

MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 143

Population Ecology of Three Species of Neotropical Rodents

BY

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at St. Louis*

ANN ARBOR

MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN

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INTRODUCTION

Many rodent populations have been studied by ecologists in the past thirty years, but since temperate regions of the world have been emphasized, most data concerning the demographic characteristics of these mammals come from areas that exhibit distinct and sometimes very harsh climatic fluctuations. Few data are available on populations of tropical rodents. Because some tropical areas (particularly the lowlands) are characterized by temperatures that are equable year-round and by a diverse mammalian fauna, selective factors operating on populations of tropical rodents might be expected to differ in degree, if not in kind, from those operating on temperate or arctic rodents. Differences in selective regimes may, in turn, cause tropical rodents to differ significantly from more northern species in methods of population regulation and in reproductive and survival rates. While latitudinal gradients in the demographic characteristics of rodents are of considerable ecological and evolutionary interest, the present lack of tropical studies has prevented such comparisons from being made.

This report summarizes a twelve-month study of small mammal populations in two forests in the Panama Canal Zone. The objectives of the study, which began on June 6, 1966 and ended June 7, 1967, were threefold: (1) to compare and contrast the demographic changes in five populations of three species of rodents in a year's cycle; (2) to examine the relationship between seasonal changes in the reproductive biology of the species and environmental changes; and (3) to determine movement patterns and sizes of home ranges of individuals of each species. In addition to providing comparative data on the autecology of three species of tropical rodents, information derived from this study can be used to compare the demographic characteristics of phylogenetically or ecologically related species of temperate and tropical North American rodents.

The year's field work resulted in an accumulation of data from about 3,000 captures and recaptures of the following species: *Liomys adspersus* Peters (spiny pocket mouse, family Heteromyidae), *Oryzomys capito* Olfers (rice rat, family Muridae), and *Proechimys semispinosus* Tomes (spiny rat, family Echimyidae). Additional information was gained from 784 individuals of the three species that were sacrificed and preserved.

Of the rodents covered in this report, *L. adspersus* and *O. capito* are mouse-sized (adult head-body length about 125 mm) and *P. semispinosus* is rat-sized (adult head-body length about 230 mm). Each species is primarily terrestrial and nocturnal. As currently understood, *L. adspersus* is restricted in distribution to the semi-arid savanna country of the Pacific coast of western and central Panama where it is most common in thorny scrub and weedy fields (Handley, 1966). Like most heteromyids, it is principally a granivore.

The known range of *O. capito* includes eastern Costa Rica to the north and thence southward throughout low and medium elevations in the northern half of South America as far south as Paraguay and northeastern Argentina (Hall and Kelson, 1959; Cabrera, 1957, 1960). In Panama this species is found at low elevations in evergreen and deciduous forests. It is probably omnivorous. *P. semispinosus*, found throughout the forested parts of Panama at lower elevations, ranges from northeastern Nicaragua (Buchanan and Howell, 1965) south through Colombia to northern Peru and northwestern Brazil (Moojen, 1948). Its diet includes fruit and other plant material.

ACKNOWLEDGMENTS

Many people and institutions contributed to the success of this study. For his constant encouragement and guidance throughout the work I extend my sincere appreciation to Dr. E. T. Hooper. I also wish to thank Drs. W. H. Burt, A. G. Kluge, J. MacFadden, and W. H. Wagner for criticising the manuscript and for assistance in other ways. Dr. L. A. Lowenthal was most generous in instructing me in histological techniques and in providing me with the unlimited use of her laboratory facilities. Mr. George Barrett, Jr., of Almirante, R. P., gave able assistance throughout the field work, and Drs. J. A. Duke, Battelle Memorial Institute, and K. E. Blum, then a graduate student at Florida State University, helped with botanical problems. Miss Darleyn Weber of the Smithsonian Institution identified many of the plant specimens that I collected in my study areas.

I also wish to acknowledge the assistance of the following agencies and institutions in the Panama Canal Zone: U.S. Air Force Southern Command, for permission to use the Rodman Depot as a study site; U.S. Army Tropic Test Center, for permission to use a site at Fort Sherman as one of my trapping grids; U.S. Army Southern Command, for permission to live and work on the Fort Sherman Military Reservation for 10 days each month; Middle America Research Unit, for laboratory facilities and supplies; Smithsonian Tropical Research Institute, for a field vehicle and a recording hygrothermograph; and Panama Canal Company's Hydrographic Branch, for weather records and a rain gauge.

I was graciously aided in many ways by the personnel of the Middle America Research Unit (MARU) in Balboa, C. Z., and wish to thank Drs. K. M. Johnson, Director of MARU, and M. L. Kuns, then a Senior Biologist there, for their encouragement, interest, and support. Dr. Kuns took the aerial photographs of my study areas. Mr. Manuel Correa of MARU kindly retrapped the Rodman grid in December 1967.

This study was part of the Smithsonian Institution's "Mammals of Panama" project, and the field work was funded by the Smithsonian Institution Research Foundation and a National Science Foundation grant to Dr. C. O. Handley, Jr. Dr. Handley aided the project in many ways and allowed me to study specimens under his care at the U.S. National Museum. My special thanks are extended to him.

The University of Michigan's Computer Center provided free computer time. Mrs. Fran Stephenson wrote the computer program for the study of home range overlap.

While at the University of Michigan, I was supported by a State College Fellowship, a Department of Zoology Teaching Fellowship, and a National Institutes of Health predoctoral fellowship 1-F1-GM-35, 960-01, 02.

STUDY AREAS

Two forests located at opposite ends of the Panama Canal Zone were selected as sites for live-trap grids because of their differences in habitat and rainfall, their relative freedom from human disturbance, and their accessibility (Fig. 1). The Pacific site was located at the Rodman Naval Ammunition Depot ($8^{\circ} 57' N$, $79^{\circ} 37' W$), hereafter called Rodman, elevation about 50 m, eight km west of Balboa. Rodman lies within the Dry Tropical Forest life zone of Holdridge and Budowski (1956). The Atlantic site was located on the Fort Sherman Military Reservation ($9^{\circ} 20' N$, $79^{\circ} 57' W$), hereafter called Sherman, elevation about 5 m, three km west of Cristobal. Sherman lies within the Moist Tropical Forest life zone of Holdridge and Budowski (1956).

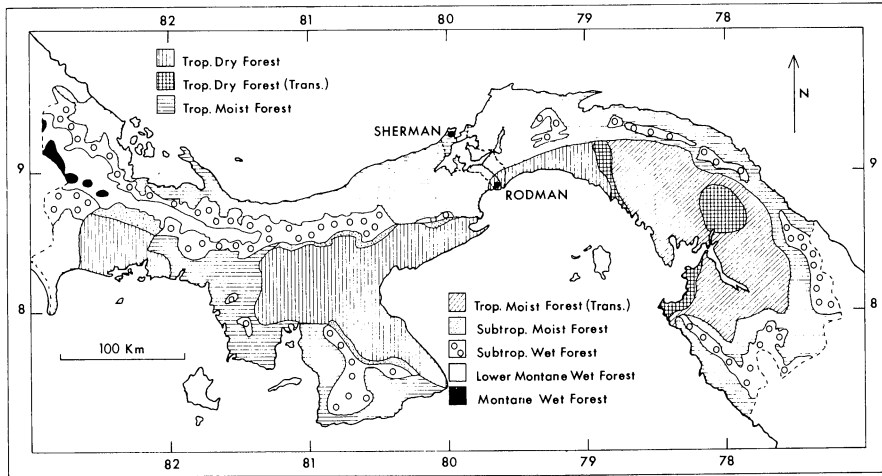


FIG. 1. Life zones of Panama. Redrawn from Holdridge and Budowski (1956). Abbreviations: Trop. = tropical; Trans. = transitional.

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CLIMATE AND PHOTOPERIOD

Because both study areas were located at low elevations near oceans, they experienced a nearly equatorial climate with respect to temperature, which averages about $80^{\circ} F$ each month throughout the Canal Zone (Fig. 2). Rainfall, however, exhibits a seasonal pattern in the form of a four-month dry season (January through April) and an eight-month wet season (May

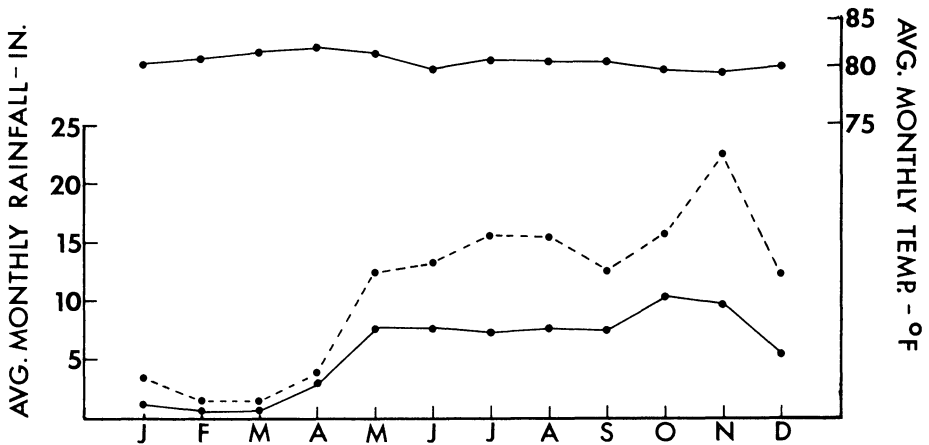


FIG. 2. Mean monthly temperature (Balboa and Cristobal combined) and rainfall at Balboa (solid line) and Cristobal (dashed line) in the Panama Canal Zone based on 65 and 94 years of continuous records, respectively.

through December) (Fig. 2). The Atlantic side of the Canal Zone receives nearly twice as much rain annually as the Pacific side (130 in versus 70 in), but both sides receive less than four inches per month during the dry season. Further accounts of Canal Zone climate are given in Allee (1926) and Kaufmann (1962).

In the year's study, rainfall was about 16 inches above normal on the Pacific side, primarily owing to heavy rains in October 1966, and about two inches below normal on the Atlantic side, although Cristobal recorded 35 inches of rain (12 in above normal) in November 1966 (records of the Panama Canal Company). Rainfall was recorded at each study site during the periods of trapping, and these records (Table 1) indicate that June 1966 was the wettest period at Rodman, August 1966 at Sherman. Rainfall in trapping sessions at Rodman was rather evenly distributed between night and day, but at Sherman, it tended to occur at night or just before dawn.

Annual changes in photoperiod at 9° N are relatively slight. Records from Barro Colorado Island, midway between my two study sites, indicate that the differences between the length of days at summer and winter solstices is about 65 minutes (Kaufmann, 1962). Average daily rate of change is about 0.29 minutes (8.7 minutes per month) throughout the year.

VEGETATION

RODMAN NAVAL AMMUNITION DEPOT.—The Rodman Depot, a fenced area of 1,015 ha, consists of a series of small hills and valleys covered with second growth forest. The highest hill attains an elevation of 168 m, and small water-courses flow through the valleys. Two major streams, the Rio Velasquez and a branch of the Rio Cocoli, pass through the Depot and flow northeasterly to empty into the Panama Canal. Since the end of World War II, the Depot has been little disturbed by man's activities.

TABLE 1
DATES OF TRAPPING AND RECORDED RAINFALL

Location	Dates	Rainfall (inches)	
Rodman	June 6-15, 1966	6.53	
	July 5-14	1.31	
	August 4-13	2.51	
	September 2-11	1.94	
	October 3-12	4.69	
	November 1-10	5.04	
	November 30-December 9	5.13	
	January 2-11, 1967	0.00	
	January 31-February 9	0.00	
	February 27-March 8	0.00	
	March 29-April 7	0.00	
	April 26-May 5	4.91	
	May 29-June 7	2.28	
	Sherman	June 20-29, 1966	1.34
		July 18-27	5.09*
		August 19-28	13.68
		September 15-24	3.18
October 18-27		3.85*	
November 15-23		4.00	
December 13-21		1.19	
January 16-25, 1967		0.04	
February 13-21		0.27	
March 15-23		1.02	
April 11-20		0.10	
May 10-19		4.23	

* Rain gauge disturbed one day

The site selected for a live-trap grid was a fairly level forested area near the southwest corner of the Depot. Except for cleared areas along the shoulders of roads and around ammunition bunkers, continuous forest surrounded the grid. Major topographical features include a stream that ran approximately diagonally from the northwest to the southeast corners and a slight rise of one to two meters near the center of the grid (Fig. 3). These two features strongly affected the local distribution of plants on the grid.

