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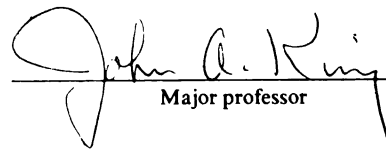
Comparative Life History of Proechimys semispinosus
in two Contrasting Environments in the Republic
of Panama.

presented by

Larry Paul Bowdre

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Ph.D. degree in Zoology


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COMPARATIVE LIFE HISTORY OF PROECHIMYS
SEMISPINOSUS IN TWO CONTRASTING ENVIRONMENTS
IN THE REPUBLIC OF PANAMA

By

Larry Paul Bowdre

A DISSERTATION

Submitted to
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ABSTRACT

COMPARATIVE LIFE HISTORY OF PROECHIMYS SEMISPINOSUS IN TWO CONTRASTING ENVIRONMENTS IN THE REPUBLIC OF PANAMA

By

Larry Paul Bowdre

In the Republic of Panama the spiny rat, Proechimys semispinosus occurs both on the Pacific slope where rainfall is strongly seasonal and on the Caribbean slope where rainfall is less seasonal. Spiny rats were collected for 18 months from Santa Rita de la Chorrera on the Pacific slope and from Almirante on the Caribbean coast. Spiny rats trapped in the field were autopsied each month and two laboratory colonies were established to study the life history characteristics of the two populations.

Spiny rats in Almirante breed the year around. Here the testes of males did not regress in size seasonally and females reproduced the year around. Spiny rats in Santa Rita breed seasonally. From October through January (late wet season and early dry season) the testes of males were regressed in size and females restricted their reproductive activity. During this period only 26% of adult females were reproductively active whereas 89% were reproductively active the remainder of the year.

In the laboratory spiny rats from both sites bred the year around. Those from Santa Rita were smaller, had larger litters, and grew faster than those from Almirante. Length of gestation for both populations averaged 64 days. Litter size was 3.0 and 2.0 for the Santa Rita and Almirante populations, respectively. Males were heavier in weight by 30 days of age. The sex ratio was 50:50 for all laboratory and field populations.

Litter size was positively correlated with maternal weight and length. The weight of neonates was negatively correlated with litter size but not maternal weight. Some females were reproductively active by 60 days of age.

The life history features of the two populations of spiny rat in Panama are discussed with respect to r- and K-selection theory and found to be in agreement with most predictions of the theory.

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At Gorgas Memorial Laboratory I received the unselfish support of the entire scientific and administrative staff. I would especially like to thank Dr. Martin D. Young for his advice and encouragement during the study. Mr. Alexander Clark ably administered the logistic portion of my study. Dr. Pedro Galindo, my advisor in Panama, helped me to adjust to the country and provided much advice and logistic help. Dr. Margaret Grayson kindly provided animal cages and Dr. Aristides Herrer graciously supplied me laboratory space, animal handlers, and his advice and kindness. Dr. John Edgecomb and Dr. Carl M. Johnson and their staff furnished histological sections of testes. Dr. Estorgio Méndez helped identify Panamanian rodents and gave this time and advice generously. I wish to thank Drs. Howard A. Christianson, David C. Baerg, and

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E.W. Zelnick, Chief of the Engineering Division of the Panama Canal Company, provided me with meteorological information for Balboa Heights. Clyde S. Stephens of the Research Department of the Chiriqui Land Company provided meteorological data for Bocas del Toro. The Seccion de Hidrometeorologia, Division de Planeamiento, of the Instituto de Recursos Hidraulicos y Electrificación provided meteorological data for Capiarra and Arraiján.

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INTRODUCTION

The objective of this study was to test the theory of r- and K-selection as an explanation of geographical variation in some aspects of the life history of rodents.

The life history of an organism is a combination of morphological, physiological, ecological, behavioral and reproductive adaptations. Naturalists have long been aware of the great diversity of species and study has revealed that the life history of each is an adaptation to its particular habitat. Darwin (1859) recognized that the diversity of organisms is the result of the great variety of physical and biological environments occupied by organisms and convincingly argued that environments preserve inherited variation through natural selection to perfect adaptation of a species to its habitat.

Some species, however, may occupy a variety of habitats. The ability of organisms to occupy different habitats depends not only on their ecological tolerance but also by local adaptation, i.e., genetic modification through natural selection resulting in genetically different populations within the same species. The evolution of differences in life history patterns is the result of the differential survival and reproduction of individuals

with slightly different heritable traits. Each environment will select organisms with life history patterns best adapted to it. This population differentiation may occur in spite of unrestricted gene flow if selection pressures are sufficient (Camin and Ehrlich, 1958; Ehrlich and Camin, 1960; Endler, 1973).

Rodents provide a good subject for the study of life history evolution because of their great diversity and nearly cosmopolitan distribution.

Geographical variation in the life histories of rodents

In this section I will provide examples of geographical variation among some life history attributes of rodents and show the diversity of explanations offered prior to the initiation of this study.

Litter size was known to be positively correlated with latitude (Lord, 1960; Moore, 1961; Jackson, 1965; Smith and McGinnis, 1968; Kilgore, 1970), and altitude (Hoffman, 1958; Dunmire, 1960; Smith and McGinnis, 1968; Spencer and Steinhoff, 1968). Lord (1960) argued that litter size increases with latitude because increasing latitude leads to more severe winters and consequently increased mortality and lower population density. Litter size increases with latitude because populations of animals respond by increasing reproduction by the principle of Christian and Lemunyan (1957) who showed an inverse relationship between population density and litter size.

Moore (1961) accepted Lack's (1954) hypothesis that litter size is the largest number of young that a parent can feed and will increase with day-length and latitude in a diurnal species. Jackson (1965) supported Lord's (1960) thesis and added that predation is more direct at high latitudes but diffuse (with many buffer species) at low latitudes resulting in stable populations near the carrying capacity of the environment with reduced adult mortality and smaller litters. Smith and McGinnis (1968) concluded that litter size increases with latitude and altitude because mean annual production does not, and litter size must be increased with latitude to compensate for shorter breeding seasons found at higher altitudes and latitudes. Spencer and Steinhoff (1968) believed that litter sizes are small in climates with long reproductive seasons because of the correlation between litter size and adult mortality. In climates with short reproductive seasons a female breeds fewer times in her lifetime, and there is selection for larger litters.

The studies cited above did not control for parity or age and it is now generally known that the litter size of many rodents increases with parity and/or age (Biggers et al., 1962; Williams, 1965). Because of this, all or part of the litter size variation reported by these investigators could be due to different age distributions. Bowdre (1971) did control for parity and reported that litter sizes of Sigmodon hispidus increased with latitude and were larger on sites with seasonal changes in climate

and vegetation regardless of latitude or altitude. Bowdre (1968) reported similar diversity between different sites in Costa Rica but did not control for parity. Generally, throughout Central America the east (Caribbean) coast is evergreen but the west (Pacific) coast is seasonally dry causing the food sources of Sigmodon to deteriorate periodically. On the eastern side of Central America (Sigmodon probably breeds the year around but on the west side breeding is probably restricted to the growing season (Green, 1964; Goertz, 1965; Petersen, 1970; Baker, 1983; Bowdre, 1968; but see Bonoff and Janzen, 1980; Fleming, 1970).

The prevalence of pregnancy has been shown to vary geographically. Lord (1960) noted that breeding was more seasonal in northern than in southern populations of Rattus norvegicus. Neither Lord (1960) nor Jackson (1965) however, found any change in prevalence of pregnancy correlated with latitude in Rattus rattus. Moore (1969) reported that southern species of Nearctic ground squirrels breed twice whereas northern species breed only once each year. Fleming (1969) found that births of Proechimys semispinosus were less seasonal on the wet side than on the dry side of the Isthmus of Panama. Delany and Neal (1969) noted that in Uganda Lophyromys has small litters and a less seasonal breeding period, but Mastomys has large litters and a more seasonal breeding pattern. Other investigators have found populations of Mastomys in other

parts of Africa with less restricted breeding seasons (see Delany and Neal for references). Hoffman (1958) reported that Microtus montanus in northern California has large litters and a short breeding season but Microtus californicus in southern California has smaller litters and a longer breeding season.

Body size was also reported to vary geographically. The body size of small rodents was reported to be larger on islands than on the mainland (Zimmerman, 1950; Hesse et al., 1951; Jewell, 1966; Berry, 1964; Tomich, et al., 1968:361). Tropical species of Peromyscus are larger than most temperate species (Hooper, 1968). Bowdre (1968) noted that Sigmodon hispidus from the wet side of Costa Rica were larger than ones observed on the dry side. Peromyscus from the tropics are known to be larger regardless of age, but the other reports cited above confounded size with age.

Rates of growth and development were shown to vary geographically between species of Citellus. Pengelley (1966) reported that Citellus lateralis collected at 6000 feet had a longer gestation, larger size at birth, and faster rate of development than species of Citellus collected in low altitude deserts. Pengelley explained this as adaptive. King (1958) described differential rates of development between Peromyscus maniculatus bairdii and P. m. gracilis.

The hypotheses posited above to explain geographical

variation in e.g. litter size obviously cannot satisfactorily explain the geographical variation in body size or rates of growth and development. A set of uncoordinated hypotheses explaining life history variation is not as satisfactory as one all-encompassing theory. Such a theory is desirable because it deepens and broadens understanding, unifies diverse phenomena, explaining them by the same underlying processes, and enhances testability (Hempel, 1966; Bunge, 1967).

The theory of r- and K-selection

In this section I will show the logical development of the theory of r- and K-selection and show how predictions of the theory can be deduced from it. The theory of r- and K-selection was invented to explain geographical variation in life history traits. The theory is usually attributed to MacArthur and Wilson (1967) but was outlined earlier by Dobzhansky. Dobzhansky (1950) proposed that natural selection arises from different sources in temperate and tropical environments. In the tropics it arises in a species primarily from interactions with other organisms but in temperate areas it arises mostly from physical forces like cold or drought. Organisms challenged by such physical forces will be characterized by increased fertility and accelerated development.

Analogously, Margalef (1959) noted that natural selection is more directed in early ecological succession

than in later succession. He predicted that more mature communities should be characterized by long-lived species with low reproductive rates. Both Dobzhansky (1950) and Margalef (1959) acknowledged the influence of Schmalhausen (1949) in the development of these ideas.

The theory of r- and K-selection is grounded on two fundamental principles. First, in an uncrowded environment the intrinsic rate of natural increase, r , is the best measure of fitness and under natural selection r will always increase (Fisher, 1930). The intrinsic rate of natural increase is defined by Euler's equation

$1 = \int_0^\infty e^{-rx} l(x)m(x)dx$ where x is age, $l(x)$ is the proportion of those born who survive to age x or more and $m(x)$ is the average number of offspring born to an individual of age x . Second, in a crowded environment the carrying capacity, K , is the best measure of fitness and under natural selection this will always increase (MacArthur, 1962); Crow and Kimura (1970:29); MacArthur and Wilson (1967:146). Increasing K is equivalent to increasing population size with no change in resources or maintaining population size with decreased resources (Cody, 1966). r and K are related by the logistic equation $dN/dt = rN(1 - N/K)$.

Bringing these two principles together, MacArthur and Wilson (1967) argued that in uncrowded environments organisms maximizing r will replace those not maximizing r and in crowded environments organisms maximizing K will

replace those not maximizing K . MacArthur and Wilson reasoned that in seasonal climates the environment is periodically uncrowded and selection is for increasing r (r -selection) but in nonseasonal climates the environment is always saturated and selection is for increasing the carrying capacity (K -selection).

Cole (1954) and Lewontin (1965) showed that selection for increasing r should lead to early maturity and increased fecundity. Smith (1954:283) and Bonner (1965:17) noted the negative correlation found in organisms between rate of development and body size and Rensch (1960:161) demonstrated that length of gestation time, age of sexual maturity, and longevity increase with body size.

Combining the principles of Fisher and MacArthur and adding the assumptions of Cole, Smith, Rensch, Bonner and Lewontin, several predictions can be deduced from the theory of r - and K -selection. If populations of organisms living in seasonal environments are less crowded on the average than those living in nonseasonal environments, the former should experience r -selection (selection for increasing r at the expense of decreasing K). Individuals in this population should breed earlier (and consequently have a shorter gestation, be smaller, have a shorter life span, and reach sexual maturity earlier) and have a greater fecundity (larger litter size than individuals from populations living in a less seasonal site). Since rapid development is more effective in increasing r than increased

fecundity (Smith, 1954; Cole, 1954; Lewontin, 1965), less genetic variance for development time than for fecundity should be expected (Lewontin, 1965:85). The relation between development time (generation time, T), net reproductive rate, R_0 , and r is apparent from the following equations: $R_0 = \int l(x)m(x)dx$, $N_t = N_0 e^{rt}$. If $R_0 = N_t/N_0$ then $R_0 = e^{rT}$ and $r = \ln R_0 / T$. The intrinsic rate of natural increase varies directly as the inverse of generation time but only as the natural logarithm of net reproductive rate.

Method of investigation

There are two scientific methods available for testing this theory, the experimental and the comparative method. Although the experimental method has been used successfully in life history studies (e.g. Tinbergen, 1967), it is not very applicable to a study of the evolution of litter size, body size, etc. in rodents because of the comparatively long generation time of rodents. The comparative method (see Cole, 1954:134; Cain and Harrison, 1958; Tinbergen, 1959, 1963; Lack, 1965) can contradict or support theoretical predictions just as the experimental method does. Although intergeneric or interspecific comparisons are often made, intraspecific comparisons should be more fruitful because of the better control of confounding variables (Lack, 1965:227). With the experimental method one can control the conditions of the experiment and test those that determine the outcome but in a natural

experiment one must determine the conditions which control the outcome.

The test species, *Proechimys semispinosus*

The geographical variation in life history features of rodents reviewed above includes both interspecific and intraspecific comparisons. The interspecific comparisons show the strongest correlations but intraspecific variation is more interesting because it eliminates that part of the differences confounded by phylogeny. For this reason the decision was made to use one species of rodent to test the theory of r- and K-selection.

In 1970 I was offered the opportunity to study the spiny rat, *Proechimys semispinosus*, at the Gorgas Memorial Laboratory in the Republic of Panama. The Republic of Panama provides strongly contrasting environments with overlapping faunas in a space convenient for easy study. Gorgas was interested in my developing a laboratory colony of the spiny rat and learning more about its biology because of its apparent involvement in a number of important human tropical diseases. Study of *Proechimys* appealed to me because I knew from Fleming's (1969) work that it occurred on both the dry and wet sides of Panama and that its breeding season was more restricted on the dry side. Differences that I found in *Sigmodon hispidus* between dry and wet sites in Mexico and Costa Rica suggested to me that I might find similar differences in the spiny rat

in Panama.

The life-history studies reviewed earlier generally emphasized the variation of one life-history attribute. Here I planned to study the geographic variation of several attributes simultaneously.

The species Proechimys semispinosus ranges from southeastern Honduras, east and central Nicaragua and Costa Rica through Panama into South America (Hall, 1981). It is not found in dry western parts of Honduras, Nicaragua, or Costa Rica but it is found in dry western Panama near water courses (Aldrich and Bole, 1937). In South America Proechimys semispinosus is found in Colombia, Ecuador, northern Peru, northwestern Brazil, and southern Venezuela (Moojen, 1948; Mares and Ojeda, 1982:416). Proechimys probably evolved in the Amazonian region of South America during the Miocene (Reig et al, 1980:307), but may not have entered Panama until the late Pleistocene (Webb and Marshall, 1982:43; Rich and Rich, 1983:27).

