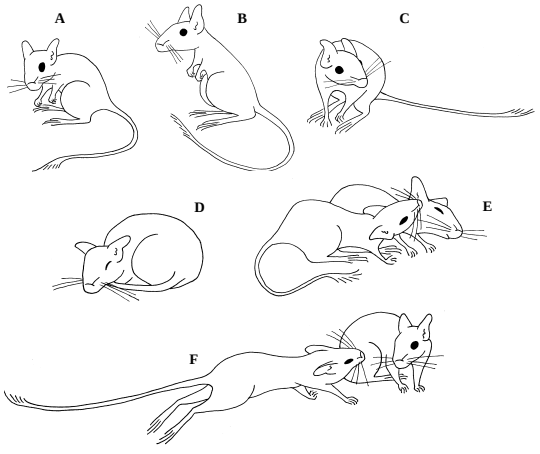


Figure 3: Behavior of *Proechimys [Trinomys] yonenagae* in captivity. A, B: stand alert postures; **C:** alert frozen posture; D: the commonest sleeping position; E: nasal-auricular contact; F: attack.

When housed in cages, pairs of *P. (T.) yonenagae* did not breed and no signal of oestrous activity was revealed by vaginal smears. Nonetheless, when pairs were kept in larger cages or in colonies breeding occurred. A male could be kept with a female throughout parturition without canibalizing the litter. Cannibalism was also a rare event when breeding took place in the colonies. Spiny rat offsprings are precocious and well accepted either by adult males or females. Strong bonds seem to develop between siblings.

Locomotion and exploratory behavior

Spiny rats move primarily by means of an asymmetrical quadrupedal bound gait with forelimbs and hind limbs alternately striking the ground. While walking they frequently stop and reorient their body in jerky 180° turns. They can dart to the shelters as result of a noticeable event or without any recognisable cause. Such movements can be intercalated with hopping and nasal-auricular (Figure 3 E) contact with a co-specific. While hopping the animals make one or a series of upward leaps and may sharply turn the head or foreparts while in the air. This category is commonest in young animals and is frequently contagious.

The animals are capable of leaping up higher than 20 cm vertically but show no highly developed climbing ability, although they may reach higher elevations on objects such as pile of boards or bricks by making series of short upward jumps. In the colonies leaping up occurs when the animals are cornered by the care-keeper or during agonistic encounters. Alert

frozen postures are common. The animal typically rears and stretches its upper body and head forward (Figure 3 C). Rearing alert postures has both front feet off the ground with a curved or upright body posture (Figure 3 A, B). All alert postures are associated to walking, running and digging. When an individual is leaving the shelter it is common to observe a posture of what can be called risk assessment whereupon the animal scrutinises its surroundings with scanning movements of the head while keeping half of the body inside the shelter.

Digging at the shelter entrance is the most frequent behavior when the animals are awake in the colonies. *P. (T.) yonenagae* digs with alternate strokes of the forefeet. The hind feet kick the loosened dirt away from the abdomen or shelter entrance (Figure 4). It occurs very often also in animals kept individually in cages and it corresponds to 11% of all behavioral categories observed during the night.

Though upright rearing is easily achieved and common in animals housed in cages, it is rarely observed in the colonies. It usually occurs when the care-keeper enters into the maintenance room offering food.

Maintenance behaviors

Foraging rats move slowly forward with their nose lowered near the ground. A food item found by one of them may be taken by another one; in this case the former animal will promptly withdraw. Foraging behavior spreads frequently among animals.

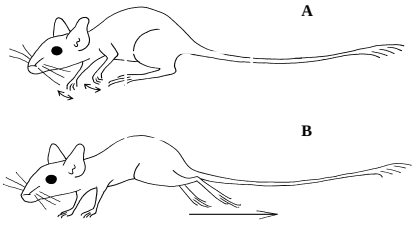


Figure 4. *Proechimys [Trinomys] yonenagae* digging. A: the spiny rat dig with alternately strokes by the forefeet; B: the hind feet kick the loosened dirt away from the abdomen.

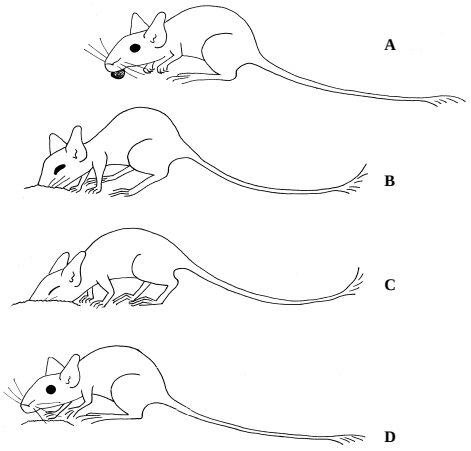


Figure 5. *Proechimys [Trinomys] yonenagae* caching food by digging movements of the snout (A - C); D. the forepaws are used to cover the burrow with substrate.