Common plants collected or otherwise identified on the Rodman grid are listed in Table 2. Most of the botanical names follow Allen (1956).

Structurally, the forest consisted of a single stratum of trees, ranging from 4 to 20 m in height, that formed an incompletely closed canopy. The forest was quite low compared with others in the area principally because of the absence of two typical Pacific slope trees, *Anacardium excelsum* and *Enterolobium cyclocarpum*, both found elsewhere on the Depot. *Calycophyllum candidissimum* and *Ficus* sp. were emergent on the grid. The most common members of the canopy, *Cordia alliodora*, *Guazuma ulmifolia*, and

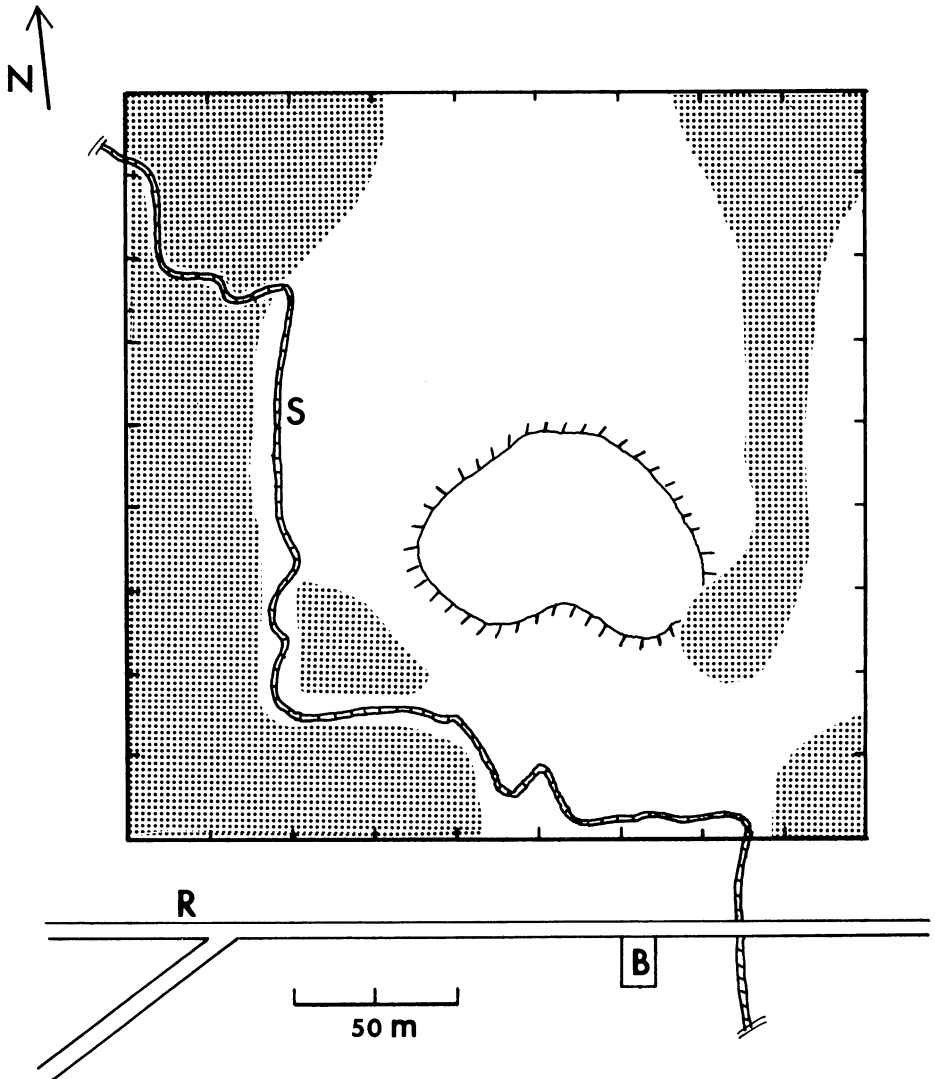


FIG. 3. Live-trap grid at Rodman. Stippled areas indicate low, moist, palm-dominated areas. A slight rise occurs near the center of the grid. Abbreviations: B = ammunition bunker; R = road; S = stream.

Luehea seemanii, averaged 24 cm or less in DBH (Table 2), indicating that the forest is relatively young. Typical views of the forest are shown in Figures 4 and 5.

Three species of palm, *Bactris balanoidea*, *Corozo oleifera*, and *Scheelea rostrata*, were conspicuous members of the flora. *Bactris* and *Corozo* were generally restricted to lower areas that were often flooded in the rainy season (Fig. 3). Because of the general lack of tall trees, *Scheelea* was an important member of the canopy (Figs. 4, 5b). The shrub layer was well developed and

TABLE 2
COMMON PLANTS ON THE RODMAN AND SHERMAN GRIDS

Rodman	Sherman
	Trees
<i>Andira inermis</i> H.B.K. (24)	(Greater than 10 m in height)
<i>Annona reticulata</i>	<i>Anacardium excelsum</i> (Bert. and Balb.)
<i>Annona spraguei</i> Safford. (26)	Skceels
<i>Apeiba tibourbou</i> Aubl. (23)	<i>Andira inermis</i> (14)
<i>Bunchosia cornifolia</i> H.B.K. (9)	<i>Apeiba tibourbou</i>
* <i>Bursera simaruba</i> (L.) Sarg. (22)	<i>Bombacopsis fendleri</i>
<i>Byrsonima crassifolia</i> (L.) H.B.K. (24)	<i>Bombax barrigon</i> (Seem.) Dcne.
<i>Calycophyllum candidissimum</i>	<i>Eugenia jambos</i> L.
(Vahl.) DC. (31)	* <i>Ficus insipida</i> Willd. (100)
<i>Cecropia obtusifolia</i> Bertol. (19)	* <i>Inga</i> sp. (45)
<i>Cecropia peltata</i> L. (16)	<i>Luehea seemanii</i> (42)
<i>Cochlospermum vitifolium</i> (Willd.)	
Spreng. (14)	<i>Mangifera indica</i> L. (66)
* <i>Cordia alliodora</i> (Ruiz. and Pav.)	
Rocm and Schult. (20)	<i>Protium panamensis</i>
<i>Ficus</i> sp. (92)	* <i>Spondias mombin</i> (46)
* <i>Guazuma ulmifolia</i> Lam. (20)	* <i>Terminalia</i> sp. (65)
<i>Inga</i> sp. (27)	<i>Viola</i> sp.
<i>Lonchocarpus</i> sp. (6)	<i>Vochysia ferruginea</i>
* <i>Luehea seemanii</i> Tr. and Pl. (24)	(Less than 10 m in height)
<i>Miconia argentea</i> (Swartz.) DC.	* <i>Belotia panamensis</i>
* <i>Sapindus saponaria</i> L.	* <i>Gustavia superba</i> (H.B.K.) Berg.
* <i>Spondias mombin</i> L. (24)	* <i>Myrcia</i> sp.
<i>Terminalia</i> sp. (23)	* <i>Psychotria grandis</i> Sw.
<i>Vochysia ferruginea</i> Mart. (15)	
<i>Xylopia frutescens</i> Aubl. (15)	
	Palms
* <i>Bactris balanoidea</i> (Oerst.) Wendl.	* <i>Astrocaryum standleyanum</i> L. H. Bailey
* <i>Corozo oleifera</i> (H.B.K.) L. H. Bailey	<i>Bactris</i> spp.
* <i>Scheelea rostrata</i> (Oerst.) Burret	* <i>Corozo oleifera</i>
	<i>Manacaria saccifera</i>
	<i>Scheelea rostrata</i>
	Shrubs
<i>Hirtella racemosa</i> Lam.	<i>Cephaelis tomentosa</i> (Aubl.) Vahl.
<i>Psychotria cuspidata</i> Bredem.	<i>Heisteria</i> sp.
<i>Psychotria undata</i> Jacq.	<i>Heliconia</i> sp.
	<i>Piper</i> sp.
	<i>Pothomorphe</i> sp.
	<i>Psychotria cuspidata</i>
	<i>Psychotria marginata</i> Sw.
	<i>Psychotria psychotriaefolia</i> (Seem.)
	Standl.
	<i>Psychotria racemosa</i> (Aubl.) Wild.
	Ground Layer
<i>Adiantum lucidum</i> Sw. (fern)	<i>Bromelia penquin</i>
<i>Chusquea simpliciflora</i> Munro	
(bamboo grass)	<i>Rynchospora cephalotes</i> (L.) Vahl.
<i>Cyperus luzulae</i> (L.) Retz. (sedge)	(sedge)
<i>Olyra latifolia</i> L. (grass)	<i>Selaginella</i> sp.
<i>Panicum maximum</i> Jacq. (grass)	

Most common trees are marked with an asterisk (*). Mean DBH (in cm) of trees is indicated in parentheses.



FIG. 4. Aerial view of part of the Rodman grid. For orientation, see Figure 3. Note the open nature of the canopy with emergent palms, *Scheelea rostrata*. Photograph by Dr. M. L. Kuns.

consisted in many places of a tangled, nearly impenetrable mass of thorny vines, young palms, and shrubs, principally *Hirtella racemosa*, which was most common in the higher, better drained areas. Occasional clearings created by fallen trees were choked with shrubs, saplings, and several species of grass including *Chusquea simpliciflora*, *Olyra latifolia*, and *Panicum maximum*. The ground, usually leaf-covered, was generally free of vegetation. In low, moist areas, *Bactris* leaves comprised the ground cover. In higher areas, ground cover varied from sparse to heavy and was comprised of seedlings, young palms, vines, and fallen leaves. Sedge and grass were uncommon everywhere except in clearings. Along the bank of the stream, a fern, *Adiantum lucidum*, was common.

Within the year, marked seasonal changes occurred in the appearance of the forest. In the rainy season the stream was often high and roily, and small feeder streams emptied into it. In October and November, standing water was common over many parts of the grid. As a result of storms and heavy wind in October, several trees and many branches were blown down across grid lines. After rains, the ground in many places was washed clear of debris by rushing torrents of water.

With the cessation of rain in late December, the forest began to dry out. The water level in the stream decreased in January and February, and by March the stream was dry. At the same time, standing water disappeared, and the ground gradually became very dry and hard. During the dry season,



FIG. 5. Views of forest on the Rodman and Sherman grids.

- a. Vegetation on the slight rise in the middle of the Rodman grid. Note small diameter of the trees and the open canopy.
- b. Two dominants in the Rodman forest: *Luehea seemanni* (tree in center of picture) and fronds of *Scheelea rostrata*.
- c. A grove of large mango trees, *Mangifera indica*, in the Sherman forest.
- d. An area of lower elevation in the Sherman forest showing dense undergrowth. The small tree, *Psychotria grandis*, is common here.

several deciduous trees, e.g., *Calycophyllum candidissimum*, *Cochlospermum vitifolium*, *Bursera simaruba*, and *Spondias mombin*, lost their leaves, and the ground was covered with dry, brittle leaves that made silent passage through the forest impossible. Dry season was the time of flowering for many trees including *Cochlospermum vitifolium*, *Cordia alliodora*, *Inga* sp., *Lue-*

hea seemanii, and *Triplaris melaenodendron*. By April deciduous trees were acquiring new leaves while leaves on other trees were dry and wilted.

After the rainy season began, on April 27, 1967, the appearance of the forest quickly changed. With more frequent rains, plants took on a greener appearance, and nondeciduous trees began to acquire new leaves. Plant growth accelerated and new palm sprouts and leaves and *Chusquea* shoots blocked the grid lines. Fallen leaves quickly became water-logged and matted. By early June the stream had flowing water in it again.

FORT SHERMAN MILITARY RESERVATION.—The topography, soil characteristics, and general vegetation of the Fort Sherman area have been described by McCullough et al. (1956). Much of the military reservation is covered with rugged, forested hills reaching a maximum elevation of 122 m. The live-trap grid was located in the Limon Bay lowlands about two km south of the Fort Sherman Post at an elevation of above five m. Immediately west of the grid the lowlands give way to a series of ridges that reach a height of 87 m. Passing near the grid is the Rio Aquadulce that flows northeastward into Limon Bay.

The site selected for a live-trap grid was a relatively level area in continuous forest, which was about 55 years old and several hundred meters from the nearest road. Topographically, the grid was rather saucer-shaped with a 1–3 m depression in the southwest quarter (Fig. 6). In the rainy season, two temporary streams joined near the south edge of the grid to form a large pool of standing water that was sometimes 0.5 m deep.

