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Breeding spiny rats *Proechimys semispinosus* in captivity

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INTRODUCTION

During the past three years, the New World hystricomorph rodents of the suborder Caviomorpha (Wood, 1955) have been the subject of intensive investigation at the National Zoological Park. Of particular interest to us has been the family Echimyidae which shows the closest affinities to the octodontoid caviomorph families including the Capromyidae and the Octodontidae (Dawson, 1967; Packard, 1967). The family

Echimyidae includes 14 genera and some 43 species. The genus *Proechimys* is widely distributed from Nicaragua in Central America at approximately 12° north latitude to central South America at approximately 22° south latitude. The island of Trinidad is also included within the range of the genus (Walker, 1964; Moojen, 1948).

The family Echimyidae exhibits a great deal of morphological diversity when its species are compared; however, *P. semispinosus* is rather conservative with respect to its external morphology, and may be taken as the living species which most nearly resembles the ancestral rodents which gave rise to the entire suborder of the South American hystricomorphs or caviomorphs in the sense of Wood (1955). As such, *P. semispinosus* represents a stem form and a knowledge of its behaviour and ecology could prove very instructive when comparative behavioural studies are undertaken on other members of the Caviomorpha. Furthermore, *Proechimys semispinosus* is susceptible to a number of viral infections which would render it useful as a laboratory animal if a methodology could be developed for sustained captive breeding. In addition, this species could provide an alternative to the guinea pig which is at present the most widely used caviomorph rodent for experimental studies of disease.

On 4 December 1967, the National Zoological Park received eight specimens (three males and five females) of *P. semispinosus* which were collected in Panama by Mr N. Smythe. Collection of the specimens and shipment to the National Zoological Park was coordinated by the Smithsonian Tropical Research Institute. Two of the females were pregnant on arrival and littered successfully. All observations reported in this paper are based upon the two litters delivered by wild-caught females plus 12 other litters bred in captivity.

GENERAL COMMENTS ON FREE-LIVING SPECIMENS

Proechimys semispinosus is a medium sized rodent with rat-like body proportions. The dorsal fur is somewhat spinescent but not to the same extent as one finds in some of the other genera of echimyids (e.g. *Hoplomys*). More rigid, spinescent hairs are found primarily along the central midline of the dorsum. The tail is sparsely haired. The coloration of the animal is agouti-brown on the back, sides, and outer edges of the legs; the ventrum and inner surfaces of the limbs are white. The tail is bicoloured with the ventral portion white.

In Panama this species is typically nocturnal. The animals dwell in burrows either of their own construction or they utilise crevices under rocks or at the bases of tree stumps. Generally such burrows are located in the vicinity of streams. Although capable of leaping up to 1 m (3 ft) vertically, *P. semispinosus* is essentially terrestrial and shows no highly developed climbing ability. Other species of echimyids are arboreal to a greater or lesser extent (e.g. *Echimys lamarum*) and one species (*Clyomys laticeps*) is semi-fossorial. In the evening, the animal leaves the burrow to forage on the forest floor, eating a variety of fruit and plant material and caching food in its burrow system. The burrow of a given individual appears to be defended against adults of the same sex, although there is considerable overlap of neighbouring home ranges. The young are raised in the maternal burrow and suckle until over one month of age. At about four to five weeks of age, they begin to forage outside the burrow, and the family group apparently breaks up when the young are about two to two and a half months old (Enders, 1935). Thus, it is an animal that is essentially non-communal in its habits, which caches food in the burrow system, is nocturnal, and adapted to a tropical rainforest ecology.

CAPTIVE MAINTENANCE

Individual specimens of *Proechimys* have been housed in metal holding cages measuring 35 × 30 × 60 cm (14 × 12 × 24 in) with a door of 6 mm ($\frac{1}{4}$ in) wire mesh. Although individuals will do well in a cage of these dimensions, it is strongly recommended that breeding be carried out in a larger cage. For this reason, we constructed cages of 60 × 30 × 76 cm (24 × 12 × 30 in) divided into two compartments of equal size by a plywood partition 12 mm ($\frac{1}{2}$ in) thick which contained two sliding access doors each measuring 12 × 12 cm (5 × 5 in). This cage was made of wood and has a slide top constructed of a wooden frame enclosing a 6 mm ($\frac{1}{4}$ in) mesh hardware cloth.

Pairs could be held in this cage and allowed access to one another by means of the small doors in the centre divider. Breeding was accomplished in this cage but cages of still larger dimensions are

preferable since post-copulatory fighting occurs frequently.