Populations of Proechimys semispinosus from both Almirante and the La Chorrera area (see Study Areas) are currently considered to be of the same subspecies (Proechimys semispinosus panamensis (Handley, 1966:786; Hall, 1981:873)).

In Panama, the spiny rat, Proechimys semispinosus, or mocangue as it is known locally, is abundant throughout forested areas at lower elevations.

Proechimys semispinosus is similar in size to the

common Norway rat, Rattus norvegicus. An adult male Proechimys ranges from 361 to 507 millimeters in total length and will weigh as much as 610 grams. The tail is less than half of the total length and measures from 141 to 220 millimeters in an adult male. The length of hind foot (from the tip of the longest claw to the heel) varies from 47 to 62 millimeters and the height of the ear from the notch measures from 20 to 30 millimeters in an adult male. Generally an adult female is 5% smaller than the male.

The pelage of the spiny rat is an agouti color evenly distributed on the sides but dark on the mid-dorsal line because of the dark stiff flattened spine-like hairs found there. The underparts of the body, tail, and the posterior of the legs are white.;

In this study I will test the validity of r- and K-theory as an explanation of differences in some life history attributes of Proechimys semispinosus between two seasonally different sites in the Republic of Panama. I will argue that data for Proechimys semispinosus support r- and K-selection theory at the intraspecific level.

STUDY AREAS

Two study areas were selected as sites for live trapping because of their differences in climate and their large populations of Proechimys. One site was located in extreme northwestern Panama near the town of Almirante, 345 kilometers west and 70 kilometers north of Panama City in the province of Bocas del Toro (see Figure 1) and hereafter referred to as Almirante. Another study area was located in central Panama near Santa Rita de la Chorrera, hereafter called Santa Rita, 36 kilometers west and 10 kilometers south of Panama City in the province of Panama (see Figure 1).

Almirante study area

Almirante is a deep port on the Caribbean Sea where a railroad maintained by the Chiriqui Land Company, a subsidiary of the United Fruit Company, brings bananas from the coastal plantations between Almirante and Changuinola. Live trapping of small mammals was confined to the near vicinity of Mile-2 Station located one mile north of Almirante along the railroad. This is a low wet area just above sea level with low hills to the south and west leading to ridges which rise to the continental divide.

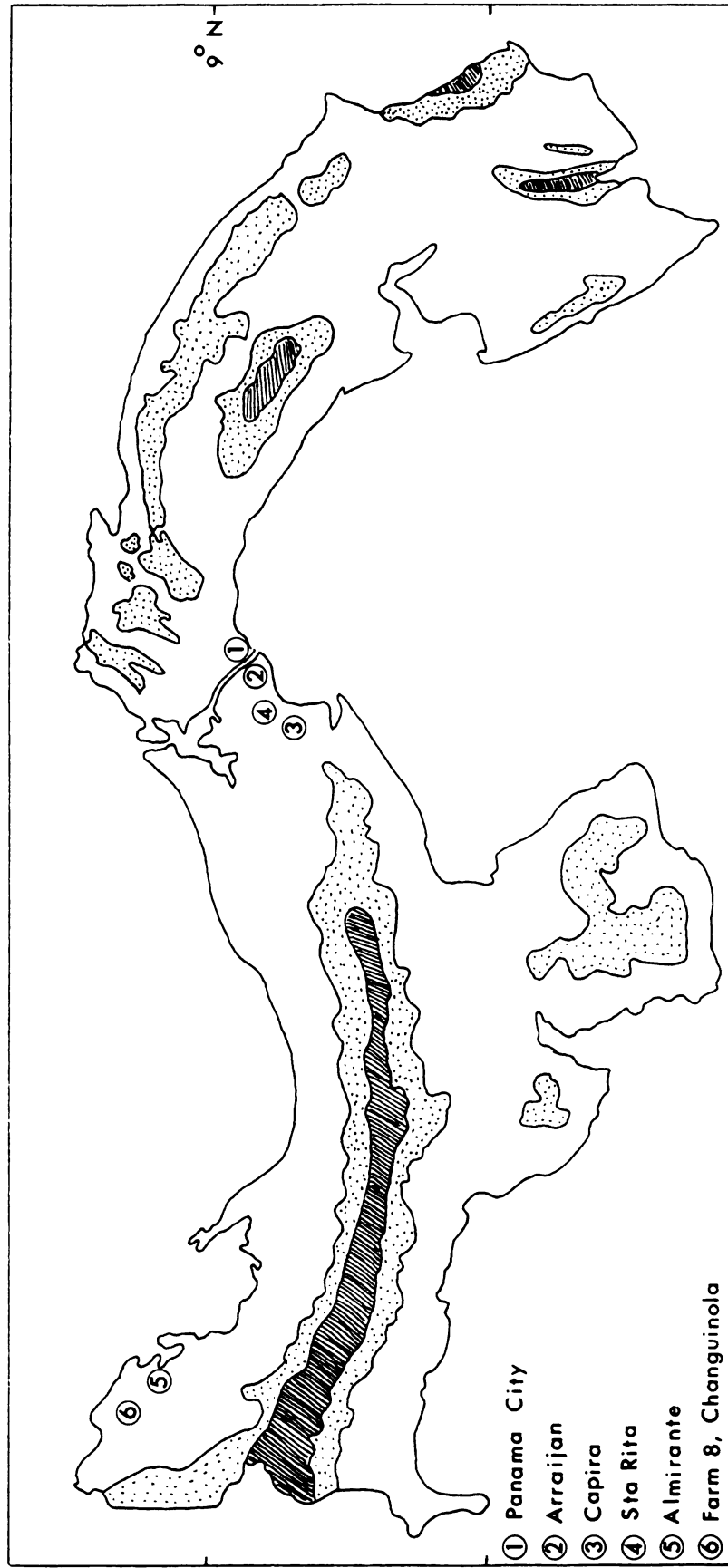


Figure 1. Key study localities in the Republic of Panama.

Climate of the Almirante study area

No climatic data was available for Almirante; however, the Research Department of the Chiriqui Land Company has declared (by personal communication) that the climate of Almirante is nearly identical to that of Farm-8, Changuinola. Rainfall data for Farm-8, Changuinola are shown in Figure 2. Rainfall for northwestern Panama in 1970 and 1971 was above normal and the rainfall total for 1970 was the heaviest recorded in 50 years. The total rainfall from September 1970 through August 1971 was 3483 millimeters whereas the average rainfall from 1926 through 1971 was 2487 millimeters. The total rainfall in 1970 was 3937 millimeters. It is apparent from Figure 2 that Almirante has two wet seasons and two dry seasons but the dry season is not as dry as it is on the Pacific side.

Temperatures in the Almirante area during the period of collections are summarized in Figure 3 and varied from a low temperature of 15.8° Celsius to a high of 33.6° Celsius while the monthly averages of the daily low temperature varied only 2° Celsius ($20-22^{\circ}$ Celsius) and the high only 1° Celsius ($32-33^{\circ}$ Celsius).

Vegetation of the Almirante study area

The Caribbean lowlands surrounding Almirante fit into the Tropical Moist Forest of Holdridge and Budowski (1956). These lowlands are swampy since water tables are high during part or all of the year and there is a series of plant

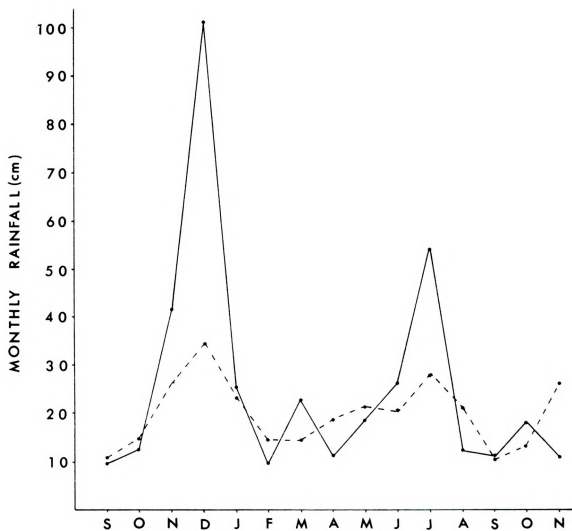


Figure 2. Rainfall recorded at Farm-8, Changuinola, Bocas del Toro, Panama during the years 1970-1971. Dotted line indicates 45 year average.

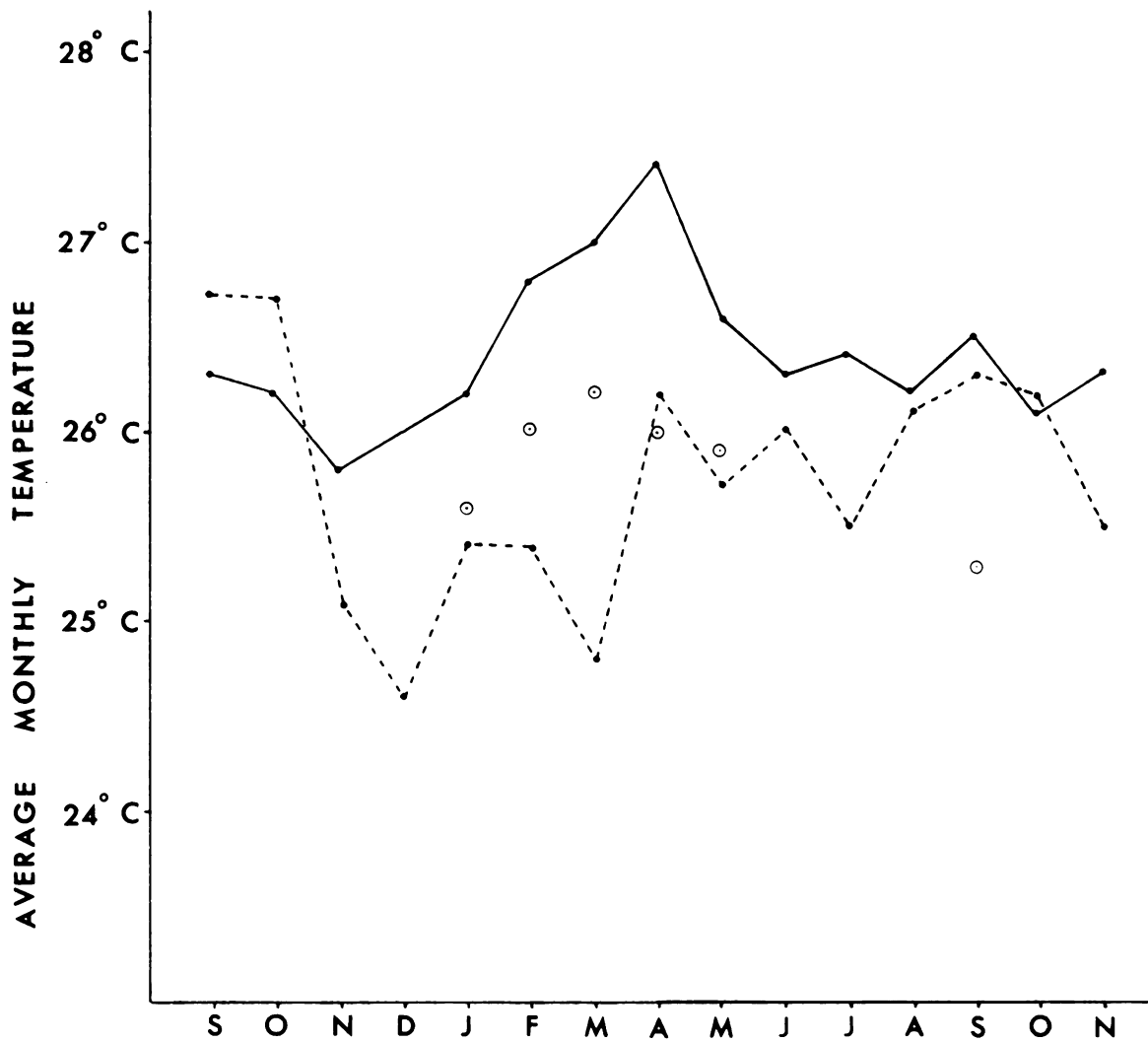


Figure 3. Average monthly temperature at Balboa Heights (solid line), Changuinola (dashed line), and Capira (circles). This statistic was obtained by averaging daily maxima and minima.

associations recognized by Holdridge and Budowski (1956) dependent on the height of the land above the water table and the salinity of the water. The mangrove association is found in the lowest areas where the water is more saline and consists of the red mangrove (Rhizophora mangle), the black mangrove (Avicennia marina), and the white mangrove (Languncularis racemosa). Nearly pure stands of orey (Camptospermia panamensis) which is tolerant of brackish water occurs extensively over the area just above sea level in the orey association. On slightly higher ground where alluvial fresh water stands much of the time, there are large forests of the silica palm (Raphia taedegeera) which form the silica palm association. Still farther inland is another swamp association, the cerillo-sangrillo association where cerillo (Symphonia globulifera) and sangrillo (Pterocarpus officinalis) are common in the upper story and the coquillo palm (Manicaria saccifera) is common in the lower canopy.

Mile-2 Station consists of a small wooden house used occasionally by Gorgas Memorial Laboratory as a field station and located on the west side of the railroad tracks. North and south of the station there are numerous freshwater marshes which become more and more brackish as one approaches Almirante. The freshwater marshes are surrounded by dense impenetrable stands of Calathea, Heliconia, Cecropia, and Piper among others. A portion of the silica palm association can be seen immediately across

the railroad tracks east of the station. This association then dominates the region between the railroad and the coast to the east. Behind the station to the west the ground slopes gradually upward and is covered with cerillo and sangrillo in the upperstory and the coquillo palm (Manicaria saccifera) in the understory. The upperstory trees are thinly distributed here allowing a dense undergrowth including the coquillo palm and numerous vines and shrubs. Most trapping was done along the railroad tracks, and along the edges of the clearings and marshes in stands of bamboo and Heliconia. Unlike Santa Rita the vegetation in Almirante is lush and green the year around.

Fauna of the Almirante study area

Mammals trapped on the Almirante site and returned to Panama City are shown in Table 1. This fauna was limited by both trap choice and trap size.

Santa Rita study area

Santa Rita is a small rural community located on the Pacific slope. This region lies between 50 and 200 meters above sea level and is characterized by low rolling hills cut by frequent seasonal streams emptying into the Rio Caimito which has water the year around.

Table 1. Mammals trapped on the Almirante and Santa Rita study areas. Numbers of individuals brought back to the laboratory for study are indicated in parenthesis.

Almirante study area

Marsupials

Philander opossum (1)

Didelphis marsupialis (10)

Rodents

Oryzomys caliginosus (30)

Nectomys alfari (2)

Sigmodon hispidus (80)

Rattus rattus (5)

Proechimys semispinosus (176)

Santa Rita study area

Marsupials

Caluromys derbianus (36)

Marmosa robinsoni (10)

Philander opossum (85)

Metachirus nudicaudatus (3)

Didelphis marsupialis (175)

Chironectes minimus (1)

Rodents

Sciurus granatensis (1)

Sciurus variegatoides (1)

* Liomys adpersus (0)

Nectomys alfari (2)

Zygodontomys microtinus (24)

Sigmodon hispidus (127)

Rattus rattus (6)

Proechimys semispinosus (963)

Diplomys labilis (37)

* Scores were trapped but released immediately without being tallied.