Structurally, the Sherman forest consisted of two fairly well-defined strata of trees—an upper stratum 15 to 30 m in height and a lower stratum 8 to 10 m in height (Table 2). Dominant members of the upper stratum included *Ficus insipida*, an unidentified species of *Inga*, *Mangifera indica*, and *Spondias mombin* all of which had large DBHs (Table 2). The occurrence of numerous large mango trees (*Mangifera indica*), many of which were probably more than 50 years old (J. Duke, pers. comm.), clearly indicates that human activities have strongly affected this region in the past (Fig. 5c). Of the trees in the lower stratum, *Gustavia superba* and an unidentified species of *Myrcia* were most common. Typical views of the forest are shown in Figures 5c and 5d.

Although at least five species of palms were recorded on the Sherman grid, they were not as conspicuous as at Rodman. Most examples of *Corozo oleifera* and *Manacaria saccifera* were restricted to low, moist areas in the southwest and northeast corners of the grid, respectively (Fig. 6). *Astrocaryum standleyanum* and *Scheelea rostrata*, common members of the lower stratum of trees, were distributed throughout the grid.

Several species of *Psychotria* (Table 2) and *Piper* were dominant elements of the shrub layer (Fig. 5d). Lacking at Sherman were tangles of thorny vines and sprawly trees such as *Hirtella racemosa*, and thus the undergrowth was more penetrable by man. Heavy woody vines were common, but epiphytes were conspicuously lacking, which probably indicates that the dry

As at Rodman, marked seasonal changes occurred within the Sherman forest. In the rainy season, standing water covered many of the low areas of the grid, and the "pool" near the south edge was nearly always full. Water draining from the grid after moderate rains sometimes passed over the tops of my boots, but it usually drained off quickly. Even after a particularly hard rainfall of 4.7 inches one afternoon in August, the grid was well drained by the next morning.

By late December the grid had started to dry out, and in January the ground, most streams, and the "pool" were nearly dry. By the middle of January, *Bombacopsis fendleri* and *Spondias mombin* had lost their leaves, and though not completely deciduous, *Ficus insipida* and *Mangifera indica* were dropping leaves. At this time, many other plants were acquiring new leaves. A thick layer of crisp, dry leaves carpeted the forest floor throughout the dry season until the middle of May when trapping was completed. Although the rains had started early in May, the forest and streams were dry until at least the middle of that month.

VERTEBRATE FAUNA

Nearly 70 species of terrestrial, arboreal, or aerial mammals were captured or observed or left signs of their presence in each forest (unpublished data). In addition to *L. adspersus*, *O. capito*, and *P. semispinosus*, five other rodent species (*Nyctomys sumichrasti*, *Oryzomys concolor*, *Nectomys alfaris*, *Sigmodon hispidus*, and *Zygodontomys microtinus*) were trapped on the Rodman grid; besides *O. capito* and *P. semispinosus*, five additional rodent species (*Sciurus granatensis*, *Heteromys desmarestianus*, *Oryzomys bicolor*, *O. caliginosus*, and *Tylomys panamensis*) were trapped on the Sherman grid. Ecological relationships between the various rodents are discussed elsewhere (Fleming, 1970a).

I have little direct evidence of predation on the three species studied. One tayra (*Eira barbara*) was found feeding on a spiny pocket mouse. The stomach of a four-eyed opossum (*Philander opossum*) contained the tail of a young spiny rat. Rodent fur was found in the stomach of two species of opossums, *P. opossum* and *Didelphis marsupialis* (Fleming, unpublished). At Sherman a semiplumbeous hawk (*Leucopternis semiplumbea*) that had been perched on a branch directly above me dropped on a rice rat that I had just examined and released. The mouse escaped unharmed and was caught again the next day. Slud (1960) described similar behavior in this hawk at "La Selva," Costa Rica. Other potential predators seen on or near the grids included several species of snakes (e.g., common boa, *Constrictor constrictor*; rainbow boa, *Epicrates cenchria*; spotted rat snake, *Spilotes pullatus*; and fer-de-lance, *Bothrops atrox*), two owls (mottled owl, *Ciccaba virgata* and spectacled owl, *Pulsatrix perspicillata*), and several species of omnivorous or carnivorous mammals (brown-masked opossum, *Metachirus nudicaudatus*; grison, *Galictis allamandi*; ocelot, *Felis pardalis*; and perhaps the puma, *F. concolor*, and jaguar, *F. onca*).

MATERIALS AND METHODS

Field techniques followed the "classic" pattern for small mammal studies. Identical grids covering 5.06 ha (12.5 acres) were established in both forests and consisted of 100 trapping stations arranged in ten rows, ten stations per row with a distance of 25 m between stations and rows. Each station was marked by a 1 m steel reinforcing rod. One National live-trap measuring 310 x 140 x 140 mm or 310 x 165 x 165 mm was placed on the ground within one meter of each steel rod. An additional 22 traps at Rodman and 7 to 10 at Sherman were tied to trees, logs, and vines at suitable places around the grid, but because only three individuals, one of each species, were caught in "tree traps," these are ignored in this account. The "tree traps" caught mainly opossums and scansorial or arboreal rodents.

In June, 1966, traps were baited with banana slices only. From July to the end of the study, sunflower seeds were added as bait. To reduce trap disturbance by opossums, carrots were alternated with bananas in grid traps starting in February. From October to the end of the study all ground traps were covered with a tarpaper jacket to protect the animals from the rain and predators.

The trapping schedule followed the lunar month, and nights with the brightest moon were avoided (see Table 1 for schedule). At Rodman all traps were operated for nine consecutive nights each month. At Sherman all traps were operated for nine consecutive nights except in November, December, February, and March when they were operated for only eight nights. In all, the Rodman grid was trapped 13 times and the Sherman grid 12 times. In the final trapping sessions, all animals caught on the grids were killed and preserved. Traps were checked each morning and left set during the day because, with the exception of a few "trap-repeaters," only one animal was ever trapped in the day. No prebaiting was used.

Animals caught on the grids were marked by toe-clipping and released after being examined. The following information was recorded for each individual: location of capture, identification number, age, sex, sexual condition, evidence of molt, and behavior upon release. Four age classes, based on size and pelage, were established for each species. These classes were: juvenile, subadult, young adult, and adult. Age-related molts are distinctive in each species, making the assignment of animals to one of the four classes quite easy. Characteristics of the various age classes are summarized in Table 3.

Sexual condition of each individual was noted at each capture. For males, this included relative size and position of testis. For *O. capito* and *P. semispinosus*, testis position was quite labile, making this information of little use in deciding whether an individual was fertile. For *L. adspersus*, in contrast, the customary designations of abdominal, inguinal, or scrotal for testis position offer a valid indication of fertility. Data recorded for females included condition of vagina (open or closed), condition of nipples

TABLE 3
AGE CLASSES IN *Liomys adspersus*, *Oryzomys capito*, and *Proechimys semispinosus*

Species	Age class	Body length (mm)	Pelage
<i>L. adspersus</i>	Juvenile	<100	Aristiforms thin; conspicuous buffy setiforms lacking
	Subadult	101-115	Molting into adult pelage
	Adult	116+	Adult pelage complete; buffy setiforms present
<i>O. capito</i>	Juvenile	83-104	Pelage thin, dull brown-gray in color
	Subadult	99-115	Pelage thick and dark brown dorsally
	Young adult	116-120	Adult pelage fresh; buffy hairs cover dorsum and sides
	Adult	120+	Adult pelage becoming worn and paler
<i>P. semispinosus</i>	Juvenile	112-150	Aristiforms thin; dorsal coloration dull brown
	Subadult	151-200	Lateral setiforms agouti; molting into adult pel.
	Young adult	200-220	Adult pelage fresh
	Adult	220+	Adult pelage slightly worn to worn

Body lengths of subadults and young adults are somewhat variable. In *P. semispinosus* males in all age classes are generally larger than females.

(small, medium, lactating, or recently lactating), and presence or absence of palpable embryos.

Each month when the grids were trapped a supplementary line of 70 to 130 National live-traps baited with banana and sunflower seeds was operated at least 2 km from the grids. Traps in these lines were placed in different locations each month but always in habitat similar to that of the grid. In April, May, and June at Rodman, and in April and May at Sherman, trap lines were run near the grids (distances ranging from 50 to 400 m) in an attempt to recapture animals that might have emigrated from the grids. At Rodman areas to the northeast, south, and west of the grid were trapped in this manner. At Sherman areas to the southeast, north, and east of the grid were trapped.

All animals captured in the supplementary and peripheral lines were killed and preserved. Measurements recorded for each individual included weight and length of head and body, tail, hind foot, and ear (from notch). External sexual condition was recorded for every female, and testis size (length x width) was recorded for each male. Skins (prepared flat) and skulls were dried, and reproductive organs (testes, epididymides, seminal vesicles,

ovaries, and uteri) were fixed in 10 per cent formalin. Stomachs of some *L. adpersus* and *O. capito* were preserved in formalin; those of *P. semispinosus* were examined while fresh.

The preserved reproductive organs of many individuals were examined histologically. Both ovaries of most females were sectioned. For most males whose tubules of the cauda epididymis were not macroscopically visible one testis and epididymis was examined along with a representative sample of organs from males with swollen tubules. Slices of testis and epididymis and whole ovaries were embedded in Tissuemat, serially sectioned at 10 μ , and selected sections mounted on slides and stained with hematoxylin and eosin. The slides were examined for the presence or absence of sperm in the testis and epididymis or for the number of fresh corpora lutea or size of follicles in each ovary. In nearly all cases, epididymal tubules that were macroscopically visible contained large numbers of spermatozoa so that males whose testis was not sectioned were considered fertile when their tubules were swollen.

RESULTS

TRAP RESPONSE

Since most methods for estimating mammalian population size require as a basic assumption that animals are being sampled randomly, there should be no differential trap responses between marked and unmarked individuals, sexes, and species in multispecies studies. Leslie et al. (1953) have described methods for testing randomness of capture within small mammal populations, but their methods assume that no dilution either by births or immigration occurs during the testing periods. Since none of the populations of the three species in this study was entirely free from these restrictions (breeding was aseasonal in two of the species and immigration was possible in all species), other methods for documenting the species' trap responses had to be used. As a result, the following statistics were compared between marked and unmarked individuals, sexes, populations, and species: rate of capture, mean number of captures per month, and tendency to skip trap sessions between recaptures.

RATE OF CAPTURE OF MARKED AND UNMARKED ANIMALS.—This statistic was determined by totaling the number of marked and unmarked individuals whose initial capture occurred on day 1, 2 . . . , 9 of each session. Data for 12 sessions at Rodman and 11 sessions at Sherman were combined, and a daily rate of capture for each population and species, sexes combined, was calculated and is shown in Figure 7. The different frequency distributions were compared, using the Kolmogorov-Smirnov two-sample test.

Results of this analysis showed that two species, *L. adpersus* and *O. capito*, were alloresponsive (Tanaka, 1956), as marked individuals were captured at a significantly faster rate than unmarked individuals (Fig. 7a, b; $P < .05$). *P. semispinosus* was isoresponsive (Tanaka, 1956), as marked and unmarked individuals were captured at the same rate (Fig. 7c). There were

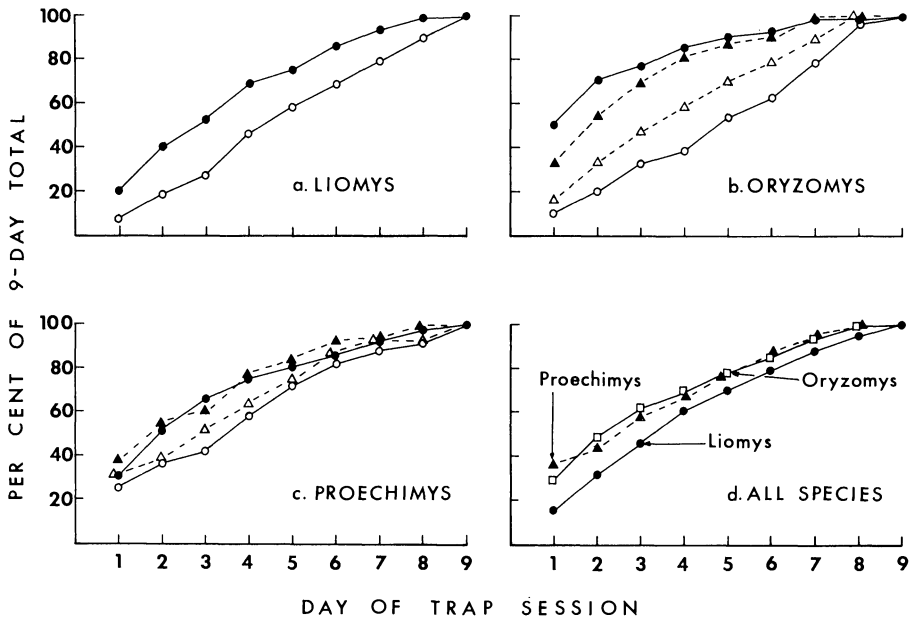


FIG. 7. Rates of capture at Rodman (circles) and Sherman (triangles) of marked (solid figures) and unmarked (open figures) individuals of three species.

no interpopulational differences for *O. capito* and *P. semispinosus* when data from marked and unmarked animals at each site were combined. Interspecific comparisons showed that the capture rates of *O. capito* and *P. semispinosus* were similar and were significantly higher than those of *L. adspersus* (Fig. 7d).