Our most successful breeding cage, in terms of reduced post-copulatory fighting, measured 1·8× 1·2×1·1 m (72×46×43 in). The bottom, sides and rear are of solid wood. The cage is divided into two equal parts by a centre divider containing a 48×48 cm (19×19 in) metal access door which slides vertically and is controlled by means of a cable from outside the cage. The front and top of the cage are covered with 6 mm (¼ in) mesh hardware cloth. The framed hardware cloth on the front of the cage has a built-in sliding door which permits access to, and cleaning of, the cage. The floor, back and walls at the intersection of partition and sides are reinforced with light gauge aluminium sheeting to prevent gnawing.

Although litter-mates can be kept together well into adulthood, we have never been able to keep a male with a female throughout parturition without resulting cannibalism of the litter. Furthermore, although several adults can be placed in one small holding cage, breeding will not take place. We believe the simultaneous encounter technique and isolation of the pregnant female is important in encouraging breeding, within cages of the above dimensions.

Wood shavings were provided in the cages, and cardboard nest boxes measuring 21×11×19 cm (8½×4½×7½ in) were provided for shelter. The animals were maintained at a temperature which varied from 18·3 to 25·6°C (65–78°F) and a relative humidity of 70 to 90%. Twelve hours of light and 12 hours of dark served as the standard photoperiod.

Strips of paper were given to pregnant females for nesting material. Shortly before parturition the female will gather nesting material into her nest chamber, but males or non-pregnant females seldom construct nests.

The animals were fed a diet of chopped vegetables including sweet potatoes, Irish potatoes, carrots, kale and lettuce. In addition, chopped fruit, such as apples, oranges, grapes, strawberries and bananas, were included with the starch diet together with a grain mixture consisting of equal parts of whole cracked corn, wheat, rolled oats and sunflower seeds. This diet may be supplemented with dog biscuits or monkey chow. Mealworms and crickets are taken avidly as dietary supplements, and even earthworms are taken by some individuals. Two cases of maternal cannibalism have been recorded and on two occasions wild mice *Mus musculus* which entered the cages were caught and eaten. Water in crocks is avialable to the animals at all times.

GENERAL BEHAVIOUR IN CAPTIVITY

As mentioned, the animals are nocturnal and, during the period when the lights are left on, generally remain in their nest boxes resting and sleeping. When the lights go out, the animals immediately become active and leave the nest box. They move primarily by means of the quadrupedal ricochet with forelimbs and hind limbs alternatively striking the ground. In a new cage, the animals frequently mark by depositing small quantities of urine at various points within the cage. Urine marking may also be induced when the animals are mildly disturbed, especially when an alien is allowed access to the cage of a resident. The animals are prone to cache food in their nest boxes or at a point nearby.

Initially, males will fight vigorously when allowed access to one another, and anoestrous females are quite prone to repulse males by attacking them. The animals fight on their hind legs and are able, while rearing up on their hind legs, to walk bipedally, thus exposing the snow white underside. The animals will grapple with one another while on their hind legs and strike at one another with their forefeet. Rapid escape leaps will occur if one animal is vanquished. Generally, in a male-female encounter, the animals will settle down without harming one another to any great extent if the cage is large enough.

METHODS OF BREEDING, AND MATING BEHAVIOUR

By using the adjoining compartment cages, the males could be allowed access to females and it was possible, after a few minutes observation, to see whether the females were receptive or not. By running successive encounters, it was generally possible to mate a female within a few days. Utilising a vaginal smear technique we were unable to demonstrate cyclic changes in vaginal cornification which generally accompany the oestrous cycle of myomorph rodents. It appears that full oestrus and ovulation are induced by the courtship and mating activities of

the male. A receptive female does show cornified cells in her vaginal smear. The following observations concerning mating behaviour are based on four natural matings, observed in the evening, which resulted in successful pregnancies.

The male, upon entering a female's territory, generally proceeds to make contact with her in the following manner. He may utter a 'whimper' call, which resembles the sound produced by young animals when they are separated from their mother, and this call apparently serves to inhibit aggressive behaviour on the part of the female. The female may also emit a 'whimper' call, although the pitch varies depending upon her motivational state and even approximates to a trill. Initially the female is somewhat disturbed by the male's presence and may show varying degrees of hair erection. She often urine marks in the cage. The male sniffs the urine spots of the female and proceeds to follow her, initiating driving behaviour.