Food is usually held in the forepaws. It is not always promptly consummed and can be partly hidden in caches. Caching is accomplished by digging movements of the snout, the forepaws being used to cover the burrow with substrate. Small items like wood shavings or blocks are scatter hoarded as well (Figure 5).

Faeces are dropped indiscriminately about the pen while urine is deposited by all animals at selected areas like the corners of the cage or of the coloniy or inside one of the shelters. All animals explore the urine of other individuals; urine marking behavior was however never observed.

The commonest sleeping position is the rounded posture, with all four feet under the body and the head pulled in (Figure 3 D).

The components of grooming behavior are: wash, groom, lick penis, and scratch. Self-grooming is seldom seen in *P. (T.) yonenagae*, corresponding to 0.9 % of all behavioral categories observed in animals kept individually in cages during the night. In the colonies, it is usually associated to resting or huddling. Although provided with sandbathing areas, spiny rats did not sand bathe or roll.

Stretching and yawning, which are considered comfort movements, were not observed in the present study.

Social behavior

A fairly complex network of allogrooming associations establishes between members of the same cage or colony. Most commonly, grooming is directed by adult females and males to juveniles. Allogrooming is also observed among animals of the same sex and between males and females.

Often an animal may just approach and nose another or two spiny rats may nose each other's pelage. Reciprocal nasal-auricular contact is also a frequent prelude to huddling and other forms of social behavior. When two or more animals are kept together, either in cages or in colonies, they always rest side by side in a rounded posture. Huddling involves contactual resting postures like head-over-head or head-over-rear/side, as well as vocalisations.

A prevalent contact behavior among two adults consists of both animals walking slowly or stop side by side in full body contact. Frequently it is preceded by nose-to-nose contacts.

Agonistic patterns

Adult animals of either sex can be housed in pairs or groups up to four, in standard or larger laboratory cages, with no risk of aggression. However, shortly after the colonies were established agonistic behavior occurred: aggressive grooming, lunges, chases, fights, and attacks (Figure 3 F). In aggressive grooming, the teeth were used to pull of the rump fur and biting of the tail, in generally vigorous movements. There was a tendency for the aggressive animal to orientate itself at a right angle to the other. These acts were usually directed to a specific single animal. Within one or two weeks the most aggressive forms of interactions disappeared. However, at least in each colony one animal was withdrawn due to the severity of the wounds inflicted upon it. Thereafter milder and infrequent agonistic interactions occurred: fight and attack were virtually abolished, lunge and aggressive grooming became associated to feeding or digging at the shelters entrance, side defensive posture, retreat or flee might be seen. Offensive upright posture, stand-threats, head-thrust, jump-turns, tail-up, head-up, crouch, boxing and full submissive posture were never observed.

Sexual patterns

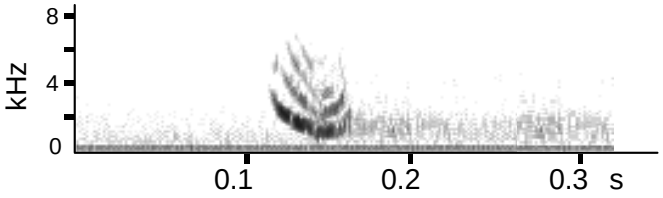
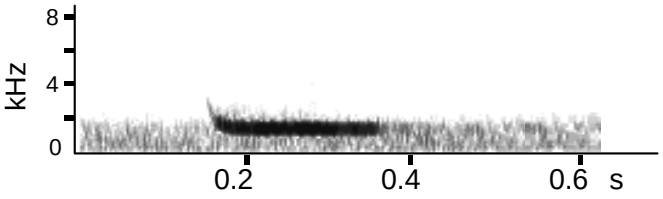
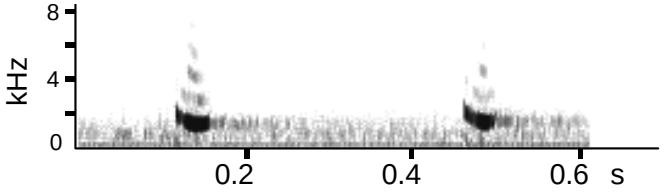
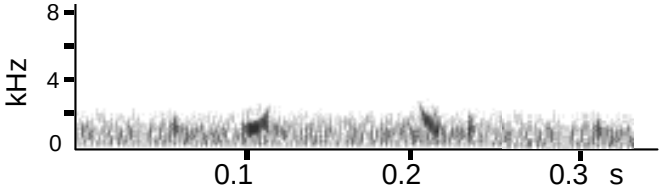
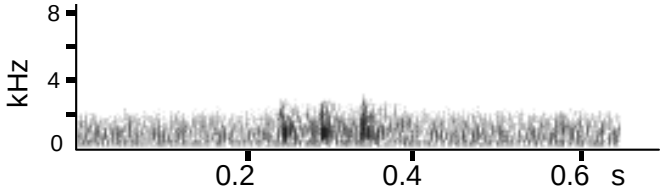
Shortly after the colony was established nasal-anal contact was the most common sexual response in *P. (T.) yonenagae*. The nasal-anal contact may be displayed either by males to females or by females to males. Intrasexual nasal-anal interactions may also occur. After the colony is well established nasal-anal interactions are given exclusively by males to females. Occasionally males will sniff the anogenital area of juveniles, both male and female, often lifting the rump of the juvenile off the ground. After a nasal-anal or a nose-rump contact a sexually excited male will slowly follow a female, then will often rapidly tap the forefeet up and down on the ground (foot tapping) and then try to mount. The female will then attempt to move away, and the male will follow her and display foot tapping.