FREQUENCY OF RECAPTURE.—In comparing recapture frequencies (expressed as the average number of recaptures per month) between sexes, populations, and species, all individuals marked and released between June 1966 and May 1967 were used. Data summarizing recapture frequencies are shown in Table 4. Significant differences in these data were determined using "t" tests. For all populations and species there were no significant differences in frequency of recapture between males and females, and there were no interpopulation differences in the rice rat and spiny rat ($P > .05$). *O. capito* and *P. semispinosus* had similar recapture frequencies ($.10 > P > .05$) as did *L. adspersus* and *P. semispinosus* ($P > .50$), but *O. capito* had a higher recapture frequency than *L. adspersus* ($.02 > P > .01$).

TENDENCY TO SKIP TRAP SESSIONS.—As seen in Table 4, some individuals of each species missed one or more months between recaptures. Percentages of *L. adspersus* and *P. semispinosus* populations with this tendency were similar (between 20 and 38 per cent) and were higher than in *O. capito* populations, in which only one individual missed any sessions between captures at Rodman. Though there were no interpopulation or interspecific

TABLE 4

TRAP RESPONSES IN *Liomys adspersus*, *Oryzomys capito*, AND *Proechimys semispinosus* AT RODMAN (R) AND SHERMAN (S)

Species	Location	Sex	Mean no. captures per indiv. per mo.	Mean length of absence (in mos.) per indiv.	Per cent indiv. absent one or more mos. between capt.
<i>L. adspersus</i>	R	M	1.78±0.20 (112)	1.96±0.25 (27)	24.1
	R	F	1.85±0.20 (108)	2.13±0.50 (36)	33.4
<i>O. capito</i>	R	M	3.73±0.76 (32)	1.00 (1)	3.2
	R	F	3.48±0.83 (24)	0.00 (0)	0.0
	S	M	2.46±0.40 (65)	1.08±0.16 (13)	20.0
	S	F	2.26±0.34 (43)	1.20±0.51 (5)	11.6
<i>P. semispinosus</i>	R	M	2.35±0.49 (55)	3.09±1.55 (11)	20.0
	R	F	1.89±0.50 (27)	1.33±0.44 (6)	22.2
	S	M	1.81±0.40 (58)	3.06±1.18 (16)	27.6
	S	F	1.97±0.50 (42)	2.81±0.77 (16)	38.2

Means are given \pm 95% confidence intervals. Number of individuals indicated in parentheses.

differences between mean length of gap in males and females ($P > .05$ in "t" tests), gaps of *L. adspersus* and *P. semispinosus* were significantly longer than those of Sherman *O. capito* ($.01 > P > .001$).

Ideally, if population densities of different species are to be determined using the same method of estimation, the animals should be responding to traps in a similar manner. Practically speaking, however, this situation is probably rare in nature. Differences in at least some components of trap response were seen in the three species, and they undoubtedly result from behavioral differences between the species. For instance, gaps in the trap records of female spiny pocket mice can probably be attributed to behavioral changes (at least with respect to traps) during the breeding season. Several individuals were caught prior to and after, but not during, the time they were pregnant or raising a litter; very few pregnant females were trapped on the grid or supplementary lines. Of the three species, *O. capito* had the least tendency to skip trap sessions, and individuals of this species could be accounted for with greatest certainty, particularly at Rodman. The presence or absence on the grid of individuals of the other two species was less certain, making monthly estimates of their population sizes by an enumeration method more tenuous.

The degree to which these slightly different trap responses influence estimates of population sizes is not known. Perhaps the most serious violation of the assumptions involved in population estimates is the nonrandom sampling that occurred in three of the five populations. When marked animals are caught at a faster rate than unmarked animals, methods such as the Lincoln Index that use a ratio of marked to unmarked animals caught

in each trapping session will tend to underestimate population size, and under these conditions Tanaka (1956) has advised against using estimation methods based on capture-recapture data. Interpretation of population densities presented next will have to be made in light of this warning and after considering the way in which the species' trap responses differed from each other.

POPULATION SIZES AND DENSITIES

Since marked and unmarked individuals of *L. adspersus* and *O. capito* were not being sampled randomly, estimates of their populations based on the conventional Lincoln Index or more recent Jolly stochastic (Jolly, 1965) methods might be subject to considerable error. Estimates of the *P. semispinosus* populations using these methods would be more accurate because this species appears to be isoresponsive to traps. To see whether conventional methods could be used on members of the *marked* populations only, the procedure for determining rate of capture of marked and unmarked animals described in the last section was applied to marked animals. Individuals caught in the session following that in which they were marked were considered "unmarked"; when captured in later sessions, they were considered "marked." The day (1-9) of first capture within those sessions was recorded, data from all months were combined, and the rates of capture for those two classes of individuals were compared using a Kolmogorov-Smirnov two-sample test. Results of this procedure showed that in two populations, those of *L. adspersus* and Rodman *O. capito*, individuals with more trap experience were caught at a faster rate than those with less experience ($P < .05$). Thus, even within the marked segments of two populations, all animals were not reacting to traps in a uniform manner.

In order to avoid using an estimation method based on assumptions known to be violated by the animals in this study, I have relied on *direct enumeration* to determine monthly population sizes. This method considers monthly populations to consist of all animals caught during a particular trapping session plus those marked previously, skipping that session, but reappearing in the traps in a later session and is based on the premise that a high percentage of the actual population enters the traps each month. Because most animals caught in a trapping session entered a trap by the seventh day (see Fig. 7d), I feel these direct counts give a reasonable estimate of the number of animals inhabiting the grids each month. As a check on these values, monthly populations were also estimated using the modified Lincoln Index of Lidicker (1966).

In calculating population densities, I added to the basic grid (5.06 ha) a strip equal in width to the average distance between successive captures for each species (see section on Movements and Home Range Sizes). At Rodman the areas used in the calculations were 8.54 ha for *L. adspersus*, 9.34 ha for *O. capito*, and 9.03 ha for *P. semispinosus*. On the side of the Rodman grid nearest the road (see Fig. 3), a strip 25 m wide was used for

each species, as no marked animals were captured across the road during peripheral trapping in May 1967. At Sherman the areas were 9.68 ha for *O. capito* and 9.20 ha for *P. semispinosus*.

For each species, monthly changes in population density are illustrated in Figure 8 and are discussed below.

L. adspersus.—The spiny pocket mouse had the highest population density of any species throughout the year at Rodman (Fig. 8). Density averaged about 10 per ha from June to October, and then it declined to about 5.5 per ha in February and March. A slight upswing owing to the recruitment of juveniles occurred in April; then followed another decline in May and early June. Although only 29 individuals were caught on the grid in June 1966, the population at that time was estimated to contain at least 71 animals. The low catch in June was likely the result of using a less attractive bait (banana only) than was subsequently employed. Based on the presumed resident status of many individuals first marked in July and August, it was estimated that 71 individuals, rather than the 29 actually caught, resided on the grid in June. In all months except July, the enumeration and Lincoln Index estimates were in quite good agreement (Fig. 8). In July the recapture of only a few animals marked in June caused the Lincoln Index to badly overestimate the population size in that month. It is possible that both methods of estimation consistently underestimated population size because of the alloresponsive behavior of this species. During the year biomass (wet weight) of *L. adspersus* varied from 208 to 629 gm per ha.

O. capito.—This species had the lowest population densities of the three species in both forests (Fig. 8). Levels were low on both grids in June 1966. Later in the rainy season densities of both populations increased, reached peaks of 3.2 per ha in October at Rodman and 4.3 per ha in November at Sherman, and then steadily declined to the same low levels that had prevailed nearly a year earlier. Throughout most of the year, the Sherman population apparently was larger than that at Rodman. Both methods of population estimation yielded similar results which likely underestimate actual densities. Biomass in this species varied from 0 to 159 gm per ha at Rodman and from 15 to 214 gm per ha at Sherman.

P. semispinosus.—Populations of the spiny rat were similar to those of the rice rat in that they were at low levels in June 1966, increased toward the end of the rainy season, and then declined throughout the 1967 dry season (Fig. 8). At Rodman, density was 1.1 per ha in June but increased nearly four-fold (to 3.8 per ha) by October and remained there for three months before declining to 0.6 per ha in June 1967. Throughout the year densities of *P. semispinosus* at Sherman were greater than those at Rodman, but fluctuations were similar: from an initial density of 2.3 per ha, the population increased to a level of about 5.0 to 5.6 per ha from September through November; this was followed by a steady decline to a density of about 1.0 per ha in May 1967. Both methods of population estimation are

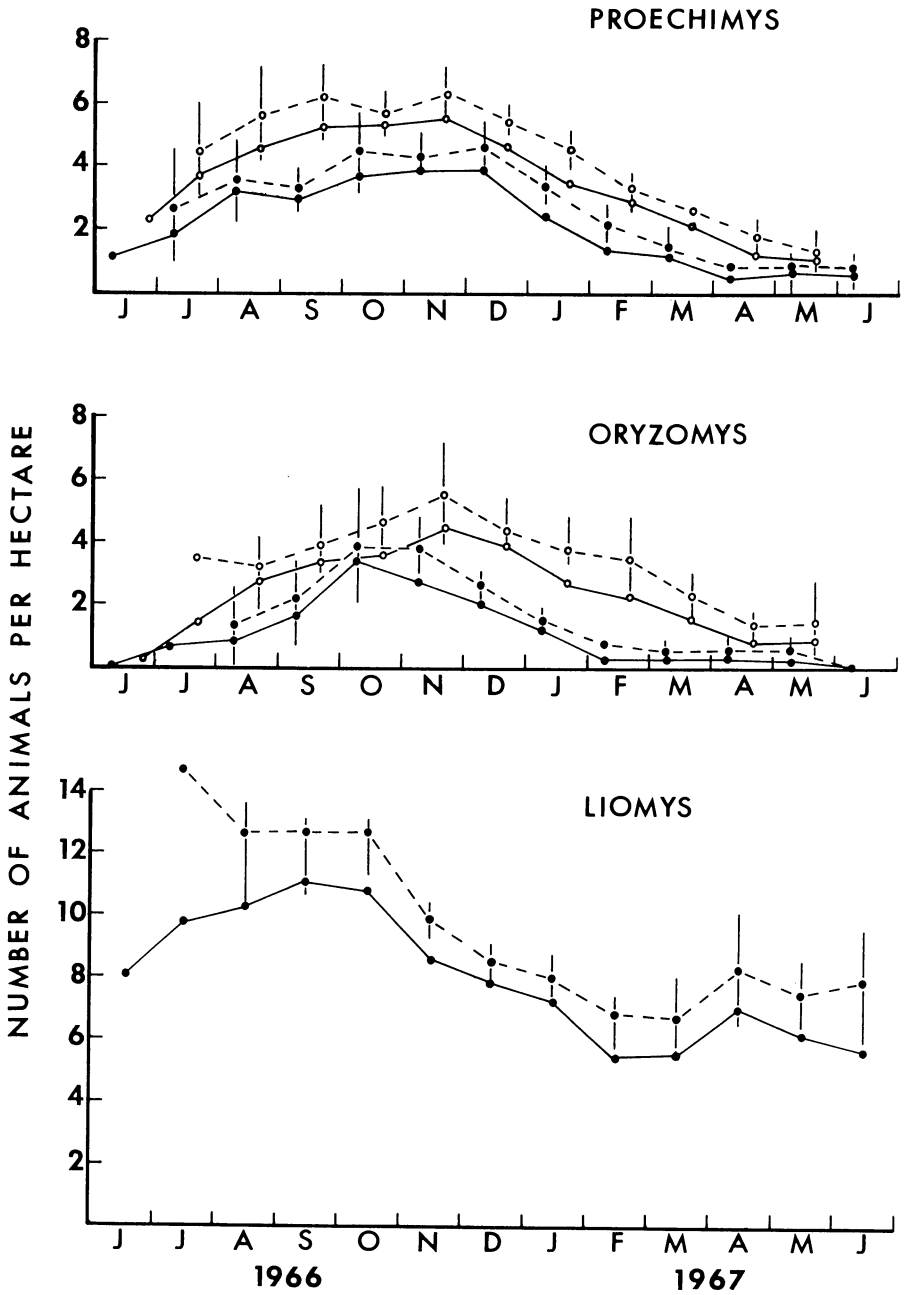


FIG. 8. Estimates of densities in a year in five populations of three species. Estimates based on actual counts (solid lines) and modified Lincoln Index (dashed lines) for Rodman (solid circles) and Sherman (open circles) populations. Vertical lines indicate 1 S.E. of Lincoln Index estimate.

in close agreement (Fig. 8) and are likely to reflect actual population densities because this species is isoresponseive towards traps. Biomass varied from 125 to 1099 gm per ha at Rodman and from 278 to 1600 gm per ha at Sherman.