Climate of the Santa Rita study area

No climatic data were available for Santa Rita; however, there was good data for Balboa Heights, Canal Zone, 35 kilometers east and 5 kilometers north of Santa Rita and enough data from Arraijan 24 kilometers east and 5 kilometers north of Santa Rita and from Capira 16 kilometers south of Santa Rita to establish that the region surrounding Santa Rita has a similar rainfall pattern to Balboa Heights (Figure 4). Comparison of Figures 2 and 4 shows that the verano dry season (mid-December through mid-April) in the Santa Rita area is more severe than it is in the Almirante area. At the end of 1971 the ten year average rainfall for Balboa Heights was 181.6 centimeters per year compared to a 45 year average of 248.7 centimeters per year for Farm-8, Changuinola.

Temperatures for the Santa Rita area are shown in Figure 3 and varied from a low of 20° Celsius to a high of 34° Celsius while the monthly averages of the daily low temperature varied only 1° Celsius (22-23° Celsius) and the high only 2° Celsius (32-34° Celsius). Available data for Capira indicate a temperature regime almost identical to Balboa Heights. The temperature varied from a low of 20° Celsius to a high of 33° Celsius during 1971 while the monthly averages of the daily low temperature varied 2° Celsius (20-22° Celsius) and the high 1° Celsius (31-33° Celsius).

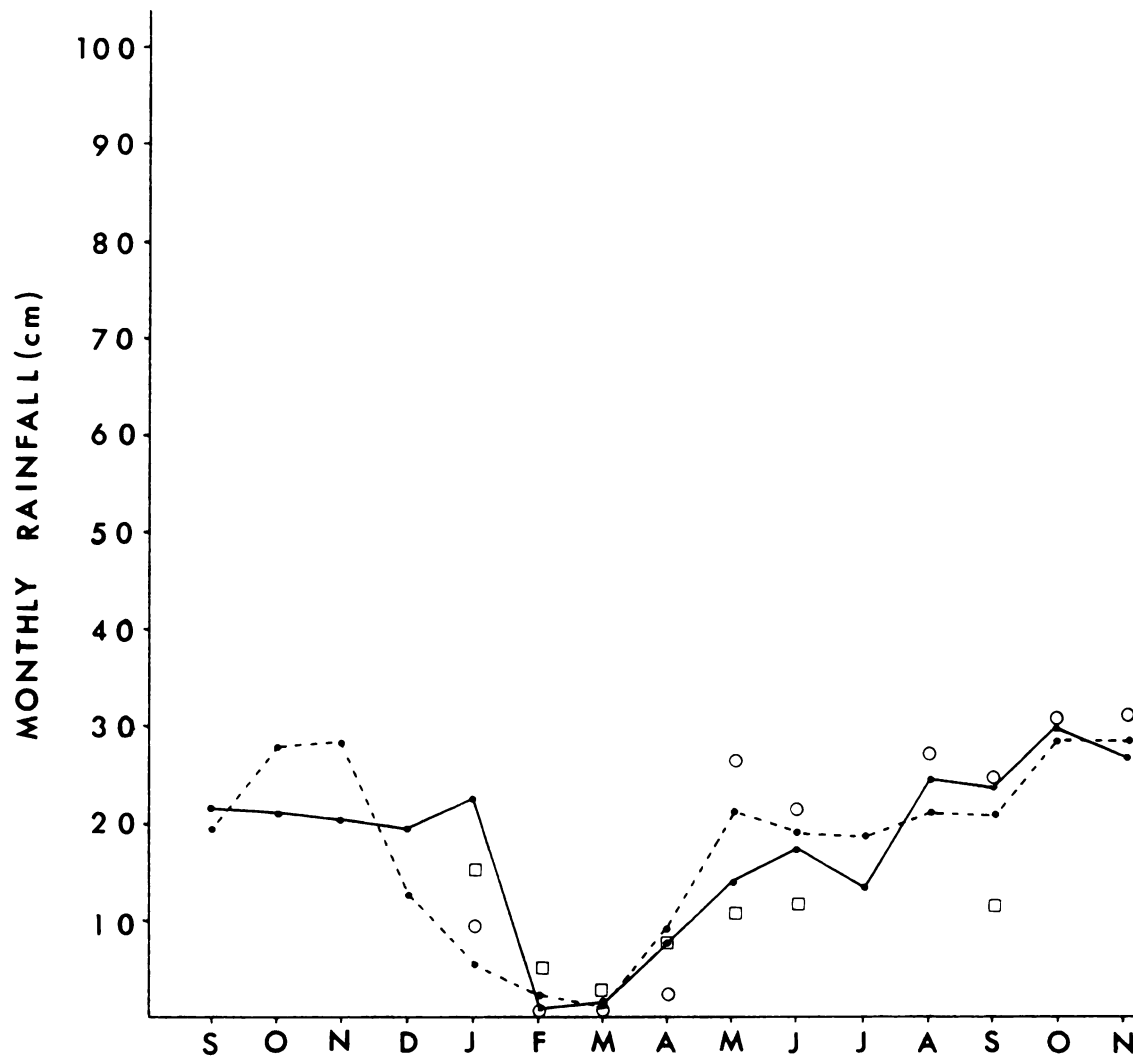


Figure 4. Rainfall recorded in the area of Santa Rita de la Chorrera during 1970-1971 (solid line) and 10 year means for Balboa Heights (dotted line). Squares and circles represent data from Capira and Arraijan, respectively.

Other climatic data from Balboa Heights show that during the dry season there is more sunshine, the relative humidity drops, and wind velocities increase. The reduced rainfall coupled with increased winds and sunshine intensifies the dry season in Santa Rita and causes the soil there to harden and crack.

Vegetation of the Santa Rita study area

Santa Rita is included in the Tropical Moist Forest of Holdridge and Budowski (1956:94) as is Almirante. In Santa Rita most of the forest has been removed and only small patches of the original forest remain on some hilltops and along a few streams and rivers. The area is covered instead, by numerous small farms where citrus, avocados, mangos, bananas, pineapples, rice, corn, yucca, ñame, and sugarcane are cultivated. Some of the more prosperous farms have a few dairy or beef cattle. The most conspicuous trees on the farms are citrus trees, the corozo palm, maintained for thatch, and the mango tree. Along the streams, the conspicuous vegetation includes espavé (Anacardium excelsum) and several species each of Ficus, Inga, Cecropia, Heliconia, Bursera, Piper, Luehea, Capparis, Chrysophyllum, Terminalia, Bixa, Amaranthus, Carica, and Bambusa. Grass is common about pastures around dwellings, along fence rows, and surrounding cultivated fields. Although the annual rainfall in the study area is sufficient to maintain some of the species

of plants indicative of the Tropical Moist Forest, the months of January, February, and March are generally very dry. Much of the herbaceous vegetation dies including grasses and many of the trees drop their leaves. The area remains dry until the rains return in April.

Although Holdridge and Budowski (1956) placed both the Almirante and Santa Rita areas in their Tropical Moist Forest, they recognized that the dry season is more marked on the Pacific side than on the Caribbean side. The severity of the dry season can be observed by examining the total rainfall for the months of February and March. The average for Cristobal (on the Caribbean coast of the Canal Zone) is 76mm, the average for Barro Colorado (in the Canal) is 90mm, Capira registered 76mm, but Arraijan registered 18mm and Balboa Heights averages 32mm of rainfall. Moist forests are found in Cristobal, Barro Colorado, and Capira, and dry forests are found in Arraijan and Balboa Heights. During the same period Almirante averages 394 mm of rainfall. Although the area between Capira and Arraijan appears much different than the Almirante area in the dry season, they do have several tree species in common including Anacardium excelsum, Cecropia obtusifolia, and Luehea seemannii. These are found along streams in the Santa Rita area. The dry season is shorter and less severe between Capira and Arraijan because here the elevated "backbone" of the Isthmus of Panama is low allowing for some Caribbean rains to reach this part of the

Pacific coast of Panama. To the west of Capira and to the east of Arraijan, however, the dry season is much longer and more severe, and many trees typical of the Moist Tropical Forest such as Anacardium excelsum cannot survive there.

Fauna of the Santa Rita study area

Mammals trapped on the Santa Rita study site and returned to Panama City are shown in Table 1. Like the Almirante site this reported fauna was limited by both trap size and trap bait choice.

METHODS AND MATERIALS

Initial effort was made to find a site on the wet Caribbean side of the Isthmus of Panama and one on the dry Pacific side where Proechimys occurred in large numbers.

Wet site

Almirante (Figure 1) was chosen as the wet site because of the abundance of Proechimys and because this was the home of a reliable collector that had worked part time for Gorgas Memorial Laboratory. Small mammals were collected intermittently from late 1970 to early 1972 and sent via railroad to Changuinola and then by air to Panama City.

Dry site

Attempts to find large populations of Proechimys near Panama City failed. In trapping near Tocumen, 20 kilometers northeast of Panama City during August and September of 1970 and near Juan Diaz 11 kilometers northeast of Panama City during October 1970, I found only small populations of Proechimys. Similarly, trapping at Juan Mina 36 kilometers north and 16 kilometers west of Panama City during September and October of 1970 revealed only a small

population of Proechimys.

During September 1970 a part-time animal collector for some of the staff members at Gorgas Memorial Laboratory reported large numbers of Proechimys near Santa Rita (Figure 1). Santa Rita is 55 kilometers from Panama City by automobile and can be reached the year around since 40 kilometers of the way is an all-weather highway and the last 15 kilometers is accessible by a gravel road which proved to be passable even in the wet season. An animal collector who lived on a small finca one kilometer west of Santa Rita was hired to obtain small mammals in the area. Animals were trapped from late 1970 to early 1972 in 15x15x18 and 23x23x70 centimeter folding live traps baited with banana. Traps were set within walking distance of the finca and transported using a home-made cart. After being carted to the finca, mammals were placed in 14x18x26 centimeter cages hand-made out of one-half inch hardware cloth and sheet metal. These were kept in a spacious thatched shelter open on four sides and made specially for this purpose. Rice hulls were used as bedding and animals were given Wayne Lab-Blox® and water ad libitum. Their diet was supplemented with oranges, yucca, ñame, and bananas. These animals were picked up and transported to Panama City once each week.



Field data

After arriving in Panama City animals were taken to the Gorgas Memorial Laboratory annex located behind the United States Embassy on Calle 37.

Females were palpated for pregnancy and held until parturition if pregnant. The remaining females were anesthetized with ether to relax their abdominal muscles and palpated again. Nonpregnant females were euthanized by chloroform and autopsied. Some females and males were selected for breeding in the laboratory. Later in the course of the study as laboratory space declined, even obviously pregnant females were euthanized and autopsied.

The length of one inguinal nipple, one lateral nipple, and the length and width of the clitoris were recorded to the nearest millimeter. The mammary tissue was examined and recorded as not developed or well-developed. The vaginal opening was recorded as closed, partly open, or open. If the vaginal area was swollen and dry or if swollen and wet, this was recorded. Among several females, vaginal smears were made by sampling the vaginal cells using a physiological saline-soaked cotton swab. These smears were examined under a microscope and the cells present were recorded. Since vaginal smears made with saline often form fern patterns when dry and since it has been suggested that these ferns may indicate estrogen levels in the female, these were photographed for later study.

The reproductive tracts of females were fixed in AFA and cleared using the technique of Orsini (1962). After being cleared, embryos and recent scars were counted and their distribution in the horns of the uterus was recorded.

Males were routinely euthanized and autopsied unless held for breeding. They were identified as testis scrotal, cauda epididymus scrotal, or nonscrotal (see discussion on the scrotum in Reproduction in field captured males). The testes were removed, the length of the left testis was measured to the nearest millimeter, and the testes were preserved by fixing them in 10 per cent formalin and later placed in 70 per cent alcohol.

Testes were analyzed among field-caught males by first grouping the material into Almirante and Santa Rita data. These two groups were each divided into material collected October through January and material collected February through September. Within each of the resulting four groups the testes lengths and body lengths were transformed using natural logarithms. The length of the left testis was then regressed by simple linear regression on body length. Within each site-season group the testes measurements were adjusted to the mean body length by the expression $y_{a_i} = y_i - b_1(x_i - \bar{x})$ where b_1 is the slope of the regression equation. The adjusted testes lengths are summarized for each of the four groups by means and 95% confidence intervals.

Dead animals were weighed to the nearest tenth of a gram on a triple-beam balance, and measured to the nearest millimeter. All measurements were made by the investigator and taken on relaxed animals just after death. Measurements included total length, tail length, length of hindfoot, and height of ear from the notch. These are standard measurements used by mammal preparators and are described in Hall (1981).

The age of field animals was estimated by comparing their body length (total length minus tail length) with the mean body length of known-age laboratory-reared animals of the same sex and of stock originating from the same site. See Growth rate for equations relating age and body length among laboratory born spiny rats. The month of conception for each field-captured spiny rat was estimated by noting its date of capture, estimating its age using laboratory growth-data, and then summing its estimated age and 64 days gestation and subtracting this from its date of capture.

Both males and females were examined for lesions on the extremities and if lesions were present, these animals were referred to investigators at Gorgas Memorial Laboratory studying leishmaniasis.

Laboratory data

Animals held in the laboratory were placed in 14x18x26 centimeter stainless steel cages and placed in



a spacious room open and covered by a wire screen on the north and west (but shaded from the sun by a porch roof). Here animals were exposed to ambient temperature and natural photoperiod. Chopped wood, rice hulls, or Absorb-Dry® was used as bedding. Animals were fed Wayne Lab-Blox® and given water ad libitum. Their diet was supplemented with spinach greens, oranges, and bananas. Cages were cleaned by washing them with soap and water and replacing the litter once each week or earlier if soiled. In the laboratory Proechimys were generally kept 1 or 2 animals to a cage. Other mammals collected at Santa Rita or Almirante were also transported to Panama City and kept in the same room as Proechimys.

All animals were exposed to similar temperatures during their confinement in the laboratory. The temperature extremes in Panama City are generally 1° Celsius lower and 1° Celsius higher in the dry season than they are in the wet seasons. The monthly mean percent relative humidity (based on the mean of the daily averages of the maximum and minimum values) averages 11 percent lower in the dry season. All animals were handled as uniformly as possible to keep variation at a minimum.

Pregnant females held in the laboratory were checked for young three times daily, and new born were counted, sexed, and toe-clipped for identification. Young were weighed to the nearest tenth of a gram and measured to the nearest millimeter on days 0, 5, 10, every ten days

until 100 days of age and then every 20 days until 200 days of age. Length measurements included total length, body length, hindfoot length, and ear length as described previously. The progress of the post-juvenile molt was fully described on the days of measurement. Observations were made to determine when the testes of males descended and when the vaginal closure membrane of females was first perforate. This membrane is perforate only at estrus and parturition (Weir, 1973).