Although breeding had occurred several times during the present study it was not possible to observe copulation. Circling, riding and chin-rump follow were also never observed in the present study.

Vocalisations

Proechimys (T.) yonenagae produces a variety of sounds, both non-vocal and vocal, which were preliminarily characterised in terms of intensity, duration and frequency (Table 1). Foot drumming is a non-vocal sound made by rapidly striking one or both hind feet against the substrate. It is heard when the animals, either females, males, adults or juveniles, were slightly disturbed as result of a noticeable event or without any recognisable cause.

Table 1. Types of sounds emitted by *Proechimys [Trinomys] yonenagae* kept in captivity

Twitter (high intensity vocalisations): Frequency between 350 - 4,200 Hz Duration: 0.050 to 0.060 s Four harmonic sounds at least Modulated (descendent and ascendent)	**Sonogram** 
Frequency between 350 - 3,500 Hz Duration: 0.190 to 0.240 s One harmonic Modulated (descendent)	
Frequency between 350 - 3,500 Hz Duration: 0.070 to 0.140 s Two harmonic sounds at least Modulated (descendent)	
Vocalisation in huddling: Frequency between 350 - 2000 Hz Duration: 0.015 to 0.017 s One harmonic Modulated (ascendent or descendent)	
Footdrumming: Three to four brief tappings on the floor with the hindfeet. Usually the sequence is repeated many times. Interval between the tappings: 0.050s	
Vocalisation in flight: High frequency and intensity, very short duration. Usually it is a three syllables phrase	Not recorded
Growl: Low frequency, high intensity, short duration. Usually it is a two or three syllables phrase	Not recorded
Squeak: Very short duration, high intensity and frequency Usually it is a only one syllable phrase	Not recorded

Twitters are harmonic, modulated, high intensity sounds which may attain different forms. They are usually emitted by an individual just after an agonistic encounter had taken place in the colonies or when a human approaches the pen. They can last for as much as 1 to 2 minutes and duets are rather common.

Squeaks are high pitched single notes which occur typically as a response to pain (animals squeak when bitten).

Another type of vocalisation, characterised by a phrase of two or three syllables can also be heard when an animal flee to the shelter. When a group of spiny rats is resting in huddling, animals utter a contagious form of vocalisation characterised by short clicks of low intensity.

Growls are a low pitched sound often given in association with agonistic encounters, and indicate aggressiveness. They are usually emitted by an animal which is approached by other while he is digging or holding food. Usually the approaching animal is intimidated by this type of vocalisation. Growls can also precede an attack. Tooth chatters was never observed.

Discussion

Our results about the behavioral repertoire of *Proechimys (Trinomys) yonenagae* can be discussed from a comparative perspective. *P. (T.) yonenagae* is a remarkable exception among members of the genus and even among the Echimyidae family of caviomorphs. While the majority of echimyids and all other *Proechimys* inhabit mesic and mostly forested environments in the neotropical region, *P. (T.) yonenagae* is a burrow-dwelling from a xeric habitat in the Caatinga Morphoclimatic Domain of Brazil.

According to Vivo (1997) the area presently occupied by the Caatinga was a mesic forest connecting the Amazonian forest with the coastal Atlantic rainforest of North-eastern Brazil and capable, therefore, of supporting rainforest mammals. During the Holocene the Caatinga suffered a major ecological change that resulted in the present semiarid conditions. *P. (T.) yonenagae* is considered to be a good example of a form which became isolated from its sister forest species and survived outside the generally preferred habitats of other conspecifics.