SURVIVORSHIP AND LONGEVITY

Because survivorship could not be measured directly (emigration was always a potentially confounding factor), *disappearance rates* were used in estimating survival rates. In calculating disappearance rates, only those animals whose age at disappearance could be estimated with an accuracy of \pm one month were used. This meant that for all species except *L. adspersus* data from animals first marked as adults had to be disregarded. Since *L. adspersus* is a seasonal breeder, all adults were arbitrarily considered to be born in February, the midpoint of the breeding season. Based on observed rates of maturation, juvenile *L. adspersus* and *O. capito* were considered to be 1-2 months old, subadults 3 months old, and young adults 4 months old. For *P. semispinosus* juveniles were judged to be 1-3 months old and subadults 4-6 months old. Whenever adequate data were available, mean ages at disappearance were calculated for each sex, population, and species. In the two year-round breeding species, *O. capito* and *P. semispinosus*, those animals born in the first half of the year were analyzed separately from those born in the last half of the year. Significant differences in disappearance rates were tested for, using the Wilcoxon two-sample test.

The above analysis considers only those animals old enough to enter traps or older. To estimate early juvenile survival, another procedure was used. The number of pregnant or lactating *resident* females captured on the grids, and therefore the expected number of litters, was totaled each month and multiplied by the average litter size to arrive at an expected number of juveniles that would be added to the trappable population approximately one month later for *L. adspersus* and *O. capito* and two months later for *P. semispinosus*. Then the number of unmarked juveniles actually trapped each month was compared with the expected number, and an index of juvenile survival, the ratio of observed to expected, was calculated. Individual *L. adspersus* and *O. capito* that were subadults when first marked were recorded in the "Observed" column in the month they would have been juveniles, usually one month earlier. Older juvenile *P. semispinosus* were likewise entered in the "Observed" column in the month when they were most likely weaned. In this analysis it was assumed that rates of juvenile emigration and immigration equalled each other.

As a check on the estimated rates of survivorship based on disappearance rates, direct and indirect estimates of longevity were made. Direct estimates, of course, were based on the trap-revealed longevities of recaptured individuals. Indirect estimates were made by studying tooth wear in the sacrificed samples. Sacrificed juveniles were aged by noting the number of erupted molars present (e.g., J2 = 2 molars erupted, J3 = 3 molars

erupted). Degree of wear seen in the upper cheek teeth of sacrificed adults was scored using an arbitrary scale ranging from 0 (no wear) to 6 (extreme wear). Typical examples of three tooth wear categories in each species are shown in Figure 9. Because absolute ages could not be applied to any of the categories except the earliest one, sacrificed animals were assigned to one of two relative ages, "young adults" (categories 1-3) or "old adults" (categories 4-6). It must be remembered that "longevities" in this study are based on survivorship, not mortality, data and thus are minimal estimates of longevity under natural conditions.

The spiny pocket mouse offered a unique opportunity to estimate longevity because it is a seasonal breeder. Based on cheek-tooth wear, sacrificed adults were assigned to a year-class representing the year in which they were born. Thus, animals with worn molars taken in the early months of the study were assigned to the 1965 year-class (it is doubtful that representatives of earlier classes would be alive in mid-1966), and animals with similar wear taken in the 1967 breeding season were assigned to the 1966 year-class. The accuracy of my assignments could be tested because in June, 1967, all individuals on the Rodman grid were killed and preserved. In all cases, known members of the 1966 year-class, based on mark and release records, were properly assigned to that class; the same was true of individuals of the 1967 year-class. Therefore, I feel confident in the ability to distinguish between year-classes in this species.

Estimates of the rate of tooth wear in members of the 1966 year-class of *L. adspersus* can be made by examining the distribution of tooth wear among monthly sacrificed samples (Fig. 10). In June 1966, individuals evidenced little wear on their cheek teeth. Each month thereafter the average amount of wear increased at a fairly regular rate. Individual variation was quite high from August to December, owing in part to variation in dates of birth of the preserved individuals. By June 1967 surviving members of the 1966 year-class had very worn cheek teeth.

L. adspersus.—The mean age at disappearance in this species, 9.22 mo, was significantly greater than that of the other two species (Table 5). The ages of males and females were similar, and the rate of disappearance was quite constant, averaging about 17 per cent per month (Fig. 11). At least 25 per cent of the members of the 1966 year-class survived one year or more. Judging from the close agreement between the expected and observed number of juveniles (Table 6), juvenile mortality may be quite low in this species.

Direct estimates of longevity were obtained for seven individuals (one male, six females), which were approximately 15-16 months of age when last captured. Among animals in the preserved sample, at least one individual of the 1965 year-class was collected in each of the following months in 1966: June (one male, one female), August (one male, one female), September (one female), and November (one female). It is likely that the latter female was around 21 months old when sacrificed. Members of the 1966 year-

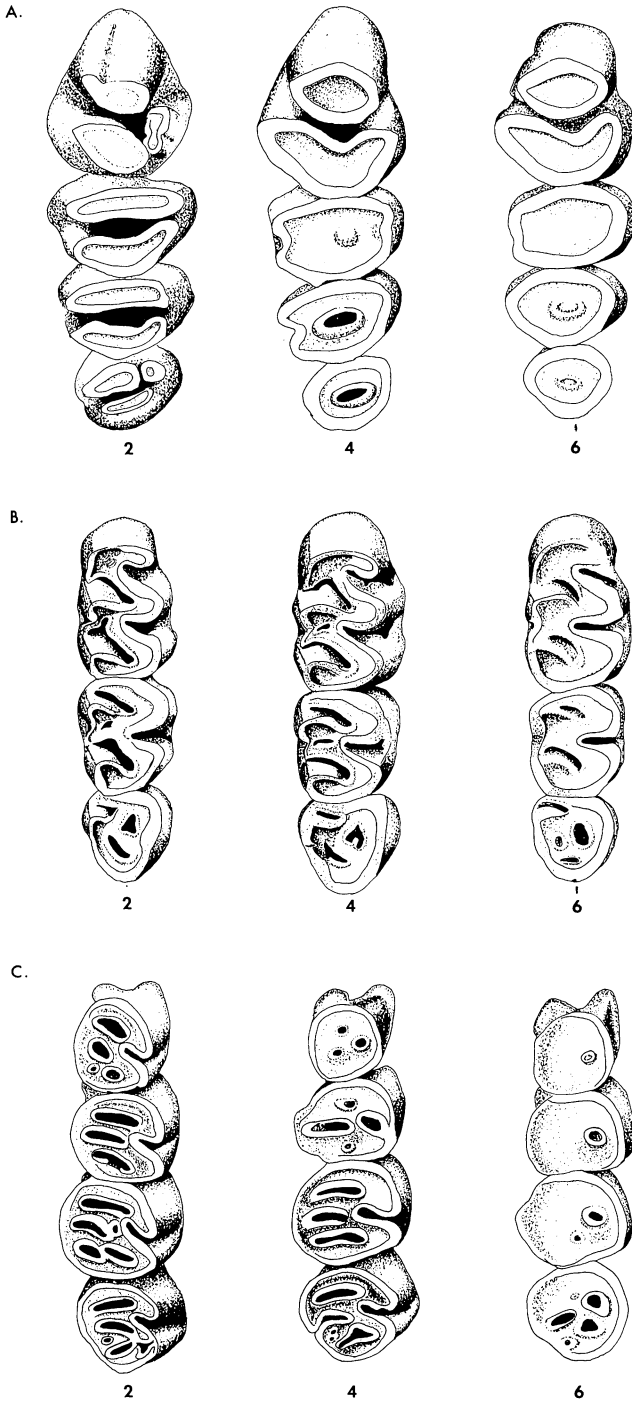


FIG. 9. Selected examples of tooth wear in right upper cheek teeth of: A, *L. adspersus*; B, *O. capito*; and C, *P. semispinosus*. Similar categories represent approximately similar amounts of wear but not similar absolute ages.

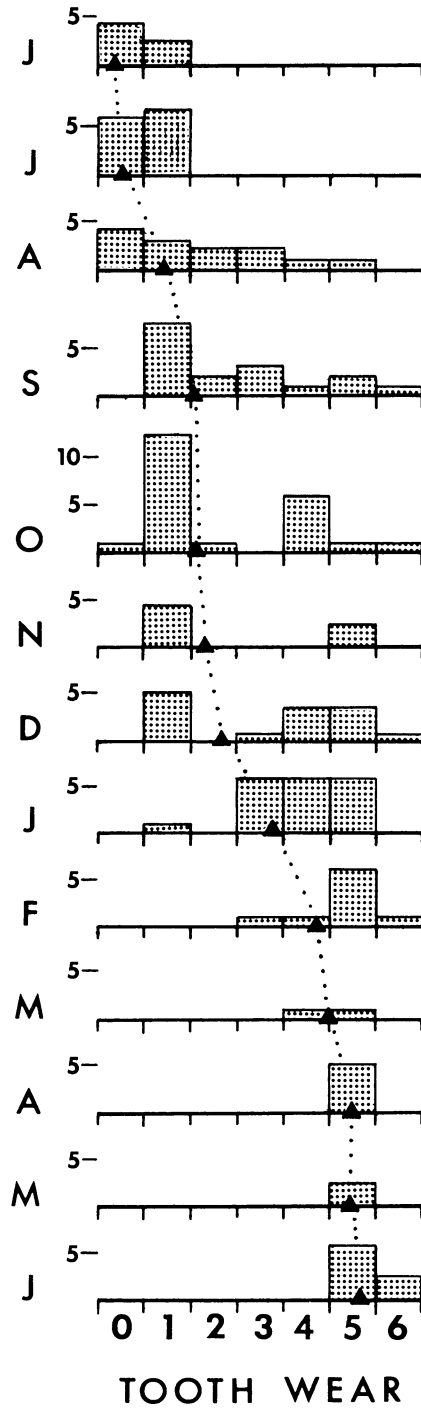


FIG. 10. Distribution of monthly samples of the 1966 year-class of *L. adspersus* by categories of wear of cheek teeth. Number of individuals indicated at left. Solid triangles indicate mean monthly values.

TABLE 5

MEAN AGE OF DISAPPEARANCE OF INDIVIDUALS IN *Liomys adspersus*, *Oryzomys capito*,
AND *Proechimys semispinosus*

Species	Location	Half of year	Sex	N	Mean age (months)
<i>L. adspersus</i>	Rodman	M	66	8.84
		F	70	9.60
<i>O. capito</i>	Rodman	First	M & F	12	4.66
		Second	M & F	21	4.00
	Sherman	First	M & F	17	5.11
		Second	M & F	37	4.76
<i>P. semispinosus</i>	Rodman	First	M & F	29	6.15
		Second	M & F	16	3.81
	Sherman	First	M & F	27	7.97
		Second	M & F	20	4.70

class comprised 95 per cent of the adult sample of 19 in January 1967, but their numbers had declined to 35 per cent of the adult sample of 31 in June 1967 (see Fig. 15). These data on survivorship indicate that while some individuals may live more than a year and a half, most members of a year-class disappear from the population by the end of the next breeding season. The data suggest that the disappearance curve for this species (Fig. 11) approximates a survivorship curve which has the formula $y = 107.52 - 6.64x$ (Fig. 12).