The length of gestation was determined by selecting females with perforate vaginas and pairing them with adult males and placing them in 25x25x35 centimeter cages. Vaginas were checked each day of the pairing for the presence of spermatozoa by microscopic examination of vaginal smears made by swabbing vaginas with cotton swabs soaked in physiological saline. When spermatozoa were observed in the vaginal smears, males were separated from the females. Corroborative evidence of length of gestation was obtained by noting the length of the time interval between successive litters when males were separated from the female on the day of birth.

Body length growth data from spiny rats reared in the laboratory were used to estimate the age, month of birth, and month of the conception (using 64 days as the length of gestation) of every field captured male and female.

Occasionally rats were bled to search for blood



parasites. Rats were supplied at various time for feeding mosquitos or provided to MARU (Middle American Research Unit) in the Canal Zone for virus studies and to the Virus Department at Gorgas Memorial Laboratory for similar work. Others were occasionally provided for the pathology department at Gorgas to be sent to the United States.

Because of the small dispersion of many of the measurements of length and weight, the standard errors are expressed to more decimal places than the number of significant figures in the means; this does not imply that these estimates are more precise than the original measurements. Many of the measurements considered in this study are discrete integers and can only be approximately normally distributed. Two-tailed tests are used throughout for all statistical analyses. All calculations were performed on a hand-held TI-59 calculator. Statistical tables provided in Steel and Torre (1960) were used to determine significance levels.

LABORATORY RESULTS

Gestation Period

A total of 50 female Proechimys were paired with males and checked daily for sperm for a total of 1100 rat-days. Sperm was observed in the vaginas of 6 Almirante females and 5 Santa Rita females that produced litters of young in the laboratory. Santa Rita spiny rats were born an average of 64.2 days (63, 64, 64, 64, and 66) after sperm was observed and Almirante young were born after 64.7 days (63, 64, 65, 65, and 66) of gestation.

When males were left with females through the gestation period and removed the day after parturition, peripartum mating occurred and a second litter was produced after an average interval of 63.5 days (63 and 64) for Santa Rita females and 64.0 days (64, 64, 64, and 64) for Almirante females.

Eighteen Santa Rita females and 11 Almirante females bred in the laboratory without being observed and gestation could not be determined.

Litter size

Among pregnant spiny rats trapped near Santa Rita and brought to the laboratory the mean litter size was



3.0(SE=0.12; R=1-6; N=68) for those giving birth and the mean embryo count was 3.0(SE=0.09; R=1-7; N=126) for those autopsied. There was no significant difference among these means ($F=0.01$; $p>0.05$; d.f.=1,192). Among pregnant spiny rats trapped near Almirante and brought to the laboratory the mean litter size was 2.0(SE=0.21; R=1-5; N=24) for those giving birth and the mean embryo count was 2.1(SE=0.15; R=1-4; N=22) for those autopsied. There was no significant difference among these two means $F=0.27$; $p>0.05$; d.f.=1,44). Among pregnant spiny rats trapped in Santa Rita and Almirante, litter size and the number of embryos were larger for Santa Rita ($F=19.34$; $p<0.005$; d.f.=1,90; and $F=13.37$; $p<0.005$; d.f.=1,146 for litter size and embryo count, respectively). However, litter size in both populations is significantly related to maternal weight after parturition ($F=8.32$; $p<0.01$; d.f.=1,26 and $F=7.69$; $p<0.025$; d.f.=1,18 for Santa Rita and Almirante respectively), and embryo count is significantly related to maternal body length at autopsy for Santa Rita ($F=10.26$; $p<0.005$; d.f.=1,123) but not Almirante ($F=4.05$; $p>0.05$; d.f.=1,23). Furthermore Santa Rita mothers were heavier than Almirante mothers at parturition ($F=24.88$; $p<0.005$; d.f.=1,46), and Santa Rita mothers were larger than Almirante mothers in body length at autopsy $F=8.00$; $p<0.005$; d.f.=1,148). Covariance analysis indicated that the litter size differences between Almirante and Santa Rita merely reflected the differences in maternal body

weight ($F=0.14$; $p>0.05$; d.f.=1,45). The same analysis of the number of embryos found at autopsy, however, showed a significant difference in embryo count independent of maternal body length ($F=13.97$; $p<0.005$; d.f.=1,147).

Growth and development

Ninety-three female spiny rats were pregnant when captured and gave birth to litters in the laboratory. Another 37 females conceived in the laboratory and gave birth to live litters.

Size at birth

There were no significant sexual differences in the average individual body weights of newborn from Santa Rita ($F=0.54$; $p>0.05$; d.f.=1,86 litters) or Almirante ($F=1.43$; $p>0.05$; d.f.=1,27 litters). Average individual body weights of Santa Rita newborn were significantly negatively correlated with litter size ($r_{23.4}=-0.46$; $t=-2.53$; $p<0.02$; n-k=28 litters) but not significantly correlated with maternal weight ($r_{24.3}=-0.006$; $t=-0.03$; $p>0.05$; n-k=28 litters). Average individual body weights of Almirante newborn were significantly negatively correlated with litter size ($r_{23.4}=-0.53$; $t=-2.76$; $p<0.02$; n-k=20 litters) but not significantly correlated with maternal weight ($r_{24.3}=-0.07$; $t=-0.32$; $p>0.05$; n-k=20 litters). Covariance analysis of mean individual body weight of newborn versus litter size showed that newborn from Santa Rita

were significantly lighter in weight than those from Almirante ($F=4.93$; $p<0.03$; d.f.=1,94 litters) independent of litter size.

Growth rate

Growth in body weight between birth and twenty days of age was not significantly correlated with weight at birth, litter size, or maternal weight (Table 2). There were no significant sexual differences in body weight growth between ages 0 and 20 days for either Santa Rita ($F=2.32$; $p>0.05$; d.f.=1,86 litters) or Almirante ($F=0.11$; $p>0.05$; d.f.=1,27 litters). There were no site differences in body weight between ages 0 and 20 days for either males ($F=1.64$; $p>0.05$; d.f.=1,55 litters) or females ($F=0.55$; $p>0.05$; d.f.=1,59 litters). Analysis of growth by linear regression of $\ln(\text{body length})$ on $\ln(\text{age})$ resulted in the following equations:

Santa Rita

$$\begin{array}{lll} \text{Males} & y=4.408(0.008)+0.204(0.002)x & r^2=0.94 \\ \text{Females} & y=4.407(0.019)+0.195(0.002)x & r^2=0.97 \end{array}$$

Almirante

$$\begin{array}{lll} \text{Males} & y=4.471(0.013)+0.197(0.003)x & r^2=0.95 \\ \text{Females} & y=4.469(0.011)+0.184(0.003)x & r^2=0.95 \end{array}$$

Growth rates, estimated by the slopes of the above regression equations, were significantly greater for males for both Santa Rita ($t=3.51$; $p<0.001$; d.f.=1491) and Almirante ($t=2.82$; $p<0.01$; d.f.=422). Males were significantly

Table 2. Partial regression coefficients for (1) growth in body weight between ages 0 and 20 days, (2) body weight at birth, (3) litter size, and (4) maternal weight.

	Santa Rita						Almirante					
	Males			Females			Males			Females		
	r	t	n-k	r	t	n-k	r	t	n-k	r	t	n-k
$r_{12.34}$	0.29	1.06	12	0.39	1.45	12	0.13	0.33	6	0.01	0.03	5
$r_{13.24}$	0.04	0.14	12	-0.30	-1.11	12	0.19	0.47	6	0.48	1.22	5
$r_{14.23}$	0.20	0.70	12	0.19	0.28	12	-0.19	-0.46	6	-0.43	-1.07	5

larger than females by day 30 in Santa Rita ($\underline{F}=8.83$; $p<0.005$; d.f.=1,96 litters) and significantly larger by day 80 in Almirante ($\underline{F}=12.04$; $p<0.005$; d.f.=1,25 litters). Growth rates, estimated by the slopes of the above regression equations, showed that females from Santa Rita grew significantly faster than Almirante females ($\underline{t}=3.29$; $p<0.01$; d.f. 966), but no significant differences in body length were found between Almirante and Santa Rita females for any age. There was a significant difference in growth rate between Santa Rita and Almirante males ($\underline{t}=2.01$; $p<0.05$; d.f.=875), and Almirante males were significantly larger (e.g., $\underline{F}=5.86$; $p<0.025$; d.f.=1,60 litters on day 5 and $\underline{F}=9.01$; $p<0.005$; d.f.=1,50 litters on day 100).

Molt

Molt comparisons between males and females from Santa Rita and Almirante are shown in Table 3. The molt began earlier among females than among males, but there was no discernible difference between sites.

Sexual maturity

The earliest vaginal perforations observed among Almirante and Santa Rita females born and reared in the laboratory were 60 days and 70 days of age, respectively. The percentages of females found perforate for the first time on each day of observation are shown in Table 4. A significantly greater proportion of Almirante females

Table 3. Comparisons of the rate of post-juvenile molt for male and female spiny rats from Santa Rita and Almirante. Age is measured in days.

Age	Stage of molt	Percentage			
		Santa Rita females	Santa Rita males	Almirante females	Almirante males
40	Molt has begun.	73%	5%		
50	Molt has begun.	100%	82%		
60	Molt has progressed up rostrum halfway or to the eyes. Molt just on tip of rostrum and there are patches around the eyes and ears.	40%	29%		33%
		60%	71%		66%
70	Molt between eyes. Molt above eyes. Molt not to eyes.	30% 52% 8%	50% 27% 23%	22% 78%	28% 71%
80	Molt to ears and there is a small dorsal patch.	86%	78%	100%	83%
90	Adult pelage. Adult pelage on all but posterior if flanks. Adult pelage not on sides. Five to nine cm. dorsal patch. Dorsal patch just appears. No dorsal patch.	2% 14% 36% 43% 4% 0%	0% 8% 34% 46% 8% 3%	50% 25% 25%	33% 66%

Continued on next page.

Table 3 (cont'd).

Age	State of molt	Percentage			
		Santa Rita females	Santa Rita males	Almirante females	Almirante males
100	Adult pelage.	19%	2%	12%	
	Adult pelage except back legs.	17%	4%		
	Adult pelage except posterior of sides.	4%	23%	12%	
	Adult pelage except sides or legs.	44%	50%	50%	78%
	Five to nine cm dorsal patch.	13%	21%	25%	22%
120	Adult pelage.	92%	68%	80%	83%
	Adult pelage except posterior of sides.	6%	23%	20%	17%
	Adult pelage except sides.	2%	9%		
Number of observations		244	203	38	45
Number of animals observed		82	58	18	17



Table 4. Percentage of laboratory reared female spiny rats with perforate vaginas seen each observation day.

Age	Almirante	Santa Rita	$G_{adj.}^1$	p
60	33% (1/3)	0% (0/23)	0.96	> 0.05
70	27% (3/11)	6% (1/18)	1.14	> 0.05
80	67% (4/6)	0% (0/9)	5.38	< 0.025
90	40% (2/5)	7% (3/44)	1.76	> 0.05
100	70% (7/10)	13% (6/45)	10.04	< 0.005
110	100% (1/1)	33% (3/9)	0.04	> 0.05
120	78% (7/9)	34% (15/44)	4.18	< 0.05

1. The 2x2 test of independence using the G-statistic with Yate's correction (Sokal and Rohlf, 1969:591).

were perforate on three of these observation days. By the age of 120 days, a significantly greater proportion of Almirante females (11/18) than Santa Rita females (10/35) had been observed perforate on some previous observation day ($G_{adj.}=3.96$; $p<0.05$; d.f.=1). The mean day of perforation could not be determined because observations were not made after 120 days and many Santa Rita females were still imperforate at that age (Table 4).

Field data (Table 5) indicated that females from both populations became reproductively active (perforate, pregnant, or with placental scars) at approximately the same size.

In the laboratory, 7 pairs of laboratory reared spiny rats from Almirante and 11 pairs of laboratory reared animals from Santa Rita bred successfully. The earliest mating among Santa Rita rats was 120 days of age when two siblings bred successfully. One Almirante female bred at 120 days of age and one male bred at 130 days after the two were paired at 100 days of age.

Testes descended earlier among Santa Rita males (Table 6).

Growth and development

New born Proechimys are covered by a thick pelage. The head is dark but the back is gray because of white hairs (about 4 millimeters long mixed in with the short

Table 5. Fraction of field captured females reproductively active (perforate, pregnant, or with placental scars) on arrival at the laboratory.

Body length	Almirante	Santa Rita	$G_{adj.}^1$	P
180-189 mm	0/3	0/13		
190-199 mm	1/2	2/11	0.005	>0.05
200-209 mm	3/4	5/16	1.04	>0.05
210-219 mm	3/3	13/23	0.76	>0.05
220-229 mm	5/5	9/16	1.87	>0.05
230+ mm	22/27	171/202	0.02	>0.05

1. The 2x2 test of independence using the G-statistic with correction (Sokal and Rohlf, 1969:591).



Table 6. Percentage of laboratory born males with descended testes at four ages.

Age	Santa Rita	Almirante	$G_{adj.}^1$	p
70	4% (2/45)	0% (0/14)	-0.02	>0.05
80	20% (8/39)	7% (1/14)	0.58	>0.05
90	56% (26/46)	12% (1/8)	3.91	<0.05
100	75% (33/44)	89% (8/9)	0.23	>0.05

1. The 2x2 test of independence using the G-statistic with Yates' correction (Sokal and Rohlf, 1969:591).

dark hairs (about 1 millimeter in length). The ventral surface is pink and covered with short white hairs with a few longer ones (about 4 millimeters long). Vibrissae (25 to 30 millimeters long) are conspicuous on the rostrum and above the eyes (15 to 22 millimeters long).

Within minutes of birth the ear pinnae unfold revealing the already perforate auditory meatus. The eyes open soon after birth, but occasionally one or both eyes will remain closed for a few hours. The tips of the toenails are always white at birth and this marking persists for a day and was used occasionally to time births not observed directly. The incisors have usually erupted before birth but in two instances were still covered by a thin membrane at birth. Although no cheek teeth are visible at birth spiny rats will nibble at solid food within hours of birth.

Molt

Juvenile Proechimys semispinosus have a brown pelage of thin aristiforms (guard hairs) and setiforms (underfur). The post-juvenile molt begins as agouti-colored hairs appear on the anterior rostrum, below the eyes and ears. The agouti coloration moves up the rostrum as the patches expand. The back is still covered with juvenile pelage with soft aristiforms raised above the surface, but if



the skin of the back is examined by parting the fur, short black hairs can be seen just erupting. The agouti coloration continues to expand on the head as agouti hairs appear above the eyes and in front of the ears. At this stage of the molt the adult pelage has advanced up the rostrum until it is almost to the eyes. The agouti-colored pelage continues moving up the rostrum until it is between or even above the eyes to the ears. Next, the agouti-colored setiforms and flattened dark-colored aristiforms appear on the back forming a conspicuously dark shiny oval patch. The agouti-colored adult pelage continues up the head until it is between the ears. The dorsal patch expands, moving to the head and down over the shoulders to the front legs and down and back over the sides until finally the rump, hips, and hind legs are covered by the agouti-colored adult pelage.

Sex ratio

Laboratory born spiny rats from Almirante and Santa Rita exhibited a 50:50 sex ratio (Table 7).

Lactation

All females observed but one had three pairs of nipples, one inguinal pair cephalad from the prominent clitoris, and two lateral pairs just above the midline, one immediately in front of the femur and one at mid-thorax.