Morphology, physiology and behavior play a role in the adaptation of an organism to its environment. Physiological data from our laboratory are in agreement with Vivo (1997) since they indicate that the only small mammal present in the dunes does not differ significantly from other species of *Trinomys* with respect to water balance adaptations to semiarid climates (Oliveira, Coimbra and Rocha, 1995; Oliveira, Mendes and Rocha, in preparation). Also Barros, Oliveira, Rocha and Branco (1998) were not able to demonstrate significant respiratory adaptations to life in burrows in the fossorial *P. yonenagae* when compared to *P. iheringi*, a *Trinomys* from the Atlantic forest.

Eisenberg (1963, 1967, as cited by Lacher, 1981) studied the behavior of heteromyids, murid and dipodid rodents and helped to establish two major concepts that should, according to Lacher (1981), be considered in any comparative behavioral study. First, "discrete behavior patterns exhibit a profound similarity;" and second, "differences in the frequency of occurrence rather in the form of the movement have proved to be the most effective criterion for delineating taxon-specific differences" (Eisenberg, 1963, 1967, as cited by Lacher, 1981, p. 5). This statement holds true to *P. (T.) yonenagae* as shown by our observations and as will be subsequently discussed.

Although *rabo de facho* shows morphological adaptations convergent with those of ricochetal rodents from Neartic (e.g., *Dipodomys*, *Microdipodops*), Australian (e.g., *Notomys*), Ethiopic and Paleartic (e.g., *Jaculus, Allactaga)* deserts, such as long hind feet and strongly pencilled tail, its gait is quadrupedal, as has been previously suggested by Rocha (1992) and not bipedal. Nonetheless, saltatorial running was prevalent in the colonies context. According to different studies, "saltatorial locomotion is

thought to be more efficient in fast, evasive movements through open areas" (as cited by Rocha, 1995, p. 547). These same physical attributes are also in favour of a stable rearing position. Indeed *P. (T.) yonenagae* can remain in upright rearing posture for a long period of time but differently from rats and mice (Silverman, 1978), animals in colonies were rarely observed in exploratory rearing. Instead *P. (T.) yonenagae* usually explores the environment by series of stops and reorientations of its body in jerky 180° turns as others caviomorphs dwellers of open habitats do (Lacher, 1981; Rood, 1972). *Rabo de facho*, as well as *Kerodon rupestris,* which displays an upright sitting exploratory posture while feeding (Lacher, 1981), may show upright rearing in response to food presented by the care-keeper. Among others caviomorphs such as *Galea spixii*, *Galea musteloides*, *Microcavia australis* and *Cavia aperea* rearing occurs only in *Galea musteloides*, as a sexual act (Rood, 1972; Lacher, 1981). Maliniak and Eisenberg (1971) reported that *Proechimys semispinosus,* a rainforest spiny rat of the subgenus *Proechimys* of rather conservative external morphology, when fighting with another male is able to rear up on its hind legs and to walk bipedally, thus exposing the snow white underside.

Hopping, which is frequent and contagious, rather than a type of locomotion may be derived from anti-predator displays, as suggested by Kleiman (1974). In this respect *P. yonenagae* would also conform to a behavioral pattern seen in others caviomorphs (Kleiman, 1974; Lacher, 1981; Rood, 1972), although not yet described in others *Proechimys*. According to Henderson (1981) wild mice show a more vigorous response of hopping than inbred strains, indicating that during domestication selection pressures maintaining high responsiveness have been relaxed. Kleiman (1974) speculates that hopping is usually associated to caviomorphs that are dwellers of open spaces (*Cavia, Galea, Chinchilla*) and most prevalent in cursorial species (*Dasiprocta*, *Myoprocta*, *Pediolagus*). It seems to be absent in arboreal forms (*Capromys pilorides*, *Erethizon*). In truly dangerous situations, anti-predator displays, such as running and jumping would lead to flight patterns which are contagious, the performance in the presence of conspecifics may induce other individuals to flee in an erratic manner which could distract the pursuer. Although during the day *P. (T.) yonenagae* is a burrower, it leaves the galleries at night and looks for food in the open dune fields. Consequently during the period of higher activity it explores open spaces. Our study thus indicates that in captivity *P. (T.) yonenagae* displays three potentially anti-predatory locomotive strategies: running, jumping and hopping, which occur in others caviomorphs.

Members of the genus *Proechimys* are know to shelter during the day under fallen brush, in hollow logs, or in holes in the ground (Emmons, 1997). *Proechimys semispinosus* dwells in burrows either of their own construction or utilises crevices under rocks or at the bases of tree stumps (Maliniak & Eisenberg, 1971).