O. capito.—The mean age at disappearance of this rice rat, 4.62 mo, was significantly lower than that of *L. adspersus* ($P < .05$; Table 5). Because of the small sample of females, data from both sexes were combined at both localities. There were no seasonal differences in mean age at disappearance at either locality, and differences between localities were not statistically significant. As seen in Figure 11, in which data from both localities are combined, the disappearance rate of this species was much higher than that of *L. adspersus*. No animals whose known age was 9 mos or older remained on the grids. Because only about one-third of the expected juveniles were accounted for (Table 7), juvenile mortality is high in this species. Similar low rates of juvenile survival were seen on both grids.

I have few direct estimates of longevity in this species. No individual was observed for more than seven months on either grid. At Rodman, one male marked as a subadult (2–3 mos old) was about eight months old when it died; its tooth wear index at death was 6. One female, also marked as a subadult, disappeared when about eight months old. At Sherman, one male and one female were estimated to have lived for eight and nine months respectively; the female's tooth wear index at death was 6.

If the degree of tooth wear seen in these two individuals whose age at death was known is representative of the populations in general, cheek teeth wear quite rapidly in this species. Relative ages of preserved subadults

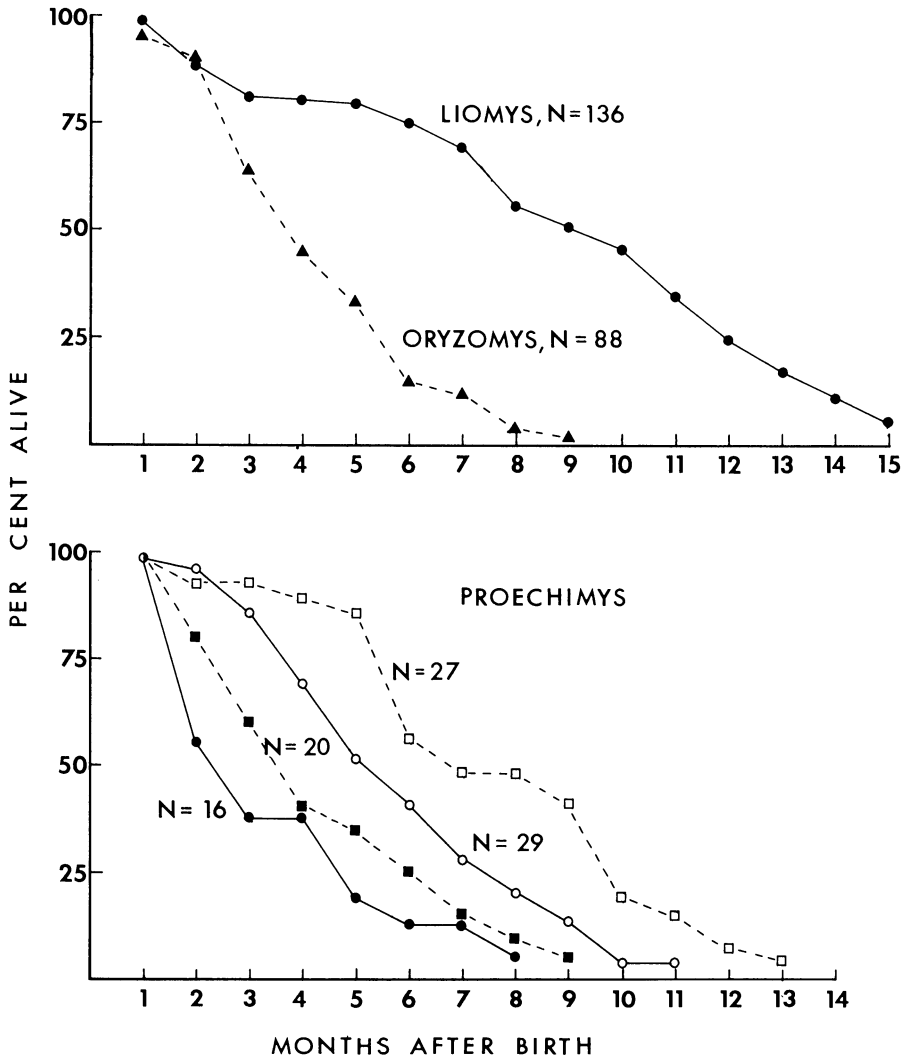


FIG. 11. Rates of disappearance of marked animals. For *Proechimys*, circles = Rodman, squares = Sherman; solid symbols = animals born in the wet season; open symbols = animals born in the dry season.

and adults (sexes combined), as judged by tooth wear, are shown in Table 8. Since 22-43 per cent of these adults were at least six months old (categories 4-6) when captured, these ages are apparently attained more frequently by animals surviving early juvenile life than indicated by the disappearance curve (Fig. 11).

Data on tooth wear suggest that the disappearance curve of this species (Fig. 11) underestimates survivorship somewhat, probably owing to emigration. To arrive at a survivorship curve that is in better agreement with

TABLE 6
 JUVENILE SURVIVORSHIP IN *L. adspersus*

Month	No. females pregnant or lactating	No. juveniles expected	No. juveniles observed	Per cent survival
Junc	0			
July	0			
August	0			
September	0			
October	0			
November	0			
December	1			
January	3	3.2	2	62
February	5	9.6	4	42
March	3	16.0	11	69
April	4	9.6	24	250
May	0	12.8	10	78
Junc	0	0.0	9*	
Total		51.2	51	100

* Not included in Total. Juveniles were assumed to become trappable one month after pregnant or lactating females were recorded.

information provided by sacrificed animals, a modification of the disappearance curve is needed. In making this modification, I am assuming that 10 per cent of the population that attains a trappable age is still alive at an age of nine months. This is a reasonable assumption based on the distribution of relative ages in the combined Rodman and Sherman preserved samples

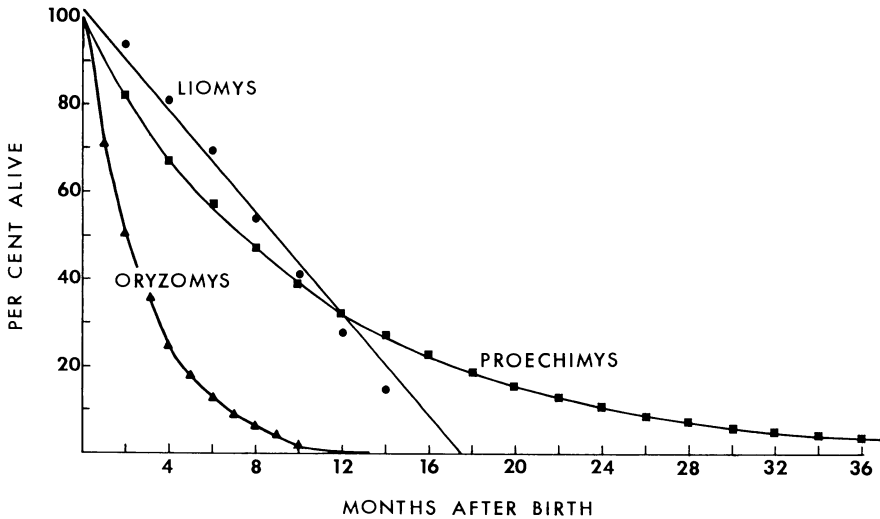


FIG. 12. Adjusted survivorship curves of three species of rodents.

TABLE 7
 JUVENILE SURVIVORSHIP IN *O. capito* AND *P. semispinosus* AT RODMAN (R) AND SHERMAN (S)

Month	No. females pregnant or lactating		No. juveniles expected		No. juveniles observed		Per cent survival	
	R	S	R	S	R	S	R	S
<i>O. capito</i>								
June	0	0						
July	1	0			5*	3*		
August	0	3	3.9	0.0	3	7*	77	
September	3	3	0.0	11.7	9	11		94
October	5	4	11.7	11.7	5	7	43	60
November	8	4	19.5	15.6	3	6	15	38
December	2	5	31.2	15.6	0	5	0	32
January	0	5	7.8	19.5	0	0	0	0
February	0	3	0.0	19.5	0	2		10
March	1	1	0.0	11.7	1	0		0
April	0	0	3.9	3.9	1	2	26	51
May	0	1	0.0	0.0	0	0		
Total			78.0	109.2	22	33	28	30
<i>P. semispinosus</i>								
June	0	2						
July	0	1			4*	2*		
August	0	1	0.0	5.0	8*	8		160
September	1	2	0.0	2.5	3*	10		400
October	1	2	0.0	2.5	3*	3		120
November	0	0	2.5	5.0	3	4	120	80
December	1	0	2.5	5.0	3	1	120	20
January	0	1	0.0	0.0	1	0		
February	1	4	2.5	0.0	0	0	0	
March	0	2	0.0	2.5	0	0		0
April	0	0	2.5	10.0	1	1	40	10
May	1	1	0.0	5.0	0	1		20
Total			10.0	37.5	8	28	80	75

* Not included in Total. Juveniles were assumed to become trappable one month (in *O. capito*) or two months (in *P. semispinosus*) after pregnant or lactating females were recorded.

(Table 8). Values for months 4 to 8 in the disappearance curve were similarly adjusted by the addition of 10 per cent to each. Because only about one-third of the expected juveniles survived to a trappable age (Table 7), 33 per cent was used as an estimate of survivorship to age one month. Values for subsequent months were derived as fractions of the population attaining an age of one month. The survivorship curve resulting from these adjustments follows the formula $\log y = 1.818 - 0.147x$ and, after the intercept is adjusted to 1.000, is shown in Figure 12. The curve indicates that few individuals live more than one year under natural conditions.

TABLE 8
AGE DISTRIBUTION IN *O. capito* AND *P. semispinosus*, BASED ON DEGREE OF
CHEEK TEETH WEAR

Species and Location	Tooth Wear Category							Total specimens
	0	1	2	3	4	5	6	
<i>O. capito</i> Rodman	5	1	3	2	1	1	1	14
<i>O. capito</i> Sherman	5	2	11	11	6	10	6	51
<i>P. semispinosus</i> Rodman	19	19	35	15	23	2	1	114
<i>P. semispinosus</i> Sherman	24	17	18	23	34	11	1	128

P. semispinosus.—Owing to small sample sizes, estimates of survivorship are likely to be least reliable for this species. According to available information (sexes combined), there was a marked difference in age at disappearance between animals born in the first half of the year (primarily the dry season) and those born in the second half of the year (the wet season). Those born in January through June at both localities had a significantly greater mean age at disappearance and lower rate of disappearance than those born in July through December ($P < .05$; Table 5 and Fig. 11). Within each half of the year, disappearance rates were higher at Rodman than Sherman ($P < .05$). As in *L. adspersus*, juvenile mortality in *P. semispinosus* was apparently rather low, as nearly 80 per cent of the expected number of juveniles were accounted for at each locality (Table 7). Although numbers are too small to have any significance, recruitment success was lowest in the first half of 1967, a time when juvenile survivorship should have been high.

Estimates of minimum longevities are available for seven individuals recaptured several times. At Rodman, three males and one female were estimated to be at least 12, 14, 20, and 13 months old, respectively, when last captured. The oldest male had a tooth wear index of 3. At Sherman, one male and two females were judged to be at least 17 months old when sacrificed, and their indices of tooth wear were 1, 1, and 3, respectively. Data on tooth wear from these individuals indicate that molar wear in this species is slow.

Sexes were combined in Table 8 as there were no significant differences in the distribution of adult males and females in the different tooth wear categories. When the proportions of "young" to "old" adults were compared at each locality using Chi-square, there were significantly more "young" than "old" animals captured at Rodman ($P < .005$), but the proportions of those classes were equal at Sherman ($P > .25$). Because there were significantly more "old" adults caught at Sherman than at Rodman, survival rates were probably higher at Sherman. The disappearance curves (Fig. 11) tend to bear this out. In both populations animals classified as "young" adults could be a year and a half old or older, and "old" adults are still older. Since 23 to 36 per cent of all sacrificed adults had well-worn teeth

(categories 4–6), it is evident that animals two years old or older are common in populations of this rodent. Once spiny rats reach adulthood, they apparently have a high survival rate.

The disappearance curves of this species (Fig. 11) clearly underestimate survivorship and, like that of the rice rat, are probably affected by emigration. To provide a more realistic picture of survivorship, the curves require modification, but, because of the problems involved with seasonal differences in rates of disappearance (survival) and differences between localities, pooling of the data seems unwarranted. However, a generalized survivorship curve can be derived by using available data and assuming that the spiny rat populations are stationary (see Discussion) and that mortality is age-constant. As indicated in Table 7, survivorship from ages 0 to 2 months was approximately 80 per cent. Using this information, a survivorship curve was drawn on semilog paper, which when combined with data on age at sexual maturity and natality rates, gave a net reproductive rate, R_0 , of 1.00. This curve, which follows the formula $\log y = 1.9902 - 0.0400x$, is shown in Fig. 12.