If she is receptive, she arches her tail over her back and walks ahead of the male, pausing to urinate from time to time. Occasionally, a female rocks on her hind legs, rising on the toes of her hind feet, walking stiff legged on all fours with her hind quarters lifted and pausing to sway from side to side by 'marking time' with her hind feet. If the female remains still either in this posture or sitting, the male will begin grooming her, generally in the vicinity of her ears and on her head, and will attempt to mount. Even a receptive female shows some initial antagonism toward the male and, after being mounted, will attempt to move forward, buck or run, eventually dislodging the male. The male has to make several attempts to mount before achieving intromission. An unreceptive female will not exhibit these behaviour patterns but instead, after urine-marking, will actively resist the attention of the male and may even attack him.

When he mounts, the male generally pats the female's rump with his forepaws after moving behind her, and then grips her with his forelimbs just in front of her hind limbs while attempting to intromit. While mounted, the male grips the skin over the female's shoulders or neck with his incisors. The receptive female maintains a lordosis posture thus making intromission easier. The male generally achieves an erection prior to mounting the female; the penis is very long and is easily observed.

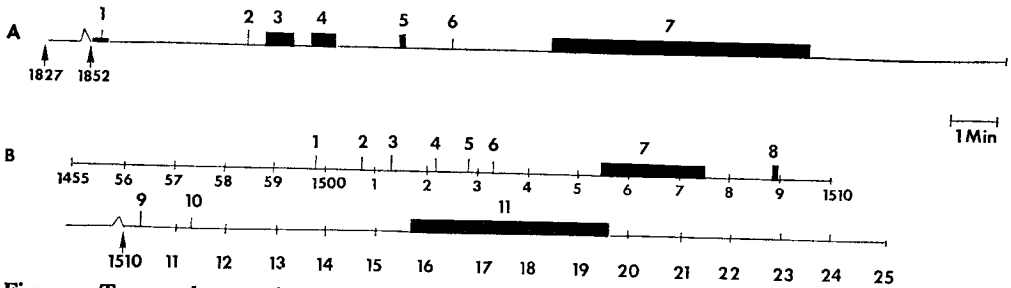

Figure 1. Temporal patterning of mounting by male *Proechimys semispinosus*. In A, the male mounted seven times with ejaculation during the terminal mount. In B, the male mounted eleven times with ejaculation during the terminal mount.

The mounting of the male is not always orientated correctly and during the initial grooming phase, the male may attempt to mount from the front while thrusting at the female's shoulder region.

In the initial stages of courtship, when the female twitters, an aggressive male may respond by growling. Indeed, a twittering female, while being courted by a male in her cage, can induce a growling or gutteral call from a male in a neighbouring cage. The male's growls, however, are dependent on his level of aggressive arousal and may grade into or change to whimpers corresponding to the degree of resistance the female offers. Consequently, it is not uncommon to find that both animals are whimpering, and a dueting situation occurs during copulation.

The male's copulation pattern consists of a multiple series of mounts, with or without intromission, culminating in a terminal mount with intromission which may have a duration exceeding 5 minutes. During the terminal mount, the

16. One-day-old spiny rat *Proechimys semispinosus* at the National Zoological Park, Washington.

thrusting rate of the male decreases during the last 2 minutes; the thrust rate initially may be from 3 to 5 per second decreasing to approximately 1 per second. At its conclusion, the male will generally sit while the female withdraws to a

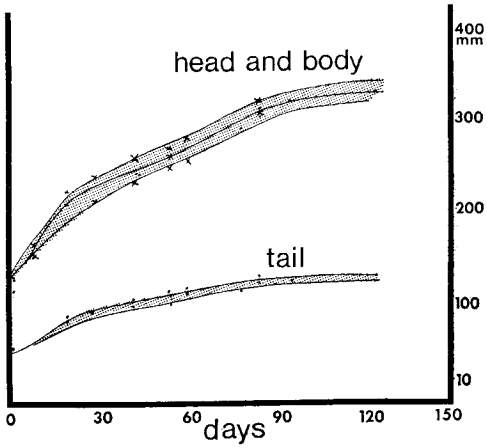

Figure 2. Growth in two litters of *Proechimys semispinosus*. The range of variation is indicated by the upper and lower boundaries of the curve.

corner. After a few moments, the male begins to wash his genitalia. The female also washes her genitalia after a mount with intromission. On one occasion a juvenile female was sitting in the corner after mating when she opened her mouth, inhaled sharply, then exhaled while dipping her head, in a way that suggested a coughing reflex.