Our results show that *P. (T.) yonenagae* is a very frequent digger even when kept in small cages. The entrance of a shelter may be a site of dispute and of agonistic display in a colony which, otherwise, shows low level of aggressiveness. Furthermore, in the sandy dunes, *P. (T.) yonenagae* builds extensive galleries which are long and deep (Rocha 1992). According to the definition of Hildebrand (1985a) *P. (T.) yonenagae* is a scratch-digger since it utilises the forelimbs and hind feet to excavate. Attend postures are frequent, and a stereotyped sequence of dig-upright attend is common. Among caviomorphs the upright attend was commonest in *Microcavia*, less so in *Galea* and rare in *Cavia* (Rood, 1972). *P. (T.) yonenagae* shows high manual dexterity when holding food, like most rat-like rodents do, and it also has powerful feet, preadaptations to an efficient scratch-digging capacity. It is important to point out though that many morphological or physiological traits usually associated to mammalian burrowers, such as small or absent external ear (pinna), relatively very short legs, reduced eyes and tolerance to high CO^2 tension are not seen in *P. (T.) yonenagae*

(Barros et al., 1998; Rocha 1995). Since digging in a loose soil as the sand does not seem to require substantial morphological modifications, the acquisition of digging may be also considered as an example of a more labile behavioral response to the environment. Digging is very important for the spiny rats from the dunes: it provides a shelter where the ambient temperatures are relatively constant and a refuge against predators. Digging may also be correlated to the type of social organisation found in colonies of *P. (T.) yonenagae* as we are going to subsequently discuss.

As stated by Kleiman (1974) very few species of caviomorphs are solitary at all times except for mating. *Proechimys* is considered a good example (Kleiman, 1974) being nocturnal, solitary (Emmons, 1997), and living in forests, a habitat that may impose a restriction on group size. Another caviomorph, *Agouti paca,* which is confined to the Amazonian rainforest of Peru, has solitary habits (Nowak, 1991). In grasslands and montane areas, most caviomorphs are colonial though the complexity of the social structure of the colony varies. In species inhabiting savannahs and open country, a colonial existence may serve as an anti-predator strategy (Kleiman, 1974); alarm calls are commonly found in these species (Eisenberg, 1974). Rood's (1972) study of *Cavia, Galea* and *Microcavia*, and Lacher's (1981) work on *Kerodon rupestris* and *Galea spixii,* in field and captive conditions, are very instructive when comparative behavioral studies are undertaken on other members of the Caviomorpha. Their results support the assumption that the social organisations of the various genera seem to be very responsive to ecological requirements. Sachser, Dürschlag and Hirzel (1998), reviewing their own data on social organisation, social status, behavioral development and endocrine stress responses, states that in captivity guinea pigs (*Cavia porcellus*) build up complex and long-lasting stable social systems generally characterised by low levels of stress.

Mature *Proechimys guairae* caged together for the first time tend to be very aggressive, inflicting serious, sometimes fatal, wounds on each other. New groups can be created with newly-weaned animals although one mature animal, usually the male, can be used with only slight risk of aggression (Lusty & Seaton, 1978). Maliniak and Eisenberg (1971) reported that *Proechimys semispinosus* in captivity would fight vigorously when allowed access to one another, and anoestrous females were quite prone to repulse males by attacking them. Furthermore, although litter-mates could be kept together well into adulthood, a male could not be kept with a female throughout parturition without resulting cannibalism of the litter. Ecological data by Fleming (1971) for *Proechimys semispinosus*, Emmons (1982) for *P. brevicauda*, Bergallo (1995) for *P. iheringi*, and Aguilera (1999) for *P. guairae* suggest territoriality since adult females do not have overlapping home range and males do.

Our data indicate that the spiny rats from the dunes are essentially communal and highly socially tolerant when kept in colonies or in cages, in contrast to other species of the genus. Agonistic encounters may occur when a colony of unfamiliar adults animals is settled, but never at random. Usually one specific animal is not accepted and must be removed from the group. Afterwards social positive behavior will predominate: nose-nose contact, nasal-auricular approach, walk or stop side by side, and huddling. Breeding occurs and cannibalism is very rare though space may be a limiting factor for procreation, as has been described for *Proechimys semispinosus* (Maliniak & Eisenberg, 1971). A complex array of interactions among females, males and juveniles indicates that bonding (Sachser et al., 1998) and tolerant alloparental behavior, which occurs in *Microcavia australis, Galea musteloides* and *Hydrochaeris hydrochaeris,* though they do not occur in *Dolichotis patagonum* (Ganslosser and Wehnelt, 1997), might be an important component of the social structure in *P. (T.) yonenagae*. Our results also indicate that parental behavior might be present among these animals. In many species of caviomorphs the male participate actively in protecting and rearing the mobile, well developed at birth, but vulnerable young (Kleiman, 1974).