AGE STRUCTURES AND SEX RATIOS

Distribution of ages and sexes at monthly intervals was determined using the combined data from grids and supplementary lines. Deviations from the expected 1:1 sex ratio for immature and mature animals were tested for by Chi-square using the same data. In instances where the null hypothesis of no difference in proportion of males to females was rejected, subsample (monthly) variation in sex ratio was tested for under the null hypothesis that monthly variations were no greater than those owing to chance. In no case was the subsample null hypothesis rejected, allowing the major null hypothesis to be clearly interpreted. Monthly changes in age structure are shown in Figure 13, and sex ratios within each population are found in Table 9.

L. adspersus.—Age structure in the spiny pocket mouse population reflected the seasonal breeding in this species (Fig. 13). When the study began in June 1966, breeding had ceased, and few immatures were taken from then until December and January. Starting in February the population was dominated to a greater extent each month by young produced in the 1967 breeding season (Figs. 13 and 15). Sex ratios did not differ significantly from unity in both immature and adult age classes (Table 9).

O. capito.—In conformance with the year-round breeding in this species, immatures were taken in every month at Sherman and in every month except February at Rodman (Fig. 13). At Rodman, juveniles and subadults were most common in the wet season, when population levels were highest. At Sherman, those age classes formed a fairly stable portion of the population throughout the year.

Sex ratio among adults in each *O. capito* population tended to be biased, significantly so at Sherman, towards males (Table 9). Among imma-

TABLE 9
SEX RATIOS IN *Liomys adspersus*, *Oryzomys capito*, AND *Proechimys semispinosus*
AT RODMAN (R) AND SHERMAN (S)

Species	Location	G or Sp	Age and sex			
			Immature		Adult	
			♂ ♂	♀ ♀	♂ ♂	♀ ♀
<i>L. adspersus</i>	R	G	31	35	89	83
	R	Sp	26	27	76	78
<i>O. capito</i>	R	G	16	15	16	9
	R	Sp	0	**	11	2
	S	G	22	27	48	**
	S	Sp	17	*	4	28
<i>P. semispinosus</i>	R	G	36	**	13	21
	R	Sp	33	28	99	**
	S	G	28	27	28	15
	S	Sp	31	27	100	**

G, grids; Sp, supplementary lines. Significant deviations from 1:1 ratio are indicated by asterisks, * = $.05 > P > .01$; ** = $P < .005$.

tures, sex ratios did not differ from unity on the grids but were biased towards one sex or the other in the supplementary catches. The greater mobility of adult males (see section on Movement Patterns and Home Range Size) may account for much of the disparity in sex ratios, particularly in the supplementary lines where more mobile animals would have a higher probability of capture. Whether the true sex ratios in these rice rat populations deviate from unity is open to question.

P. semispinosus.—Populations of the spiny rat, like those of the rice rat, contained immature individuals throughout the year (Fig. 13). At both localities, juveniles and subadults formed a larger proportion of the population during most of the wet season (June through December) than during the dry season (January through April). This seasonal change in composition is probably the result of seasonal differences in the survival rate of immatures. As indicated above, animals born in the dry and early wet seasons had a significantly higher rate of survival than those born later in the wet season. As a result, the populations contained more subadults in the wet season than in the dry season.

Sex ratios in each *P. semispinosus* population tended to deviate from unity in favor of males among adults but, with one exception, not among immatures (Table 9). Because the movement patterns of males and females were similar, it is doubtful that greater male mobility can account for the unequal sex ratios. Perhaps adult females have a higher mortality rate than males in this species.

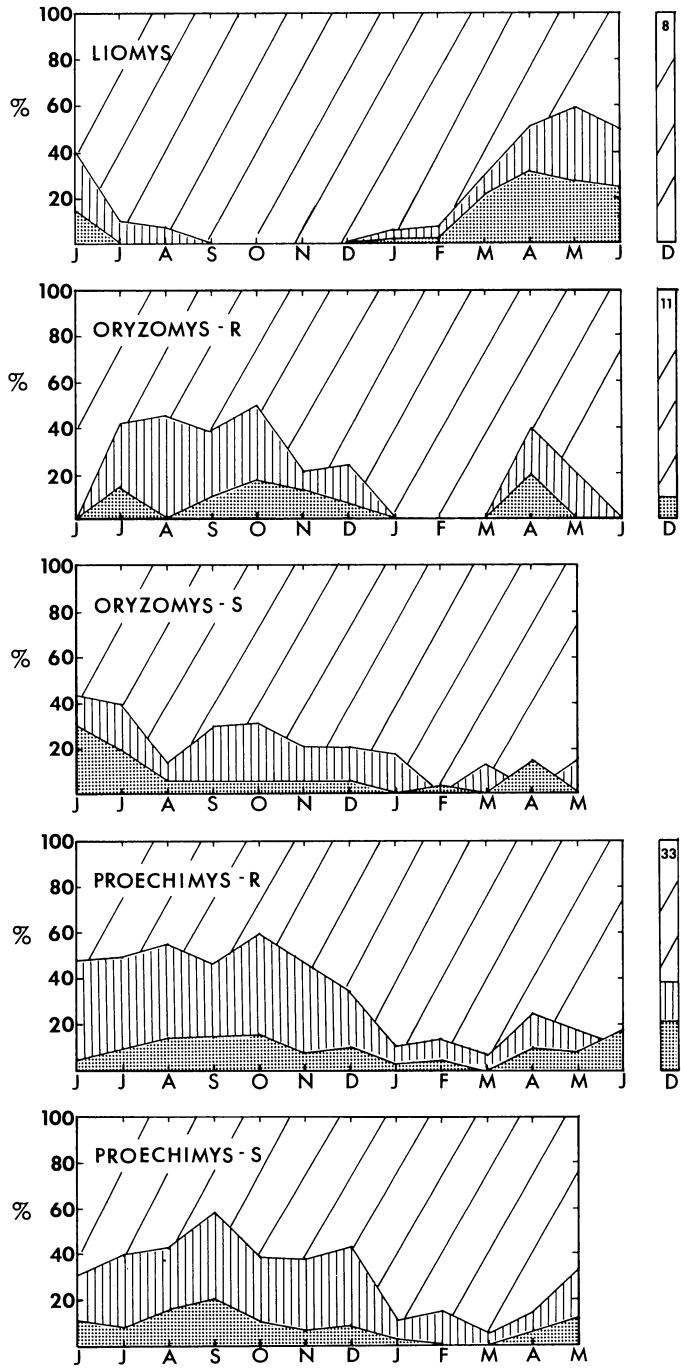


FIG. 13. Percentages of juveniles (stippled), subadults (vertical hatch), and adults (diagonal hatch) in three species at Rodman (R) and Sherman (S). Rectangles to the right of the boxes represent sample size and age composition of a collection made at Rodman in December 1967.

REPRODUCTION

Reproductive data were obtained from animals marked and released on the grids and from those collected in the supplementary lines. Because data from both sources were often complementary, they have been pooled to arrive at a fairly complete picture of the reproductive biology of the three species.

Annual productivity, defined as the number of offspring a female is potentially capable of producing in a year, was determined by noting the number of pregnancies experienced by females recaptured in two or more months. These data, expressed as number of litters produced per month, were averaged for all individuals of each species and were then converted to a hypothetical yearly rate, which when multiplied by the average litter size gave annual productivity. Some early pregnancies were missed as evidenced by capture of lactating animals that had not been previously recorded as being pregnant, and the data were corrected to account for these pregnancies. It is still possible that other early pregnancies were missed, which would cause productivity to be underestimated.

Liomys adspersus.—Annual cycle: This spiny pocket mouse is a seasonal breeder; both males and females are reproductively active for a portion of the year only. In females, judging from external signs (condition of vagina and nipples and presence of palpable embryos), breeding probably began late in November, reached a peak in March and April, and declined thereafter (Table 10). Histological examination revealed that females were anestrus from June to September 1966 and from April to June 1967 (Fig. 15). They contained maturing follicles beginning in October and corpora lutea

TABLE 10
REPRODUCTIVE CONDITION OF ADULT FEMALES OF *L. adspersus*

Month	Number of individuals			Total	% active	
	Pregnant	Lactating or postlactating	Perforate vagina			
June	0	0	0	19	19	0.0
July	0	0	0	47	47	0.0
August	0	0	0	44	44	0.0
September	0	0	0	57	57	0.0
October	0	0	1	56	57	1.8
November	0	0	0	29	29	0.0
December	1	0	1	30	32	6.2
January	4	0	7	31	42	26.2
February	5	4	4	16	29	45.0
March	4	5	3	7	19	63.1
April	4	5	1	6	16	62.5
May	0	5	1	11	17	35.3
June	0	0	2	11	13	15.4

Data from grid and supplementary lines are combined.

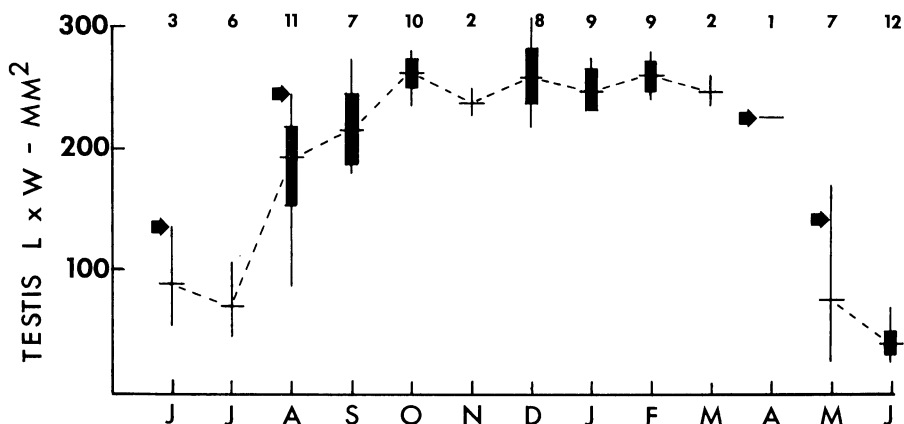


FIG. 14. Variation in size of testis, expressed in square millimeters (length x width), in adult *L. adspersus*. Standard diagrams indicate ranges, means, 95% confidence intervals, and sample size. Arrows indicate testis size of individuals from the previous year-class.

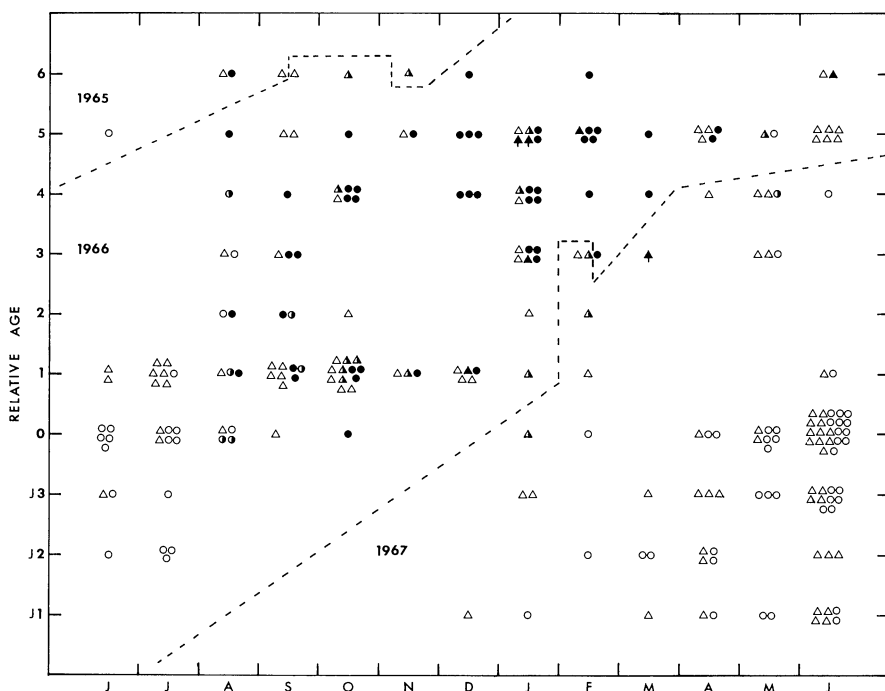


FIG. 15. Relationships of fertility to age and season in sacrificed males (circles) and females (triangles) of *L. adspersus* by year-class (separated by dashed lines). Open symbols = anestrous or infertile individuals; half-closed symbols = maturing individuals; closed symbols = fertile individuals. Pregnant females indicated by short line below symbol. Tooth wear indices indicate relative age (see text).

in the period December to March. Pregnant females were captured from December through April.