Table 7. The number of male and female spiny rats captured in the field and born in the laboratory (including both field and laboratory conceptions).

	Males	Females	χ^2	p
Spiny rats trapped near Almirante	92	82	0.58	> 0.05
Spiny rats trapped near Santa Rita	471	474	0.01	> 0.05
Almirante births in the laboratory	37	35	0.06	> 0.05
Santa Rita births in the laboratory	109	113	0.07	> 0.05
Total	713	718	0.02	> 0.05



One laboratory-born female had the 6 nipples described above plus a pair on the abdomen 4.5 centimeters cephalad of the inguinal pair.

During the period of lactation the nipples are swollen and elongated and the mammary tissue is thick and conspicuous. It is especially conspicuous around the inguinal nipples where the hair is thin and where it forms a thick 1.4x4.5 centimeter patch extending from the clitoris forward and laterally under the nipples. The mammary tissue around the lateral nipples is well-developed but less conspicuous because of the thick hair on the thorax. The areas immediately surrounding the lateral nipples are devoid of hair during the period of lactation when the nipples are erect and prominent.

Young Proechimys were observed eating soft fruit on the day of birth and one youngster gained 1% of its weight on day 9 when removed from its mother for a day. When left with the mother for longer periods young will spend a great deal of time suckling for the first three weeks. If the young are left with the mother longer, the inguinal mammary tissue recedes but the young will continue suckling on the lateral nipples. Well-developed lateral mammary tissue was observed as late as 46 days after birth and young were observed suckling as late as day 51. Most young have quit suckling by day 50 and the nipples have receded in size. Some young, if left confined with their

mother, continue suckling even though the mammary tissue is no longer conspicuous. In such situations the nipple is still enlarged and was observed as late as day 66.

Young spiny rats were observed suckling longer in this study than has been reported elsewhere. Enders (1935) reported lactation lasting 46 days in one case and Maliniak and Eisenberg (1971) noted that young are nursed until 40 days of age in captivity.

It is not known if lactation lasts as long in the field, but Enders (1935) estimated by the size of trapped young that they stay with their mother until 2 to 2½ months of age. Young spiny rats may be able to find food long before this age since in this study young did eat solid food at an early age. Other investigators have reported similar observations. Enders (1935) reported young eating solid food by the age of 11 days and Maliniak and Eisenberg (1971) remarked that young begin to eat solid food almost from the first day.

Since most male spiny rats were measured on arrival, estimates can be made of their ages (Table 8). These estimates suggest that some young are moving about at an early age.

Table 8. Frequency distribution of age estimates of male spiny rats trapped in Almirante and Santa Rita.

Estimated age(days)	Frequency of Almirante males	Frequency of Santa Rita males
10-20	1	2
20-30	4	3
30-40	1	6
40-50	3	6
50-60	5	5
60-70	0	2
70-80	4	12
80-90	2	6
90-100	2	9
100-120	8	21
120-140	6	26
140-160	2	11
160-180	6	4
180-200	6	14
200+	26	173



FIELD RESULTS

Reproduction in field captured males

Proechimys like other caviomorphs do not have a true scrotum (Weir, 1974; Pocock, 1922), but the testes will descend from the inguinal canal until the caudae epididymi or even the testes themselves are just beneath the skin. The position of the testes was labile in field-captured males and was not used for determining the fertility of field-trapped males. When handled, most field captured males pulled the testes into the inguinal canals with only portions of the caudae epididymi exposed. Males that were held in the laboratory longer were more likely to have external testes when handled. The testes of laboratory born males with descended testes remained external when examined.

The testes of most male spiny rats trapped in Santa Rita were significantly smaller during the months of October, November, December and January (Figure 5). In Santa Rita this period of four months juxtaposes the two wettest months with the first two months of the dry season.

There was insufficient evidence to show any seasonal change in the testis size of Almirante males (Table 9).

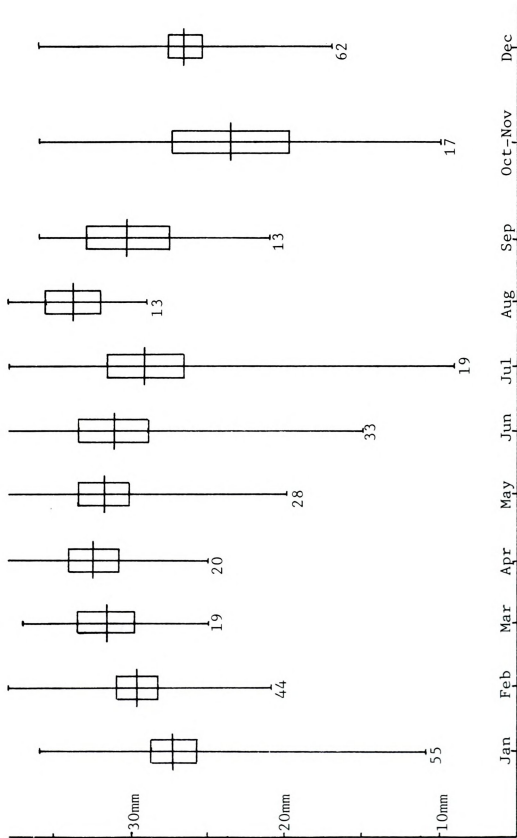


Figure 5. Mean length (mm) of left testis of Santa Rita males 220mm in body length or larger. Includes 95% C.I., range, and sample size.

Table 9. Mean length + 95% C.I. of the left testes of field trapped male spiny rats. Measurements are given in millimeters with sample size in parenthesis.

Body length	Santa Rita		Almirante	
	Oct-Jan	Feb-Sep	Oct-Jan	Feb-Sep
200-209	12.80 $\pm$ 2.39 (5)	13.28 $\pm$ 3.32 (7)	9(1)	11.33 $\pm$ 6.25 (3)
210-219	16.33 $\pm$ 4.34 (6)	20.28 $\pm$ 4.19 (14)	14(1)	16.20 $\pm$ 2.04 (5)
220-229	18.10 $\pm$ 3.17 (10)	21.62 $\pm$ 2.16 (16)	19.33 $\pm$ 10.04 (3)	18.50 (2)
230-239	21.86 $\pm$ 1.33 (22)	27.23 $\pm$ 1.63 (17) *	24.00 $\pm$ 4.97 (3)	22.83 $\pm$ 2.85 (6) **
240-249	24.80 $\pm$ 1.54 (15)	29.61 $\pm$ 1.16 (26) *	23.50 $\pm$ 5.09 (6)	26.14 $\pm$ 2.58 (7)
250-259	26.80 $\pm$ 1.89 (15)	30.88 $\pm$ 1.14 (33) *	25.86 $\pm$ 2.39 (7)	25.56 $\pm$ 2.00 (9) **
260-269	28.50 $\pm$ 1.17 (26)	32.95 $\pm$ 1.05 (42) *	23(1)	27.50 $\pm$ 2.18 (6) **
270-279	29.43 $\pm$ 1.52 (23)	34.33 $\pm$ 1.04 (27) *	31.33 $\pm$ 1.43 (3)	28.00 $\pm$ 6.27 (5)
280-289	31.89 $\pm$ 2.22 (9)	34.59 $\pm$ 1.39 (22)	31(1)	30.60 $\pm$ 3.35 (5)
290+	31.75 $\pm$ 2.89 (8)	31.88 $\pm$ 9.50 (8)	28(1)	32(1)

* Testes lengths of Santa Rita males are significantly larger during February-September than October-January.

** Testes lengths of Santa Rita males are significantly larger than those of Almirante males during February-September.

Testis size increases with body length. The natural logarithm of testis size was significantly correlated with the natural logarithm of body length for Almirante and Santa Rita males for the period of October through January ($t=10.93$, $p<0.05$, d.f.=49; $t=18.26$, $p<0.05$, d.f.=210) and February through September ($t=6.04$, $p<0.05$, d.f.=25; $t=16.14$, $p<0.05$, d.f.=143) respectively.

When testes lengths were adjusted to the mean body length for each of the four site-season combinations (see Methods), the mean testes lengths, measured in millimeters, for the periods of October through January and February through September were 24.97 ± 0.63 ($n=56$) and 29.56 ± 0.65 ($n=64$) respectively for Santa Rita and 23.66 ± 1.64 ($n=20$) and 23.98 ± 1.00 ($n=29$) respectively for Almirante. Therefore even after testes lengths were adjusted to remove the effects of body size this analysis supported the argument that the testes of Santa Rita males captured during February through September were significantly larger than those of males captured during October through January. No seasonal change in testis size was observed in Almirante males after testis size was adjusted to body size. This analysis also revealed that the testes of Santa Rita males captured during February through September were larger than those of Almirante males regardless of season of capture even though Almirante males were larger than Santa Rita males.

Analysis of a small sample of testes taken from known age laboratory born males supported the argument that the testes of Santa Rita males were larger than those of Almirante males (Figure 6).

Maximum testis length and the body length when testis growth rate stops increasing and begins decreasing can be estimated by fitting the data of Table 10 to the logistic equation $y = a / (1 + e^{b+cx})$. The mean testis lengths were fitted by nonlinear least squares to the midpoint of the body length interval using Marquardt's algorithm as described by Conway et al. (1970). The three partial derivatives of the above logistic equation described by Conway et al. (1970) are incorrect, however, and should read:

$$Y/a = 1 / (1 + e^{b+cx})$$

$$Y/b = -a e^{b+cx} / (1 + e^{b+cx})^2$$

$$Y/c = -a x e^{b+cx} / (1 + e^{b+cx})^2$$

Calculations were performed on a TI-59 hand-held calculator using a program written by the author. The three resulting logistics have the asymptotes (maximum testes sizes) 40.1 millimeters, 34.5 millimeters, and 33.8 millimeters respectively for males captured in Santa Rita during February through September, during October through January, and in Almirante in both seasons. This reflects the previous conclusion that testes are larger for males captured in Santa Rita during February through September but that the testes of males captured in Santa Rita

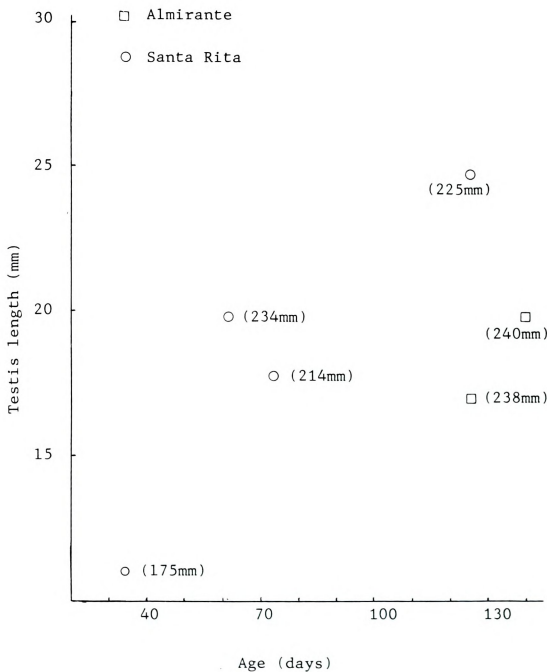


Figure 6. Testis length of young known age spiny rats from Santa Rita and Almirante. Body lengths are in parenthesis.

during October through January are similar to those of males trapped in Almirante in both seasons.

The body lengths at which inflection (body length when the rate of testes growth begins decreasing) occurs was determined by fitting the parameters obtained by solving the logistic for the second derivative:

$$y'' = -ac^2 e^{b+cx} \frac{(1+e^{b+cx} - 2e^{b+cx})}{(1+e^{b+cx})^3}$$

This analysis revealed that the points of inflection were remarkably similar, 219 millimeters, 217 millimeters, and 217 millimeters for Santa Rita during February through September, Santa Rita during October through January, and Almirante during the whole year.

In order to better understand the meaning of changes in testis size with season, histological sections of the testes from animals captured both in the dry season and the wet season will have to be studied. Some information is provided by the availability of testis sections of ten adults caught in Santa Rita during October and November. Among these, one with an adjusted testis length of 30 millimeters had enlarged seminiferous tubules with many cell layers, few interstitial spaces, and many spermatozoa. The remaining nine testes 25 millimeters in length or less when adjusted to mean body length had small seminiferous tubules with few cell layers, large interstitial spaces,

and few to no spermatozoa.

If the fluctuations in testis size do reflect fertility among males, then one would expect to find more pregnant females during the months of February through September in Santa Rita than in the months of October through January but no seasonal difference in Almirante. We will see in the next section that the reproductive activity of female spiny rats in Santa Rita and Almirante supported this proposition.

Reproduction in field captured females

During the months of October, November, December, and January only 26% (34/131) of females (estimated by body length to be 120 days of age or older) trapped near Santa Rita were pregnant on arrival to the laboratory (Table 11). During the remainder of the year 89% (188/211) were pregnant. This difference is very highly significant [$p(G\ 147.9) < 0.005$, $n=1$]. Juveniles (estimated by body length to be less than 120 days of age) and young adults (estimated by body length to be between 120 and 200 days of age) were more commonly trapped in the months of October through January. This suggested that the seasonality in the proportion of pregnant females found in the field was merely a result of a seasonal change in the age structure of the population. Although age estimates for females that gave birth to live or still born young

Table 11. Summary of monthly reproductive condition of female *Proechimys semispinosus* captured near Santa Rita and estimated by body length to be 120 days or older.

Month	Number pregnant at autopsy	Gave birth to live young	Number that gave birth to stillborn or young palpated but no birth observed	Total pregnant on arrival	Not pregnant on arrival	Percent pregnant on arrival
January	3	3	2	8	15	35%
February	9	6	3	18	4	82%
March	11	9	5	25	0	100%
April	18	14	1	33	7	82%
May	21	6	4	31	4	88%
June	16	7	1	24	2	92%
July	23	8	1	32	0	100%
August	7	1	0	8	4	67%
September	10	7	0	17	2	89%
October	2	2	5	9	19	32%
November	2	1	3	6	35	15%
December	2	4	5	11	28	29%

were not available, they were available for all other females including pregnant and nonpregnant. Analysis of these data revealed the same seasonality in the proportion of pregnant females for all age classes (Table 12).

Females from Almirante appear to be reproductively active the year around (Table 13). From October through January 93% (13/14) were pregnant on arrival and during the remainder of the year 92% (33/36) were pregnant. Among 16 juvenile sized individuals captured near Almirante, 4 were pregnant when captured in January, February, May and June.

Estimates of the month of conception (see Methods and materials) for each field trapped spiny rat are summarized in Figures 7 and 8. The large sample of spiny rats from Santa Rita provided the opportunity to analyze males and females separately. This allowed two independent estimates of the months of conception for field caught spiny rats from Santa Rita. The monthly pattern for 420 Santa Rita males was very similar to that for 378 Santa Rita females (Figure 7). Most conceptions were estimated to have occurred in May, June, and July and the fewest occurred in the months of October, November, December, and January.

The observation that males and females analyzed separately show a similar pattern increases confidence in these estimates and further supports the argument that breeding among Santa Rita Proechimys is concentrated into

Table 12. The proportion of pregnant to nonpregnant females revealed by autopsy of spiny rats trapped in the months October through January and February through September in Santa Rita.