Proechimys (Trinomys) yonenagae may be considered the most social member of the genus so far studied, and this sociality is reflected in the complex array of contactual gestures, and a correspondingly restricted aggressive repertoire. In this respect it is similar to *Microcavia*, the most abundant representative of the Caviinae in the semi-arid thorn bush country which covers much of central Argentina (Rood, 1972).

Differently from others caviomorphs (Kleiman, 1974), *P. (T.) yonenagae* does not show visual signals as tail up rump or pilo-erection. Tactile stimuli seem, however, to be important in group integration and cohesion, as well as in sexual interactions. As in most caviomorphs such as *Microcavia*, *Cavia*, *Galea*, *Dinomys*, *Dasyprocta*, *Myoprocta*, *Octodon, Octodontomys*, *Chinchilla*, *Lagostomus*, *Geocapromys*, and *Proechimys*, allogrooming is common. As in the case of *P. (T.) yonenagae*, individuals of *Myoprocta pratii*, and *Octodon degus* (Kleiman, 1974), when put in the presence of conspecifics, begin by showing nose to nose contact and then display further investigatory behavior, including sniffing and nuzzling the perineum, the rump and the neck. Most agonistic interactions terminate without escalation, although biting may occur. Scent-marking using urine and anal gland secretion, which serves primarily to increase social cohesion were never observed. However, spiny rats from the dunes are highly interested in sniffing urine of others which indicates that olfactory stimuli may help to locate and recognize of conspecifics. Urine spraying (enurination) which has been reported in sexual or defensive contexts among caviomorphs (Kleiman, 1974; Lacher, 1981; Rood, 1972) was not observed in *P. (T.) yonenagae*.

Courtship rituals are not common in mammalian species, yet male caviomorph display complex behavioral patterns, such as tail-wagging, urine spraying, body quivering and frisky hops, while interacting with females (Kleiman, 1974; Lacher, 1981). Although data from other *Proechimys* are scarce, Maliniak and Eisenberg (1971) reported that mating behavior in *P. semispinosus* involves reciprocity in vocalisations ("whimper calls"), urination by the female and sniffing by the male, ritualised patterns of locomotion by the female, grooming and mounting by the male. The male's penis is long and easily observed; the copulation pattern consists of multiple series of mountings. Male and female wash their genitalia after a mount with intromission. In our study we were not able to observe any elaborated courtship or even a single episode of copulation in *P. (T.) yonenagae* in six months of observation. Nonetheless, foot tapping was a recurrent behavior of a sexually excited male and, as far as we know, this is the first description of such behavior in a member of the genus *Proechimys*. Foot tapping, also termed trembling, is a sexual display exhibited by *Cavia*, *Dinomys*, *Dasyprocta*, *Myoprocta*, *Agouti*, *Octodontomys*, and as body trembling, in *Octodon* and *Lagostomus* (Kleiman, 1974).

As cited by Silverman (1978, p. 49) "[Robert Bolles said] an isolated laboratory rat spends 40% of its waking time on grooming." This results differ significantly from our data on *P. (T.) yonenagae* which rarely grooms. Instead among caviomorphs different forms of grooming are frequent: combing occurs in *Cavia*, *Microcavia*, *Kerodon*, but not in *Galea musteloides* or *spixii,* while face wipes and scratching occur in all the mentioned genera (Lacher, 1981; Rood, 1972).

Sand bathing behavior is common in desert rodents and has evolved in all the major deserts of the world except those from Australia (Randall, 1994). The lack of sand bathing in tropical heteromyids led Eisenberg "to conclude that sand bathing evolved in response to desert conditions" (1963, as cited by Randall, 1994, p. 415). However, non-desert rodents do sand bathe, but the behavior is more frequent and best developed in desert species (Randall, 1994). *P. (T.) yonenagae* does not sand bathe, stretch or yawn. Lacher (1981, p. 22) suggested a correspondence between stretching and movements of sand bathing, "stretching may be the origin of more complicated series of movements such as those used in sandbathing." Stretching and yawning occurred in *Microcavia*, *Cavia*,

Galea musteloides, Galea spixii, and *Kerodon rupestris* while sandbathing was observed only in *Galea spixii* (Lacher, 1981; Rood, 1972).