REPRODUCTIVE DATA

Litter sizes range from 1 to 5, with an average of 2·8 animals per litter from a sample of 13. The female has three pairs of mammae and could conceivably raise six young. Eight matings took place in the simultaneous encounter cages, and the gestation period has been found to range from 63 to 66 days, with an average of 64·8 days. Thirty-seven young have been born to date; 14 were males and 23 were females, a sex ratio of 1 male to 1·6 females. It has been possible to breed *Proechimys* in almost every month of the year and it appears that, under captive conditions, the animals exhibit no seasonal variation in receptivity. In the field, definite breeding seasons may be shown (Walker, 1964) but this is doubtless due to seasonal abundance of food which may or may not be related to a prevailing climatic condition.

FEMALE NO.	NUMBER OF LITTERS	RANGE (days)	AVERAGE (days)
7	2	65–66	65·5
8	2	63–65	64
11	1	65	
15	1	63	
19	1	66	
23	1	66	

Table 1. Gestation period in spiny rats *Proechimys semispinosus*.

FEMALE NO.	NUMBER IN LITTER	SEX ♂·♀
7	4	2·2
7	5	4·1
7	2	1·1
8	3	0·3
8	3	1·2
8	5	1·4
14	3	1·2
15	1	1·0
19	3	0·3
23	1	1·0
11	1	1·0
10	3	1·2
22	3	0·3

Table 2. Number and sexes of offspring of female spiny rats *Proechimys semispinosus*.

GROWTH AND MATURATION OF YOUNG

The young are born in a precocial condition, fully haired, with eyes open and teeth erupted. The animals begin to feed on solid food almost from the first day but are nursed until about 40 days of age. The earliest age at which conception occurred in a captive-born female was 100 days. The moult to the adult pelage begins at 70 days and may be virtually completed by 125 days of age. Growth begins to slow markedly from about 85 to 95 days of age.

DISCUSSION

Proechimys semispinosus gives birth to precocial young, in common with all other caviomorphs which have been studied to date. The gestation

period and the degree of development of the newborn young of *Proechimys* are approximately equivalent to that shown by the guinea pig *Cavia porcellus.*

The spiny rat urine marks during social encounters and these markings presumably have some communicatory significance; however, there is no ritualised urination at an aggressor as has been described for other caviomorph rodents, such as the Patagonian cavy *Dolichotis patagonum* and the chinchilla *Chinchilla lanigera.* Similarly there is no ritualised urination involved in courtship whereby the male urinates on the female during the initial phases of contact-promoting behaviour such as has been recorded for *Cavia porcellus*, *Chinchilla lanigera*, *Cuniculus paca*, *Myoprocta pratti*, *Dasyprocta aguti*, *Dolichotis patagonum*, and *Erethizon dorsatum* (Kunkel & Kunkel, 1964; Bigami & Beach, 1968; Freiheit, 1965; Morris, 1962; Smythe, pers. comm.; Kirchshofer, 1960; Shadle *et al.*, 1946).

The whining vocalisation produced during initial courtship and sustained throughout mounting, often in a duet pattern, appears to be unique for *Proechimys*, although similar vocalisations have been recorded during the initial courtship phases for *Chinchilla lanigera*, *Cavia porcellus*, and *Erethizon dorsatum. Proechimys* is similar to *Chinchilla lanigera* and *Cavia porcellus* in that the female is initially reluctant to be mounted by the male and does not show a prolonged lordosis; rather the male must attempt to mount several times and, following a mount with ejaculation, the female reverts to nonreceptivity quite rapidly. A long lordosis, such as one finds in Cricetine rodents, e.g. *Mesocricetus auratus*, *Peromyscus maniculatus*, *Mus musculus*, and *Rattus norvegicus* (Eisenberg, 1967) is not to be found in *Proechimys semispinosus.* However, the long mount with ejaculation shown by *Proechimys* differs markedly from the very brief mounts (less than 10 seconds) which are found in *Cavia porcellus* and *Chinchilla lanigera* (Young & Grunt, 1951; Bigami & Beach, 1968). The significance of the long mount with ejaculation in *Proechimys* can not be explained. It is reminiscent of a similar phenomenon described for the heteromyid rodents of the genus *Dipodomys* (Eisenberg, 1963; Eisenberg, 1967).

To date we have been able to breed *Proechimys* to the third generation and we see no barriers to establishing this species as a laboratory resource. The animals may be held in moderately small cages, and with selective breeding it should be possible to develop strains which are more docile, and amenable to reproduction in smaller enclosures. With respect to recruitment its litter size and gestation period place this species on a par with the guinea pig.

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Footnote: Tesh (19) has recently reported success in breeding *Proechimys* by administering hormones (50 units chorionic gonadotropin) to the females prior to the introduction of males. With such treatment, gestations averaged 51 days in contrast to our results using natural oestrus.