Age estimates	Pregnant/nonpregnant	
	<u>Oct-Jan</u>	<u>Feb-Sep</u>
Between 90 and 120 days	1/5(20%)	6/12(50%)
Between 120 and 200 days	2/40(5%)	13/16(81%)
Greater than 200 days	6/61(10%)	106/115(92%)

Table 13. Summary of monthly reproductive condition of female *Proechimys semispinosus* captured near Almirante and estimated by body length to be 120 days or older.

Month	Number pregnant at autopsy	Gave birth to live young	Number that gave birth to stillborn or young palpated but no birth observed	Total pregnant on arrival	Not pregnant on arrival	Percent pregnant on arrival
January	2	0	0	2	0	100%
February	2	5	3	10	1	91%
March	4	0	1	5	0	100%
April	1	0	0	1	0	100%
May	3	1	0	4	0	100%
June	4	1	0	5	2	71%
July	0	1	0	1	0	100%
August	0	0	0	0	0	-
September	0	7	0	7	0	100%
October	0	2	0	2	1	67%
November	0	0	0	0	0	-
December	3	6	0	9	0	100%

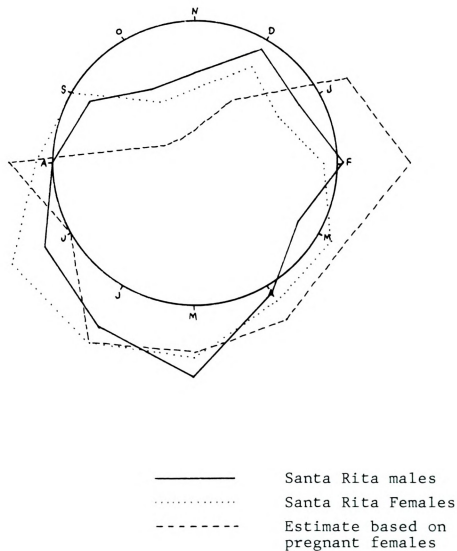


Figure 7. The monthly distribution of conceptions estimated to occur throughout the year at Santa Rita. The circle represents 8.3% or the expected monthly proportion if breeding occurs uniformly throughout the year.

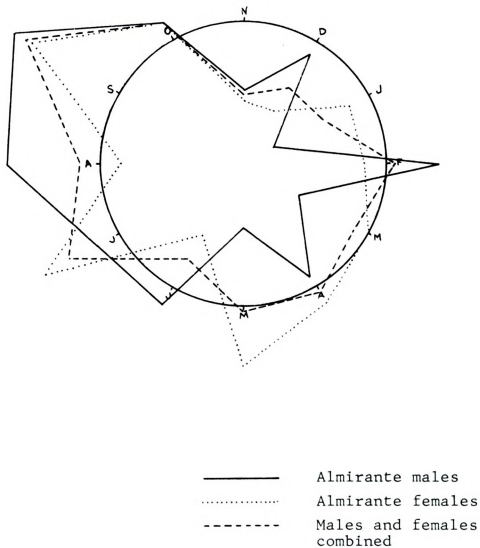


Figure 8. The monthly distribution of conceptions estimated to occur throughout the year at Almirante. The circle represents 8.3% or the expected monthly proportion if breeding occurs uniformly throughout the year.

the months of February through September.

Obviously mortality is a confounding factor here. If young are born during the period of October through January and their mortality is high they will not be captured. If it is assumed that (1) the number of adult females is constant the year around, (2) the pregnancy pattern is that shown in Table 11, and (3) the average female's pregnancy was conceived one month (half the gestation period) earlier, then the estimated pattern of conceptions would be as shown in Figure 7. Comparison of this estimate with the estimated month of conception of field trapped males and females supports the argument that the reproductive season in Santa Rita was restricted but also suggests a higher mortality for spiny rats conceived in the verano (January, February, March, and April) since the proportion of conceptions estimated by pregnancy patterns of captured females exceeds the proportion of conceptions estimated by the body lengths of males and females during these four months.

Among 84 males and 52 females from Almirante most conceptions were estimated to have occurred in the four months of July to October and the fewest in November, December, and January. The sample for Almirante was smaller and less reliable than the Santa Rita sample.

Comparison of the two Figures 7 and 8 suggests that breeding in Almirante was shifted so that breeding

was reduced a month later than it was in Santa Rita. Recall that the heaviest rains occurred in Almirante one month later than they did in Santa Rita and lasted into January.

If Proechimys semispinosus in Almirante do breed equally the year around (Table 12), then Figure 8 suggests that mortality was highest among those spiny rats conceived in November, December, and January.

Additional field results

Distribution of embryos in the uterus

Analysis of the distribution of embryos in the horns of the uterus of Proechimys was prompted by a remark by Fleming (1969:131) that implantation tended to occur more frequently in one uterine horn of the spiny rats that he examined. One caviomorph, the mountain viscacha (Lagidium peruanum), is known to nearly always (97% in one sample) carry embryos only in the right horn of the uterus (Pearson, 1949:155).

The numbers of embryos found implanted in the left and right horns of the uteri from pregnant spiny rats trapped near Santa Rita and Almirante are shown in Table 14. Neither the data from Santa Rita nor that from Almirante showed any significant difference from an equal distribution of embryos among the two horns [$\chi^2=3.43$]=0.064, d.f.=1 and $p(\chi^2 \leq 0.51)=0.475$, d.f.=1, respectfully].



Table 14. The distribution of embryos in the uterine horns of pregnant spiny rats trapped near Santa Rita and Almirante.

Site	Number of pregnant females	Uterine horn	Total number of embryos
Santa Rita	119	Right	161
		Left	196
Almirante	24	Right	22
		Left	27



When the data for both of these sites were pooled however, the number of embryos implanted in the left horns was significantly greater than those implanted in the right horns [$p(\chi^2 \geq 3.94) = 0.047$, d.f.=1].

Unilateral pregnancies among females with embryo counts of two or more were not more frequent than would be expected if an ovule was just as likely to come from the left as well as the right ovary at each ovulation and there was no migration of embryos from one horn to another (Table 15). Unilateral pregnancies among females with embryo counts of 3 or more were less frequent than would be expected by chance $0.005 < p(\chi^2 = 11.95, \text{d.f.}=1)$. There was a clear tendency for embryos to be distributed equally between the two horns of the uteri for embryo counts of three or more. McLaren (1963) has addressed this topic in mice.

Tail autotomy

Almost one-third of all spiny rats captured in the field had either no tail or one damaged with a blunt end covered by scar tissue (Table 16). A significantly higher proportion of spiny rats was tailless at Santa Rita than Almirante, $0.05 < p(\chi^2 \leq 4.02) < 0.025$. There was no sexual difference in the proportion of tailless individuals at either site, [$p(G \geq 0.27) > 0.05$ and $p(G \geq 0.93) > 0.05$ for Almirante and Santa Rita, respectively].



Table 15. Distribution of embryos in the horns of the uteri of spiny rats from near Santa and Almirante.

Number of embryos	Distribution of embryos (L,R)	Frequency	χ^2
2	2,0 or 0,2	23	$0.900 > P(\chi^2 \geq 0.02) > 0.750$, d.f.=1
	1,1 or 1,1	22	
3	3,0 or 0,3	17	$0.010 > P(\chi^2 \geq 7.40) > 0.005$, d.f.=1
	2,1 or 1,2	37	
4	4,0 or 0,4	5	$0.500 > P(\chi^2 \geq 2.25) > 0.250$, d.f.=2
	3,1 or 1,3	8	
	2,2 or 2,2	11	
5	5,0 or 0,5	0	$0.025 > P(\chi^2 \geq 8.87) > 0.010$, d.f.=2
	4,1 or 1,4	1	
	3,2 or 2,3	6	

Table 16. Tail condition for spiny rats trapped in the field.

	Tail missing	Tail damaged	Tail Intact	Totals
Almirante				
Males	10(12%)	10(12%)	63(76%)	83
Females	4(8%)	3(6%)	45(86%)	52
Santa Rita				
Males	68(16%)	48(11%)	311(73%)	427
Females	70(19%)	50(13%)	253(68%)	373
Totals	152(16%)	111(12%)	672	935



The tail is more easily broken on larger animals. An animal can be picked up and held by its tail but if it kicks or is able to get traction with its hindfeet, the tail breaks taking the posterior half of the fifth caudal vertebra with it (Enders, 1935). Among Santa Rita males 8% (15/179) of animals with a body length less than 250 millimeters were tailless, 20% (21/107) of those between 250 and 270 millimeters were tailless, and 46% of those greater than 270 millimeters were tailless. No male greater than 300 millimeters in body length was observed with a complete tail.

Several investigators have noted that spiny rats are often found tailless. Allen and Chapman (1893) described this condition in Proechimys trinitatus, Goldman (1920) wrote that the tailless condition is common among Panamanian spiny rats, and Enders (1935) observed that 20-25% of spiny rats on Barro Colorado Island were tailless. Fleming (1970) noted that a higher proportion of spiny rats was found tailless on the wetter Atlantic side of the Canal Zone. In the present study a higher proportion of tailless individuals was found at Santa Rita, a dry site.

Data from Santa Rita and Almirante show that the likelihood of tail loss increases with size (age). Since spiny rats trapped in Almirante were smaller (and probably younger, Table 8), one would expect fewer tailless

individuals there. Similarly Fleming's (1969) data showed that the population with the higher proportion of tailless individuals had a higher proportion of older (estimated by teeth wear) animals.

The direct cause of tail loss in the field is unknown. No tail loss due to intraspecific conflict was observed in the laboratory. Although spiny rats held in cages are often aggressive toward one another resulting in terrible wounds about the shoulders and flanks, no tail wounds of any kind were observed.

Sex ratio

Sex ratios among field trapped individuals did not differ significantly from a 50:50 ratio any month of the year (Table 7). The 50:50 sex ratios found in this study contradict Fleming (1969) who found that sex ratios among field-caught Proechimys semispinosus from both the Atlantic and Pacific sides of the Canal Zone favored males. Similarly, Everard and Tikasingh (1973) found that sex ratios favored males among P. guyannensis from Trinidad. Such biased sex ratios may be due to still unknown local conditions or sampling methods.

DISCUSSION

MacArthur and Wilson (1967:149) convincingly argued that r-selection will occur in a seasonal environment because the environment is periodically uncrowded and that K-selection will occur in a non-seasonal environment because the environment is always saturated with respect to resources. If it can be demonstrated that an important resource like food varies seasonally from low to high abundance for one population but remains constant for another population, then r-selection would be expected in the first population and K-selection in the second, ceteris paribus. If a single species of animal occupies two different environments then there will be selection for local adaptation to each environment and the two populations will differ in their life-history features. There should be r-selection in the seasonal environment because the less productive genotypes will be replaced by the more productive genotypes. There should be K-selection in a less seasonal environment because less efficient genotypes will be replaced by more efficient genotypes (MacArthur and Wilson (1967:149)).

It was demonstrated above that a single species of spiny rat, Proechimys semispinosus occurs in Almirante and

Santa Rita. Almirante occurs on the wet side of Panama and has a relatively nonseasonal climate but Santa Rita occurs on the dry side of Panama where the climate is seasonally wet and dry. Neither resource levels nor population densities were measured directly in Almirante or Santa Rita but these can be inferred from other sources.

The most important resource of P. semispinosus that may vary seasonally is food. Proechimys is entirely or mostly frugivorous (Enders, 1935:457; Fleming, 1969:62; Smythe, 1970a:44; Bonaccorso, 1980:66; Emmons, 1982:287; Glantz, 1982:100; Guillotin, 1982). Proechimys, like other terrestrial frugivores, depends on fruit that has fallen to the ground naturally or that has been dropped by volant or arboreal animals.

The phenology of fruit fall was not studied at Santa Rita or Almirante. A reasonable estimate could be made, however, since rainfall data were available for these two areas and since the fruitfall in the region is closely correlated with rainfall (Smythe, 1970; Frankie et al., 1974, and Foster, 1982). Rainfall patterns of the Santa Rita area are very similar to those of Barro Colorado Island. Both Smythe (1970) and Foster (1982) reported abundant falling fruit on Barro Colorado Island for only May through September. Frankie et al. (1974) studied two contrasting sites in Costa Rica, La Selva in a Wet Forest on the Caribbean side and Hacienda La Pacifica in a Dry

Forest on the Pacific side. Rainfall patterns at these two sites in Costa Rica are similar to those of Almirante and Santa Rita, respectively. The dry season at Hacienda La Pacifica is longer than it is at Santa Rita but the climate at La Selva is very similar to that of Almirante. Frankie et al. (1974) found that mature fruit was abundant the year around on the wet Caribbean side but was low late in the wet season on the dry Pacific side and increased in abundance only slightly in the early dry season. If rainfall patterns in Almirante and Santa Rita are reflected by fruit phenology as they are expressed at La Selva, Hacienda La Pacifica, and on Barro Colorado Island, then the primary food of Proechimys must be relatively constant the year around at Almirante but low during the last few months of the year at Santa Rita. On the dry side of Panama the late wet season seems to be a stressful time for terrestrial frugivores. Agoutis and pacas forage longer, range farther for food, and are trapped easier by bait (Smythe, 1982). Mortality of agoutis increases during this period (Smythe, 1978, 1982). When fruit is scarce Proechimys are easier to capture with baited traps (Fleming, 1969; personal observation).

Fleming (1969:77) showed that the population density of Proechimys semispinosus was higher on the wet Caribbean side than on the dry side of Panama regardless of season. He noted (Fleming, 1969:98) that disappearance rates were

higher on the Pacific side. Fleming demonstrated that the density of Proechimys on both the wet and dry sides of Panama increased during the wet season, but began to decrease late in the wet season and declined sharply in the early dry season. Fleming (1969:106) also demonstrated that Proechimys born in the late wet season had poor survivorship.

Glivicz (1984) studied a population of Proechimys semispinosus on the dry side of Panama near Barro Colorado during 1969-1970 and also demonstrated that population density increased during the wet season and decreased in the dry season.

The data in this study indicated that climate and the inferred fruit phenology were reflected by the breeding habits of Proechimys. In Santa Rita the percentage of pregnant females captured during the months of low fruit fall was significantly lower than the percentage captured during the months of higher fruit fall. The testes of males were significantly smaller during the period of low fruit fall than they were during the remainder of the year. Histological examination of a few testes suggested also that significantly more males were fertile during the fruiting season.

In Almirante, rainfall and presumably fruitfall were relatively constant the year around, the prevalence of pregnant females did not change seasonally, and the testes

of adult males did not vary in size.

Other frugivorous animals of Central America also synchronize their breeding to fruit abundance. This is true in squirrels (Glantz, 1982), opossums (Fleming, 1973), bats (Fleming, 1971, 1972; Morrison, 1978), and birds (Leck, 1970). The life-cycle of Proechimys like that in many other mammals is adapted so that pregnancy and lactation occur and young are produced at energetically favorable times of the year. When food levels vary seasonally, reproduction will be seasonal; when food levels remain relatively constant reproduction will occur throughout the year.

The difference in the breeding habits of Proechimys in Santa Rita and Almirante is similar to that of the seed eaters, Liomys and Heteromys (Fleming, 1974). In Costa Rica Liomys (found on seasonally dry sites) breeds in the early dry season when seeds are abundant and Heteromys (found on less seasonal sites) breeds the year around at a site when seeds can be found throughout the year.