Striking the feet on the ground to create mechanical vibrations is widespread among desert rodents and seems to have evolved independently in several families of the Sciurognathi suborder (Heteromyidae: *Dipodomys*, *Perognathus, Microdipodops, Chaetodipus*; Muridae: *Neotoma*, *Gerbillus*, *Gerbillurus*, *Meriones*, *Psammomys*, *Rhombomys*, *Tatera*; Dipodidae: *Jaculus*) of fossorial rodents around the world. It may be an effective means to transmit air-borne signals at night between distant neighbours in sparsely vegetated habitats and seismic signals underground for communication between burrows. Foot drumming occurs in similar context in all desert rodents: during territorial and agonistic encounters, during mating, and in response to predators (Randall, 1994).

Emmons (1997, p. 233) describes the sounds produced by a fleeing *Proechimys* spp. in the neotropical forests as "series of about five rapid taps of the hind feet on the ground, the only common small nocturnal mammal to do this." Eisenberg (1974) studying the vocalisation of 17 species of Caviomorphs states that they produce a variety of sounds, both vocal and mechanical, which includes tooth chattering, stamping or in some cases, quill vibrations. Foot drumming was not mentioned even in relation to *Proechimys semispinosus*. Although foot drumming has been identified in field studies of *Proechimys*, we have not been able to detect it in *Proechimys (Trinomys) iheringi* or *Proechimys (Trinomys) albispinus* housed for more than two years in our laboratory (personal observation). However, foot drumming was frequently observed in *P.* (*T.) yonenagae* kept either in cages or in colonies and seems to be related to individual recognition and predator defence. Twitters, which are vocalisations of high intensity easily recognisable, may also occur in a context of predator defence. Furthermore, a combination of foot tapping and twitter is common. *P.* (*T.) yonenagae* also emits vocalisations clearly related to social interactions, such as during huddling, or during agonist encounters (growl and squeak). According to Eisenberg (1974) when threatening each other, *P. semispinosus* will exhibit pilo-erection and tooth chatter, two behavioral categories which are absent from the repertoire of *P.* (*T.) yonenagae*. When submissive, and being approached by a conspecific, *P. semispinosus* may cluck. This sound may grade into a twitter series or whimper. Aggressive males may emit a growl as also occur in *P.* (*T.) yonenagae*. In disregard of what has been observed in *P. (T.) yonenagae*, during the long copulatory mount (Maliniak & Eisenberg, 1971), the female of *P. semispinosus* produces a wailing call, she may then be joined by the male thus creating a duet.

In spite of the scarcity of ethological data available, there are similarities and important differences at the species level that should be considered when comparing *P. (T.) yonenagae* and *P. semispinosus*, the only species thus far studied in captivity. Both species dwell burrows, are nocturnal, terrestrials, and prone to cache food. Discrete behavior patterns, such as drinking and eating exhibit similarities. However, striking differences can be observed. *P. (T.) yonenagae* is a scatter hoarder, while *P. semispinosus* is a larder hoarder. *P. semispinosus* is an animal that is essentially non-communal in its habits, with a complex pattern of agonistic and mating behaviors that appears adapted to a tropical rainforest ecology. *P. (T.) yonenagae*, the fossorial rodent of the dunes, is a highly autapomorphic species which has acquired morphological traits that permit the expression of a quadrupedal asymmetrical bound gait, the capacity for scratch-digging, for leaping up, for hopping, for foot drumming, and foot tapping by males. The combination of social tolerance, low aggressive level, and relatively simple sexual and vocal patterns suggests that the presence of a complex system of galleries was an important selective factor in *P. (T.) yonenagae*.

References

Aguilera, M. M. (1999). Population ecology of *Proechimys guairae* (Rodentia: Echimyidae). *Journal of Mammalogy, 80* (2), 487-498.

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behavior, 49*, 227-267.

Barros, R. C. H., Oliveira, E. S., Rocha, P. L. B., & Branco, L. G. S. (1998). Respiratory and metabolic responses of the spiny rats *Proechimys yonenagae* and *P. iheringi* to CO_2. *Respiration Physiology, 111*, 223-231.

Bergallo, H. G. (1995). Comparative life-story characteristics of two species of rats, *Proechimys iheringi* and *Oryzomys intermedius*, in an Atlantic forest of Brazil. *Mammalia, 59*, 51-64.

Eisenberg, J. F. (1974). The function and motivational basis of hystricomorph vocalisations. In W. I. Rowlands & B. Weir (Orgs.), *The biology of hystrichomorph rodents* (pp. 171-209). London: Academic Press.

Eisenberg, J. F. (1989). *Mammals of the neotropics* (Vol. 2). Chicago: The University of Chicago Press.