The breeding season of Proechimys appears to be opportunistic since laboratory stock from neither Almirante nor Santa Rita showed any tendency to breed seasonally.

Based on the data presented and the inferences deduced above, it appears that Proechimys semispinosus should be more r-selected in Santa Rita and more K-selected in Almirante. The theory of r- and K-selection predicts

that spiny rats from the seasonally dry site, Santa Rita, in contrast to those at Almirante, will have a larger intrinsic rate of natural increase. r - and K -selection theory predicts that there will be selection for increased fecundity and earlier age of maturity in Santa Rita. If individual life history characters have measurable additive variance and some autonomy and are subject to natural selection then selection for earlier maturity will also be selection for shorter gestation, faster growth rate, earlier molt, earlier sexual maturity, smaller neonate size and shorter life-span in the Santa Rita population.

This study found no evidence that the Santa Rita population of Proechimys differed from the Almirante population with respect to length of gestation. This is no surprise because gestation length is constrained by body size within the Caviidae (Kleiman, et al., 1974). Because of the difference between the effectiveness of development time and fecundity in reducing r (see The theory of r - and K -selection), selection will have long ago shortened development time (Lewontin (1965:85). Studies of geographical races of Drosophila serrata e.g., have shown large differences in fecundity but no differences in development time (Birch, L.C. et al., 1963).

Litter size, independent of maternal size, of Proechimys did not differ between the two sites but embryo count, independent of maternal size, did differ. Observed

litter size in the laboratory was less reliable than embryo count as an indicator of actual litter size because mothers were easily disturbed in the laboratory and often killed and cannibalized their young. This is reflected by the standard errors for litter size and embryo count (see Litter size).

Differences in the rate of molt between the two populations of Proechimys would be difficult to detect because of the low power of resolution for molt observations.

Santa Rita males became sexually mature before Almirante males in the laboratory (Table 6) but Almirante females appeared to become sexually active earlier than Santa Rita females (Table 4). It appears, however, that the data on vaginal perforation was unreliable because insufficient records of number, sex, and age of cage mates were kept for these females. Lusty and Seaton (1978) reported that the vaginal opening of Proechimys guairae averaged 55.9 days when females were caged with adult males, 82 days when caged with immature males, and did not occur when females were caged with no males.

Longevity data contradicted the predictions of r- and K-selection theory. The spiny rats from the Santa Rita field population appeared older than those from Almirante. Two lines of evidence supported this conclusion. Field trapping indicated that Santa Rita rats in the field were larger and probably older (Tables 17 and 18). Data

Table 17. Mean maternal length $\pm$ 95% C.I. and embryo count for field conceptions. Sample sizes are in parenthesis.

Embryo count	Santa Rita	Almirante
1	226.00 $\pm$ 10.71mm (7)	230.50 $\pm$ 3.18mm (4)
2	238.69 $\pm$ 7.85mm (29)	229.78 $\pm$ 3.62mm (14)
3	247.72 $\pm$ 4.61mm (51)	234.75 $\pm$ 11.16mm (4)
4	250.22 $\pm$ 4.77mm (23)	
5	252.14 $\pm$ 10.59mm (7)	
6	260.00 $\pm$ 51.64mm (2)	
Total	245.19 $\pm$ 3.14mm (119)	232.35 $\pm$ 7.58mm (22)

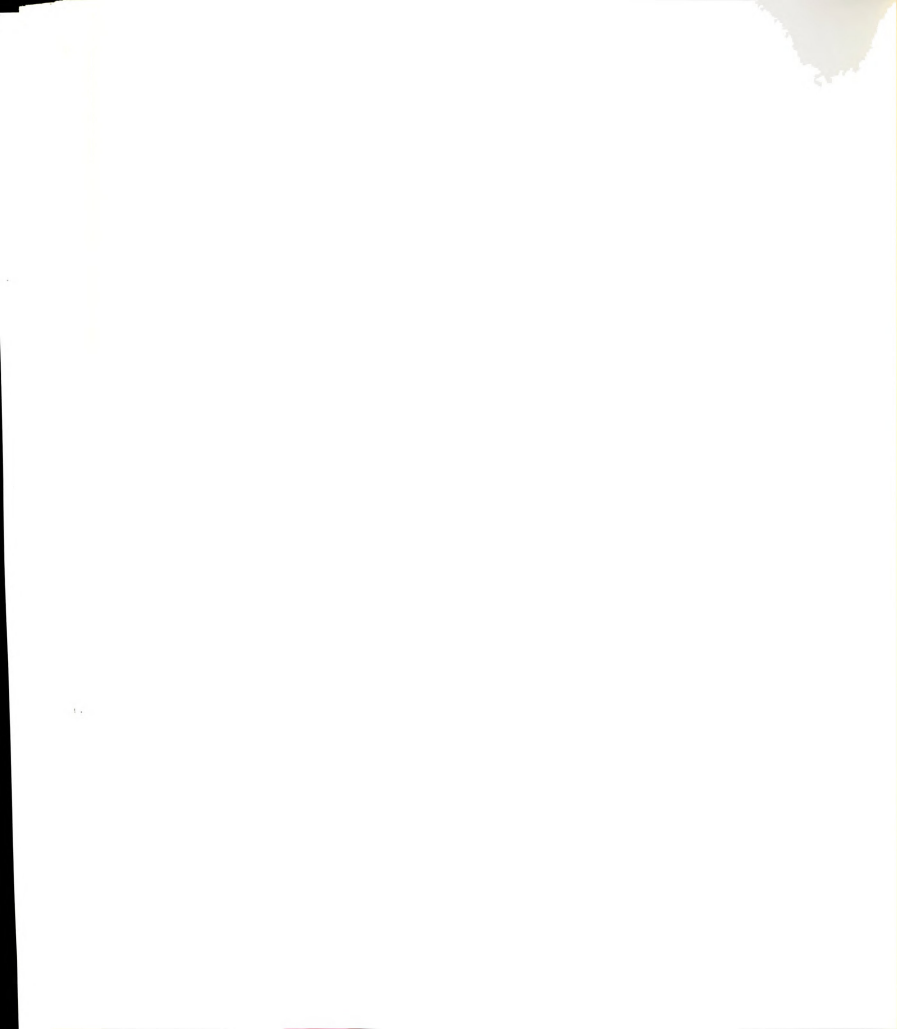


Table 18. Mean maternal weight $\pm$ 95% C.I. and litter size for field conceptions. Sample sizes are in parenthesis.

Litter size	Santa Rita	Almirante
1	385 $\pm$ 97.0g (3)	290 $\pm$ 241.4g (2)
2	372 $\pm$ 54.0g (8)	329 $\pm$ 29.4g (11)
3	428 $\pm$ 33.9g (12)	374 $\pm$ 55.4g (4)
4	423 $\pm$ 12.1g (4)	
Total	409 $\pm$ 23.0g (27)	335 $\pm$ 11.2 (17)

from tail autotomy supported the argument that the Santa Rita population was composed of older individuals if tail loss increases as a function of age. This inference has support from data published by Fleming (1969, 1970). Fleming (1969:100) reported that Proechimys were older at a wet site than at a dry site in the Panama Canal Zone. Fleming (1970:486) reported further on the same study and observed that 21% of Proechimys at the wet site were tail-less but only 13% of Proechimys at the dry site were tail-less.

I believe that the age distribution of Proechimys that I observed during 1970-1971 was unusual. The age distribution of Proechimys is the most labile of its life-history features considered here and most subject to environmental variation. I observed signs of extensive flooding in the Almirante area following the record-breaking rains of late 1970 (see Climate of the Almirante study area). Undoubtedly Proechimys living on the low wet area of my study area suffered unusual mortality during 1970. This view is supported by Mr. George Barrett, Jr., a resident of Almirante and part-time animal collector for Gorgas Memorial Laboratory, who told me that spiny rats were abundant in the vicinity of Mile-2 station prior to 1970 but were difficult to find during this study. I believe the Almirante population of Proechimys is normally older. As noted above, Fleming (1969:100) reported that a popula-

tion of spiny rats on the wet Caribbean side of Panama had significantly more old adults than did a population on the seasonally dry Pacific side. This age distribution of Proechimys is consistent with r- and K-selection theory.

The size of Santa Rita and Almirante Proechimys supported r- and K-selection theory. Neonates from Santa Rita stock were significantly smaller than Almirante neonates. Study of the size of known age Proechimys showed that males from Almirante were significantly larger than those from Santa Rita for ages 0, 5, 10, 100, and 120 days (Table 19). With the exception of neonates, no significant differences were found among females of any age, however. Growth rate data showing faster growth among Santa Rita Proechimys supported r- and K-selection theory since Santa Rita rats grew faster.

A summary of the life history features of Proechimys semispinosus examined in this study are shown in Table 20. The majority of data reported here supports the theory of r- and K-selection and it appears that differences in the life-history pattern of Proechimys semispinosus between two Panamanian sites is consistent with that predicted by r- and K-selection theory.

It has been argued that the greatest weakness of r- and K-selection theory as an explanation for patterns of covariation of life-history traits is that its support

Table 19. Mean body length $\pm$ 95% C.I. for two ages of Proechimys semispinosus from Almirante and Santa Rita.

Age (days)		Almirante		Santa Rita
100	Males	222.65 $\pm$ 3.4mm	Males	216.15 $\pm$ 2.4mm
	Females	207.96 $\pm$ 3.2mm	Females	205.38 $\pm$ 1.2mm
120	Males	232.17 $\pm$ 3.8mm	Males	225.57 $\pm$ 2.6mm
	Females	213.88 $\pm$ 3.6mm	Females	213.14 $\pm$ 1.6mm

Table 20. Summary of life-history features of Santa Rita and Almirante populations of Proechimys semispinosus.

	Santa Rita	Almirante
r-selected features	Seasonal breeding Smaller neonates More embryos Faster growth Earlier male maturity Smaller adult males	Earlier female maturity Age distribution favors young
K-selected features	Later female maturity Age distribution favors old	Aseasonal breeding Larger neonates Fewer embryos Slower growth Later male maturity Larger adult males
No difference	Gestation Litter size Molt Size of adult females	

is dependent on the taxonomic level examined. Comparisons among higher taxonomic categories offer strong support but support is weak for intrageneric or intraspecific comparisons (Stearns, 1977, 1980, 1983a, 1984a). Stearns (1984b:264) has argued that microevolution could not have produced the pattern because it results from differences among higher taxa that occurred long ago and has not changed significantly within lineages since then. I believe the present study refutes this view and shows that this pattern involving r- and K-selection characteristics can be explained by microevolutionary forces. In this study intraspecific tactics were perceptible and trade-offs among r- and K-selection attributes did occur.

Due to the logical structure of statistical inference, hypotheses can be rejected but not confirmed. The data presented above is consistent with r- and K-selection theory but does not confirm it. In fact, these data are also consistent with the hypothesis that there has been selection for larger size for Almirante rats and/or selection for smaller size for Santa Rita rats. Larger size can help a population avoid some predation, it increases the variety of food choices available, and increases the efficiency of energy acquisition (Armitage, 1981:43). Once there has been selection for size, allometric growth will lead to life history changes consistent with r- and K-selection (see Theory of r- and K-selection; Blueweiss,

et al., 1978; Western, 1979; Stearns, 1983a, 1984a).

Stearns (1983a) believes that many patterns attributable to r- and K-selection among broad taxonomic groups is due to selection on size followed by coadaptive shifts in life-history attributes. If this is true, then not all correlations between the life-history attributes are adaptive.

The life history of Proechimys semispinosus in Santa Rita and Almirante is also consistent with the hypothesis that density-dependent mortality applied to all age classes is greater in Santa Rita, or that adult mortality is high, variable, or unpredictable in Santa Rita and Almirante, and/or juvenile mortality is high, variable or unpredictable in Almirante (Stearns, 1983b:601; Parsons, 1983:12).

In this study it was assumed that the selection of the life-history parameters of Proechimys semispinosus are mediated through the density of Proechimys with respect to resources. Obviously any other forces impinging on the density of Proechimys or its resources like predation or interspecific competition will require modification of the r- and K-selection model. Many Panamanian predators feed on fruit in season but turn to animal prey when fruit is less abundant (Fleming, 1969:63; Smythe, 1970, 1978, 1982). Interspecific competition may also change seasonally (Smythe, 1970). These are just a few of the many possible dimensions of a life-history pattern

(Wilbur, et al., 1974; Parry, 1981). Until the covariance structure of the life-history attributes can be identified by study of other populations of Proechimys semispinosus, one cannot identify the life history features under strongest selective pressure.

The life history of Proechimys semispinosus in Panama appears to be consistent with r- and K-selection theory but before this hypothesis can be termed the cause of this pattern with any degree of confidence, the rival hypotheses must also be tested and the density of populations measured directly.

LITERATURE CITED

- Aldrich, J.W. and B.P. Bole, Jr. 1937. The birds and mammals of the western slope of the Azuero Peninsula (Republic of Panama). Sci. Publ. Cleveland Mus. Nat. Hist. 7:1-196.
- Allen, J.A. and F.M. Chapman. 1893. On a collection of mammals from the island of Trinidad, with descriptions of new species. Bull. Amer. Nat. Hist. 5:203-234.
- Armitage, K.B. 1981. Sociality as a life-history tactic of ground squirrels. Oecologia 48:36-49.
- Baker, R.H. 1983. Sigmodon hispidus. Pp. 490-492 in: D.H. Janzen (ed.), Costa Rican Natural History. Univ. Chicago Press, Chicago.
- Berry, R.J. 1964. The evolution of an island population of the house mouse. Evolution 18:468-483.
- Biggers, J.D., C.A. Finn, and A. McLaren. 1962. Long-term reproductive performance of female mice. II. Variation of litter size with parity. J. Reprod. Fertil. 3: 313-330.
- Birch, L.C., Th. Dobzhansky, P.O. Elliott, and R.C. Lewontin. 1963. Relative fitness of geographic races of Drosophila serrata. Evolution 17:72-83.
- Blueweiss, L., H. Fox, V. Kudzma, D. Nakashima, R. Peters, and S. Sams. 1978. Relationships between body size and some life-history parameters. Oecologia 37:257-272.
- Bonaccorso, F.J., W.E. Glanz, and C.M. Sandford. 1980. Feeding assemblages of mammals at fruiting Dipteryx panamensis (Papilionaceae) trees in Panama: seed predation, dispersal, and parasitism. Rev. Biol. Trop., 28:61-72.
- Bonner, J.T. 1965. Size and Cycle: An essay on the structure of biology. Princeton Univ. Press, Princeton, N.J.
- Bonoff, J.B. and D.H. Janzen. 1980. Small terrestrial rodents in eleven habitats in Santa Rosa National Park, Costa Rica. Brenesia 17:163-174.

Bowdre, L.P. 1968. An examination of the ecology of several small terrestrial mammals of three life zones in Costa Rica. Unpublished Organization for Tropical Studies Report.

Bowdre, L.P. 1971. Litter size in Sigmodon hispidus. Southwestern Natur. 16:121-128.

Bunge, M. 1967. Scientific Research: The search for system. Springer-Verlag, Berlin.

Cain, A.J. and G.A. Harrison. 1958. An analysis of the taxonomist's judgement of affinity. Proc. Zool. Soc. London 131:85-98.

Camin, J.H. and P.R. Ehrlich. 1958. Natural selection in water snakes (Natrix sipedon L.) on islands in Lake Erie. Evolution 12:504-511.

Caughley, G. 1966. Mortality patterns in mammals. Ecology 47:906-918.

Christian, J.J. and C.D. Lemunyan. 1958. Adverse effects of crowding on reproduction and lactation of mice and two generations of their progeny. Endocrinology 63:517-529.

Cody, M.L. 1966. A general theory of clutch size. Evolution 20:174-184.

Cole, L. 1954. The population consequences of life history phenomena. Quart. Rev. Biol. 29:103-137.

Conway, G.R., N.R. Glass, and J.C. Wilcox. 1970. Fitting nonlinear models to biological data by Marquardt's algorithm. Ecology 51:503-507.

Crow, J.F. and M. Kimura. 1970. An introduction to population genetics theory. Burgess Publ. Co., Minneapolis.

Darwin, C. 1859. The origin of species by means of natural selection. John Murray, London.

Deevey, E.S., Jr. 1947. Life tables for natural populations of animals. Quart. Rev. Biol. 22:283-314.

Delany, M.J. and B.R. Neal. 1969. Breeding seasons in rodents in Uganda. J. Reprod. Fert. (Suppl.6):229-235.

Dobzhansky, Th. 1950. Evolution in the tropics. Amer. Sci. 38:209-221.

Dunmire, W.W. 1960. An altitudinal survey of reproduction in Peromyscus maniculatus. Ecology 41:174-182.

Ehrlich, P.R. and J.H. Camin. 1960. Natural selection in middle island water snakes (Natrix sipedon L.). *Evolution* 14:136.

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

Enders, R.K. 1935. Mammalian life histories from Barro Colorado Island, Panama. *Bull. Mus. Comp. Zol.* 78:385-502.

Endler, J.A. 1973. Gene flow and population differentiation. *Science* 179:243-250.

Everard, C.O.R. and E.S. Tikasingh. 1973. Ecology of the rodents, Proechimys guyannensis and Oryzomys capito on Trinidad. *J. Mamm.* 54:875-886.

Fisher, R.A. 1930. The genetical theory of natural selection. Clarendon Press, Oxford.

Fleming, T.H. 1969. Population ecology of three species of neotropical rodents. Ph.D. Thesis, Univ. Mich.

Fleming, T.H. 1970. Notes on the rodent faunas of two Panamanian forests. *J. Mamm.* 51:473-490.

Fleming, T.H. 1971. Reproductive patterns of 40 Panamanian mammals. Handbook for tropical biology in Costa Rica. Organization for Tropical Studies, San Jose, Costa Rica.

Fleming, T.H. 1972. Three Central American bat communities: Structure, reproductive cycles, and movement patterns. *Ecology* 53:555-569.

Fleming, T.H. 1973. The reproductive cycles of three species of opossums and other mammals in the Panama Canal Zone. *J. Mamm.* 54:439-455.

Fleming, T.H. 1974. The population ecology of two species of Costa Rican Heteromyid rodents. *Ecology* 55:493-510.

Foster, R.B. 1982. The seasonal rhythm of fruitfall on Barro Colorado Island. Pp. 151-172 in: E.G. Leigh, Jr., A. Stanley Rand, and D.M. Windsor (eds.), *The ecology of a tropical forest: Seasonal rhythms and long-term changes*. Smithsonian Inst. Press, Washington, D.C.

Frankie, G.W., H.G. Baker, and P.A. Opler. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecol.* 62:881-919.

Glantz, W.E. 1982. Adaptive zones of Neotropical mammals: A comparison of some temperate and tropical patterns. Pp. 95-110 in: M.S. Mares and H.H. Genoways (eds.), *Mammalian biology in South America*. Special Publ. Pymatuning Lab. Ecol. #6.

Gliwicz, J. 1984. Population dynamics of the spiny rat Proechimys semispinosus on Orchid Island (Panama). Biotropica 16:73-78.

Goertz, J.W. 1965. Reproductive variation in cotton rats. *Amer. Midl. Nat.* 74:329-340.

Goldman, E.A. 1920. Mammals of Panama. *Smith. Misc. Coll.* 69:1-309.

Green, P.M. 1964. Density of population as a regulating factor in the reproductive potential of Sigmodon hispidus. Ph.D. Diss. Abstr., Oklahoma State Univ., Stillwater.

Guillotin, M. 1982. Activity rhythms and diet of Proechimys cuvieri and Oryzomys capito velutinus (Rodentia) in French Guiana. Terre Vie 36:337-371.

Hairston, N.G., D.W. Tinkle, and H.M. Wilbur. 1970. Natural selection and the parameters of population growth. *J. Wildl. Mgmt.* 34:681-690.

Hall, E.R. 1981. The mammals of North America. Ronald Press, N.Y.

Handley, C. 1966. Checklist of the mammals of Panama. Pp. 753-795 in: R.L. Wenzel and V.J. Tipton (eds.), *Ectoparasites of Panama*. Field Mus. Nat. Hist., Chicago.

Hempel, C.G. 1966. Philosophy of natural science. Prentice-Hall, Englewood Cliffs, N.J.

Hess, R., W.C. Allee and K.P. Schmidt. 1951. Ecological animal geography. John Wiley, N.Y.

Hoffman, R.S. 1958. The role of reproduction and mortality in population fluctuations of voles (*Microtus*). *Ecol. Monogr.* 28:79-109.

Holdridge, L.R. and G. Budowski. 1956. Report of an ecological survey of the Republic of Panama. *Caribbean For-ester* 17:92-110.

Hooper, E.T. 1968. Classification of Peromyscus. Pp. 27-69 in: J.A. King (ed.), *Biology of Peromyscus* (Rodentia). *Amer. Soc. Mamm., Special Publ.* #2.

- Jackson, W.B. 1965. Litter size in relation to latitude in two Murid rodents. *Amer. Midl. Nat.*, 73:245-247.
- Jewell, P.A. 1966. Breeding season and recruitment in some British mammals confined on small islands. *Symp. Zool. Soc. London* 15:89-116.
- Kilgore, D.L. 1970. The effects of northward dispersal on growth rate of young, size of young at birth, and litter size in *Sigmodon hispidus*. *Amer. Midl. Nat.* 84:510-520.
- King, J.A. 1958. Maternal behavior and behavioral development in two subspecies of *Peromyscus maniculatus*. *J. Mamm.* 39:177-190.
- Kleiman, D.G., J.F. Eisenberg, and E. Maliniak. 1979. Reproductive parameters and productivity of Caviomorph rodents. In *Vertebrate ecology in the northern Neotropics*, ed. J.F. Eisenberg, pp. 173-183. Washington, D.C.: Smithsonian Institution Press.
- Lack, D. 1954. The natural regulation of animal numbers. Oxford Univ. Press, Fair Lawn, N.J.
- Lack, D. 1965. Evolutionary Ecology. *J. Anim. Ecol.*, 34:223-231.
- Leck, C.F. 1970. The seasonal ecology of fruit and nectar eating birds in lower Middle America. Ph.D. Thesis, Cornell Univ., Ithaca, N.Y.
- Lewontin, R.C. 1965. Selection for colonizing ability. Pp. 77-94 in: H.G. Baker and G.L. Stebbins (eds.), *The genetics of colonizing species*. Academic Press, N.Y.
- Lord, R.D. 1960. Litter size and latitude in North American mammals. *Amer. Midl. Nat.* 64:488-499.
- Lusty, J.A. and B. Seaton. 1978. Oestrus and ovulation in the casiragua *Proechimys guairae* (Rodentia, Hystricomorpha). *J. Zool. London* 184:255-265.
- MacArthur, R.H. 1962. Some generalized theorems of natural selection. *Proc. Nat. Acad. Sci.* 48:1893-1897.
- MacArthur, R.H. and E.O. Wilson. 1967. *Island Biogeography*. Princeton Univ. Press, Princeton, N.J.
- Maliniak, E. and J.F. Eisenberg. 1971. Breeding spiny rats, *Proechimys semispinosus*, in captivity. *Int. Zoo Yearb.* 11:93-98.

- Mares, M.A. and R.A. Ojeda. 1982. Patterns of diversity and adaptation in South American hystricognath rodents. Pp. 393-432 in: M.A. Mares and H.H. Genoways (eds.), Mammalian Biology in South America. Special Publ. Pymatuning Lab. Ecol. #6.
- Margalef, R. 1959. Mode of evolution of species in relation to their places in ecological succession. Proc. Xv Int. Congr. Zool. 10:787-789.
- McLaren, A. 1963. The distribution of eggs and embryos between sides in the mouse. J. Endocrin. 27:157-181.
- Moojen, Joao. 1948. Speciation in the Brazilian spiny rats (Genus Proechimys, Family Echimyidae). U. Kansas Publ. Mus. Nat. Hist. 1:301-406.
- Moore, J.C. 1961. Geographic variation in some reproductive characteristics of diurnal squirrels. Bull. Amer. Mus. Nat. Hist. 122:1-32.
- Morrison, D.W. 1978. Foraging ecology and energetics of the frugivorous bat Artibeus jamaicensis. Ecology 59: 716-723.
- Orsini, M.W. 1962. Technique of preparation, study and photography of benzyl-benzoate cleared material for embryological studies. J. Reprod. Fertil. 3:283-287.
- Parry, G.D. 1981. The meanings of r- and K-selection. Oecologia 48:260-264.
- Pearson, O.P. 1949. Reproduction of a South American rodent, the mountain viscacha. J. Anat. 84:143-167.
- Pengelley, E.T. 1966. Differential developmental patterns and their adaptive value in various species of the genus Citellus. Growth 30:137-142.
- Petersen, M.K. 1970. Competition between the cotton rats, Sigmodon fulviventer and S. hispidus. Ph.D. Thesis, Mich. State Univ., East Lansing.
- Pocock, R.I. 1922. On the external characters of some hystricomorph rodents. Proc. Zool. Soc. London 1922:365-427.
- Reig, O.A., M. Aguilera, M.A. Barros, and M. Useche. 1980. Chromosomal speciation in a Rassenkreis of Venezuelan spiny rats (Genus Proechimys, Rodentia, Echimyidae). Pp. 291-312 in: N.N. Vorontsov and J.M. Van Brink (eds.), Animal Genetics and Evolution. Dr. W. Junk B.V. Publishers, The Hague.

- Rensch, B. 1960. Evolution above the species level. Columbia Univ. Press, N.Y.
- Rich, P.V. and T.H. Rich. 1983. The Central American dispersal route: Biotic history and paleogeography. Pp. 12-34 in: D.H. Janzen (ed.), Costa Rican Natural History. Univ. Chicago Press, Chicago.
- Schaffer, W.M. 1974. Optimal reproductive effort in fluctuating environments. Am. Nat. 108:783-790.
- Schmalhausen, I.I. 1949. Factors of evolution. Blakiston, Philadelphia.
- Smith, F.E. 1954. Quantitative aspects of population growth. Pp. 277-294 in: E.J. Goell (ed.), Dynamics of population growth. Princeton Univ. Press, Princeton, N.J.
- Smith, M.H. and J.T. McGinnis. 1968. Relationships of latitude, altitude, and body size to litter size and mean annual production of offspring in Peromyscus. Res. Pop. Ecol. 2:115-126.
- Smythe, N.D.E. 1970a. Ecology and behavior of the agouti (Dasyprocta punctata) and related species on Barro Colorado Island, Panama. Ph.D. Thesis. University of Maryland, College Park, Maryland.
- Smythe, N. 1970b. Relationships between fruiting seasons and seed dispersal methods in a neotropical forest. Am. Nat. 104:25-35.
- Smythe, N. 1978. The natural history of the Central American agouti (Dasyprocta punctata). Smith. Contr. Zool. 257:1-52.
- Smythe, N. 1982. Population regulation in some terrestrial frugivores. Pp. 227-238 in: E.G. Leigh, Jr., A. Stanley Rand, and D.M. Windsor (eds.), The ecology of a tropical forest: Seasonal rhythms and long-term changes. Smithsonian Inst. Press, Washington, D.C.
- Sokal, R.R. and F.J. Rohlf. 1969. Biometry. W.H. Freeman and Company, San Francisco.
- Spencer, A.W. and H.W. Steinhoff. 1968. An explanation of geographic variation in litter size. J. Mamm. 49:281-286.
- Stearns, S.C. 1977. The evolution of life history traits: A critique of the theory and a review of the data. Ann. Rev. Ecol. Syst. 8:145-171.

Stearns, S.C. 1980. A new view of life-history evolution. *Oikos* 35:266-281.

Stearns, S.C. 1983a. The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. *Oikos* 41:173-187.

Stearns, S.C. 1983b. A natural experiment in life-history evolution: Field data on the introduction of mosquitofish (Gambusia affinis) to Hawaii. *Evolution* 37(3): 601-617.

Stearns, S.C. 1984a. The effects of size and phylogeny on patterns of covariation in the life history traits of lizards and snakes. *Am. Nat.* 123:56-72.

Stearns, S.C. 1984b. Models in evolutionary ecology. In population biology and evolution, ed. K.Wöhrmann and V. Loeschke, Pp. 261-265. Springer-Verlag, Berlin, Heidelberg.

Steel, R. and J. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill, N.Y.

Tinbergen, N. 1959. Comparative studies of the behavior of gulls (Laridae): A progress report. *Behavior* 15:1-70.

Tinbergen, N. 1963. On aims and methods of ethology. *Z. Tierpsychol.* 20:410-433.

Tinbergen, N. 1967. Adaptive features of the blackheaded gull, Larus ridibundus L. Pp. 43-59 in: D.W. Snow (ed.), *Proc XIV Int. Orn. Congr.*

Tomich, P.Q., N. Wilson, and C.H. Lamoureux. 1968. Ecological factors on Manana Island, Hawaii. *Pacif. Sci.* 22:352-368.

Webb, S.D. and L.G. Marshall. 1982. Historical biogeography of recent South American land mammals. Pp. 39-52 in: M.A. Mares and H.H. Genoways (eds.), *Mammalian Biology in South America*. Special Publ. Pymatuning Lab. Ecol. #6.

Weir, B.J. 1973. Another Hystricomorph rodent: Keeping casiragua (Proechimys guairae) in captivity. *Lab. Animals* 7:125-134.

Weir, B.J. 1974. Reproductive characteristics of Hystricomorph rodents. *Symp. Zool. Soc. London.* 34:265-301.

Western, D. 1979. Size, life history and ecology in mammals. Afr. J. Ecol. 17:185-204.

Wilbur, H.M., D.W. Tinkle, J.P. Collins. 1974. Environmental certainty, trophic level, and resource availability in life history evolution. Amer. Nat. 108:805-817.

Williams, G.C. 1966. Adaptation and natural selection. Princeton Univ. Press, Princeton, N.J.

Williams, R.H., J.L. Carmon, and F.B. Golley. 1965. Effect of sequence of pregnancy on litter size and growth in Peromyscus polionotus. J. Reprod. Fertil. 9:257-260.

Zimmerman, K. 1950. Die Randformen der Mitteleuropäischen Wühlmause. Pp. 454-471 in: A. Jordans and F. Peus (eds.), Syllegomena Biologica Festschrift. Leipzig.

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