Emmons, L. H. (1982). Ecology of *Proechimys* (Rodentia, Echimyidae) in Southeastern Peru. *Tropical Ecology, 23* (2), 280-290.

Emmons, L.H. (1997). *Neotropical rainforest mammals*: *A field guide* (2a ed.). Chicago: The University of Chicago Press.

Fleming, T. H. (1971). Population ecology of tree species of neotropical rodents. *Miscellaneous Publications of the Museum of Zoology, 143*, 1-77.

Ganslosser, U., & Wehnelt, S. (1997). Juvenile development as part of the extraordinary social system of the Mara *Dolichotis patagonum* (Rodentia: Echimyidae). *Mammalia, 61* (1), 3-15.

Henderson, N. D. (1981). A fit mouse is a hoppy mouse: Jumping behavior in 15-day-old *Mus musculus*. *Developmental Psychobiology, 14* (5), 459-472.

Hildebrand, M. (1985a). Digging of quadrupeds. In M. Hildebrand, D. M. Bramble, K. F. Liem, & D. B. Wake (Eds.). *Functional vertebrate morphology* (pp. 89-109). Cambridge, MA: The Belknap Press.

Hildebrand, M. (1985b). Walking and running. In M. Hildebrand, D. M. Bramble, K. F. Liem, & D. B. Wake (Eds.), *Functional vertebrate morphology* (pp. 38-57). Cambridge, MA: The Belknap Press.

Kleiman, D. G. (1974). Patterns of behavior in hystricomorph rodents. In W. I. Rowlands & B. Weir (Orgs.), *The biology of hystrichomorph rodents* (pp. 171-209). London: Academic Press.

Lacher, T. E. (1981). The comparative social behavior of *Kerodon Rupestris* and *Galea spixii* and the evolution of behavior in the Caviidae. *Bulletin of Carnegie Museum of Natural History, 17*, 1-71.

Lara, M. C., Patton, J. L., & Silva, M. N. F. (1996). The simultaneous diversification of South American echimyid rodents (Hystricognathi) based on complete cytochrome b sequences. *Molecular Phylogenetics and Evolution, 5* (2), 406-413.

Lehner, P. N. (1996). *Handbook of ethological methods* (2a ed.). Cambridge, MA: Cambridge University Press.

Lusty, J. A., & Seaton, B. (1978). Oestrus and ovulation in the Casiragua *Proechimys Guairae* (Rodentia, Hystricomorpha). *Journal of Zoology, London, 184*, 255-265.

Maliniak, E., & Eisenberg, J. F. (1971). Breeding spiny rats *Proechimys semispinosus* in captivity. *International Zoo Yearbook, 2*, 93-98.

Martin, P., & Bateson, P. (1988). *Measuring behavior*: *An introductory guide*. Cambridge, MA: Cambridge University Press.

Nowak, R. M. (1991). *Walker's mammals of the world* (Vol. 2) (5a ed.). Baltimore: The John Hopkins University Press.

Oliveira, E. S., Coimbra, T. M., & Rocha, P. L. B. (1995). Determinação de alguns parâmetros fisiológicos do roedor *Proechimys* sp. n. Em *Livro de Resumos da X Reunião Anual da Federação de Sociedades de Biologia Experimental* (p. 354). Serra Negra, SP: FESBE.

Randall, J. A. (1994). Convergences and divergences in communication and social organisation of desert rodents. *Australian Journal of Zoology, 42* (4), 405-433.

Reis, A. C. S. (1976). Clima da caatinga. *Anais da Academia Brasileira de Ciências, 48* (2), 325-335.

Rocha, P. L. B. (1992). *Ecologia e morfologia de uma nova espécie de* Proechimys *(Rodentia: Echimyidae) das dunas interiores do rio São Francisco (BA)*. Dissertação de Mestrado, Instituto de Biociências da Universidade de São Paulo, São Paulo.

Rocha, P. L. B. (1995). *Proechimys yonenagae*, a new species of spiny rat (Rodentia: Echimyidae) from fossil sand dunes in brazilian caatinga. *Mammalia, 59* (4), 537-549.

Rood, J. P. (1972). Ecological and behavioral comparisons of three genera of argentine Cavies. *Animal Behavior Monographs, 5*, 1-83.

Sachser, N., Dürschlag, M., & Hirzel, D. (1998). Social relationships and the management of stress. *Psychoneuroendocrinology, 23* (8), 891-904.

Silverman, P. (1978). *Animal behavior in the laboratory*. London: Chapman and Hall.

Vivo, M. (1997). Mammalian evidence of historical ecological change in the caatinga semiarid vegetation of northeastern Brazil. *Journal of Comparative Biology, 2* (1), 65-73.