Adult males undergo a similar reproductive cycle. Testes and epididymides, abdominal in most adult males in June and July 1966, began to increase in size August and were largest October to April (Fig. 14). Testes of males born in 1966 began to regress at the end of April 1967, and at this time young of the year that had attained adult size (115 mm+ body length) still had small testes. Thus, infertile males lacking spermatozoa in their testes and epididymides formed the bulk of the population in June and July 1966 and in April, May, and June 1967 (Fig. 15). Though most of the individuals at these times were young of the year, males from earlier year-classes were infertile also. Reproductive activity began earlier (in August and September) in males than in females.

Annual productivity: Based on the records of 19 individuals, each female spiny pocket mouse produces an average of 1.44 litters per year. Most (22 of 24) females on the grid produced only one litter each in the 1967 breeding season, but two females were known to have produced two litters each. All adult females living on the grid bred at least once in 1967. Because females apparently undergo reduced activity (at least around traps) when pregnant, only five pregnant females were dissected. The number of embryos in these individuals ranged from two to four with an average of 3.2 (Table 11). This value is close to the 3.5 young per litter produced by captive *Liomys pictus* (Eisenberg, 1963). Combining data on frequency and size of litters and assuming little or no litter mortality, adult *L. adspersus* produce, on the average, 4.5 young per year.

Age at sexual maturity: Young females born early in the breeding season may come into estrus before that season ends (Fig. 15). In April 1967 two subadults had swollen vaginas that corresponded in appearance to the proestrous condition of *Perognathus longimembris* described by Hayden et al. (1966). One preserved female of the 1967 year-class was pregnant. In the United States National Museum's Panama collection, at least four young females of this species were pregnant and a fifth was lactating when collected

TABLE 11

ANNUAL PRODUCTIVITY OF *Liomys adspersus*, *Oryzomys capito*, AND *Proechimys semispinosus*

Species	N	Avg. no. litters per year	Avg. litter size	Avg. no. young per female per year
<i>L. adspersus</i>	19	1.44	3.2 (2-4) N = 5	4.5
<i>O. capito</i>	34	6.06	3.92 ± 0.56 (2-5) N = 14	23.7
<i>P. semispinosus</i>	15	4.68	2.49 ± 0.02 (1-5) N = 51	11.6

Means are given ± 95% confidence intervals. Ranges of observations are indicated in parentheses.

in the 1962 dry season in western Panama. Eisenberg and Isaac (1963) reported that the earliest age of conception in captive *L. pictus* was 98 days. Field data from this study indicate this situation may also obtain in *L. adspersus*. Although some females may attain sexual maturity at about three months of age, it is probable that most do not become pregnant until the following breeding season when they are nearly one year old.

Males apparently take longer to reach sexual maturity than females. No young males were fertile in the breeding season in which they were born (Fig. 15). Testes of most males caught in the periods June through August 1966 and May and June 1967 measured 20–150 mm² (length x width) and were devoid of sperm. Meiotic activity within primary spermatocytes was noted in testes 35 mm² and larger, but seminiferous tubules usually lacked secondary spermatocytes before testes reached a size of 100 mm². In males with a testis size of 150–220 mm², active spermiogenesis was occurring, but there was little or no sperm in the cauda epididymides. Few individuals with testes within this size range were taken compared with larger numbers with smaller or larger testes, suggesting that testis growth is rapid during this stage of sexual maturation. Males with testes 240 mm² or larger were actively producing large numbers of spermatozoa which filled the epididymal tubules causing them to expand greatly in size. Eisenberg (1963) measured the scrotal sac (testis plus epididymis) of maturing *L. pictus* and found that testis growth did not level off until males were approximately five months of age. The situation appeared to be similar in *L. adspersus* so that males, like many females, do not breed until nearly one year of age.

Oryzomys capito.—Annual cycle: In Panama this species of rice rat breeds year-round. Females and males in both populations in the Canal Zone were reproductively active throughout the year (Table 12 and Fig. 16). Although number of individuals is small, there were no discernible peaks of reproductive activity, and at least 50 per cent of the females of all ages caught each month were in breeding condition. As determined from the sacrificed sample, testes of adult males did not appear to vary significantly in size during the year (Fig. 17). This was supported by observations of released individuals. Adults recaptured several times over a period of several months showed no noticeable fluctuations in testis size as determined by palpation. Four adults collected at Sherman contained small numbers of spermatozoa along with many spermatogonia and primary spermatocytes in their cauda epididymides. This perhaps indicates that, while the population as a whole never becomes reproductively quiescent, individual males may undergo periodic lulls in reproductive activity.

Annual productivity: Based on the records of 34 individuals, females of this species are capable of producing 6.06 litters each per year (Table 11). Females in both populations had similar rates of litter production. Several females were known to produce two litters in rapid succession which suggests that females undergo a post-partum estrus. As seen in Table 11, litter size in this species is 3.92. Litter size in *O. capito* in Panama is probably com-

TABLE 12
 REPRODUCTIVE CONDITION OF FEMALES OF *O. capito* AND *P. semispinosus*
 AT RODMAN (R) AND SHERMAN (S)

Month	Number of individuals								Total	% active		
	Pregnant		Lactating or postlactating		Perforate vagina		Imperforate vagina					
	R	S	R	S	R	S	R	S				
<i>O. capito</i>												
June	0	1	0	0	0	0	0	0	0	2	—	100.0
July	1	2	0	0	0	1	0	2	1	5	100.0	60.0
August	1	6	0	0	1	1	1	0	3	7	66.7	100.0
September	4	8	0	0	0	0	2	3	6	11	66.7	72.8
October	8	6	0	0	2	4	5	1	15	11	66.7	91.0
November	10	8	0	0	0	1	2	6	12	15	83.5	60.0
December	2	5	0	1	1	1	3	6	6	13	50.0	53.9
January	0	6	0	1	0	0	3	4	3	11	0.0	63.6
February	0	5	0	1	1	1	0	5	1	12	100.0	58.3
March	1	2	0	0	0	0	0	4	1	6	100.0	33.3
April	0	3	0	1	0	0	2	1	2	5	0.0	80.0
May	1	2	0	0	0	0	0	0	1	2	100.0	100.0
<i>P. semispinosus</i>												
June	1	2	0	0	1	2	1	1	3	5	66.7	80.0
July	0	2	1	1	2	1	3	4	6	8	50.0	50.0
August	3	10	0	2	4	3	1	2	8	17	87.5	88.4
September	6	7	1	0	1	1	0	4	8	12	100.0	66.7
October	2	5	1	1	5	8	0	3	8	17	100.0	82.5
November	1	4	1	2	2	6	5	8	9	20	44.5	60.0
December	2	1	1	2	5	4	3	7	11	14	72.8	50.0
January	2	5	0	0	1	6	3	6	6	17	50.0	64.8
February	8	7	0	0	1	2	2	6	11	15	81.8	60.0
March	1	5	0	1	0	0	1	5	2	11	50.0	54.6
April	7	2	0	1	0	0	0	2	7	5	100.0	60.0
May	2	5	0	0	0	0	0	1	2	6	100.0	83.5
June	1		0		0		0		1		100.0	

Data from grids and supplementary lines are combined.

parable to values of 3.0, 5.0, and 3.7 to 6.0 reported for *Oryzomys palustris* in the United States by Svihla (1931), Conaway (1954), and Negus et al. (1961), respectively. Combining rate of litter production (6.1 per year) with average litter size (3.9), each female can produce an average of 23.7 young per year (Table 11). Because few females live a year in the wild, their reproductive output is probably much less than this hypothetical value.

Though based on a small number of observations, there was a tendency in *O. capito* for the number of embryos *in utero* to be larger in larger (older) individuals. Three females less than 110 mm in body length had an average of 2.3 embryos while 11 females greater than 110 mm in body length averaged 4.5 embryos. Young females of *O. palustris* have smaller litters than

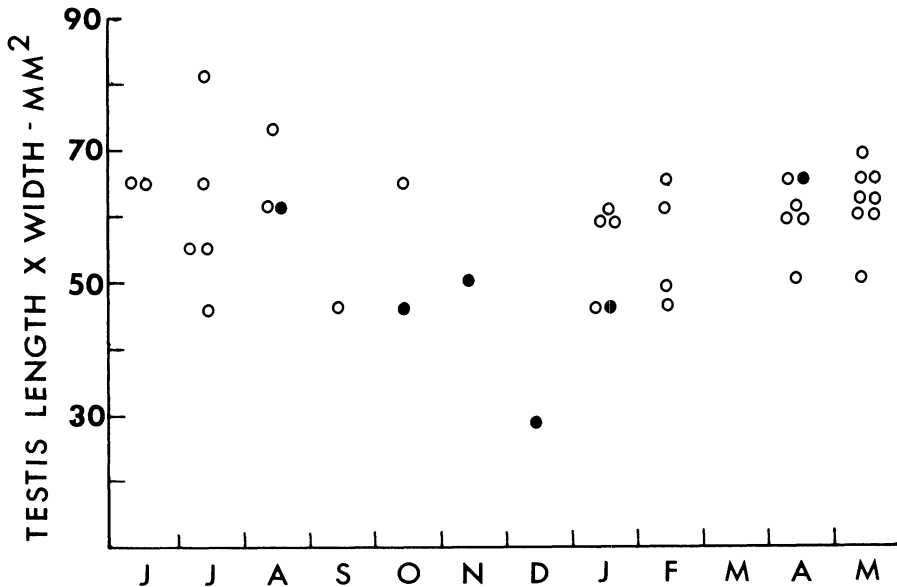


FIG. 17. Testis size in sacrificed adults of *O. capito*. Symbols as in Figure 14.

older ones (Svihla, 1931). An average of 2.1 embryos was found in each uterine horn in 11 specimens. Two cases of unilateral pregnancies were observed, and in each the embryos occurred in the left uterine horn. Left ovaries of these individuals contained corpora lutea of pregnancy while the right ovaries were inactive. A similar situation occurs in *O. palustris* (Negus et al., 1961).

Age at sexual maturity: As in *O. palustris* (Conaway, 1954), male and female *O. capito* become sexually mature at an age of less than two months. Several females in juvenal pelage were pregnant or the vagina was perforate. Those juveniles were probably less than 50 days old, judging from the growth rate of 14 laboratory reared *O. capito*. Males in which the body length was 105 mm or more (55–65 days of age) had large numbers of spermatozoa in the seminiferous tubules and epididymides. Minimum testis size in fertile males was 45 mm². Too few individuals were preserved to follow sexual maturation in detail in this species.

Proechimys semispinosus.—Annual cycle: Like the rice rat, adult spiny rats are reproductively active throughout the year. In both populations usually 50 per cent or more of the adult females were active each month (Table 12). Proportions of pregnant to nonpregnant adults were similar in both wet and dry seasons at both localities, but there was a significantly higher proportion of pregnant females in the period January through June than in July through December at Rodman (Chi-square = 13.31; $P < .001$). Pregnant females were taken in every month except July at Rodman and in every month at Sherman.

Although fertile males were found throughout the year (Fig. 18), size of testis in males 220 mm or more in body length varied seasonally (Fig. 19). Mean monthly testis sizes were similar in Rodman and Sherman adults so that those data are combined in Figure 19. In both populations, testes of adults collected in October and November were significantly smaller, both absolutely and relatively, than those of adults taken in August, September, March, and April ($P < .05$ using the Wilcoxon two-sample test). Since the observed fluctuations are within the range in which males are considered fertile (testis size $195 \text{ mm}^2 +$), the physiological significance of these fluctuations is not known. It may be that some males undergo reduced spermatogenic activity, but fertile males still form a significant portion of the population in October and November. The fluctuations in testis size apparently do not affect breeding activity because the proportion of pregnant to non-pregnant females was similar in the period of reduced testis size (September to February) and increased testis size (March to August) in both populations (Rodman Chi-square = 0.88, $P > .50$; Sherman Chi-square = 4.62, $.10 > P > .05$). Rainey (1956) noted fluctuations in the size of adult *Neotoma floridana* testes but felt that male fertility was not affected by these fluctuations.

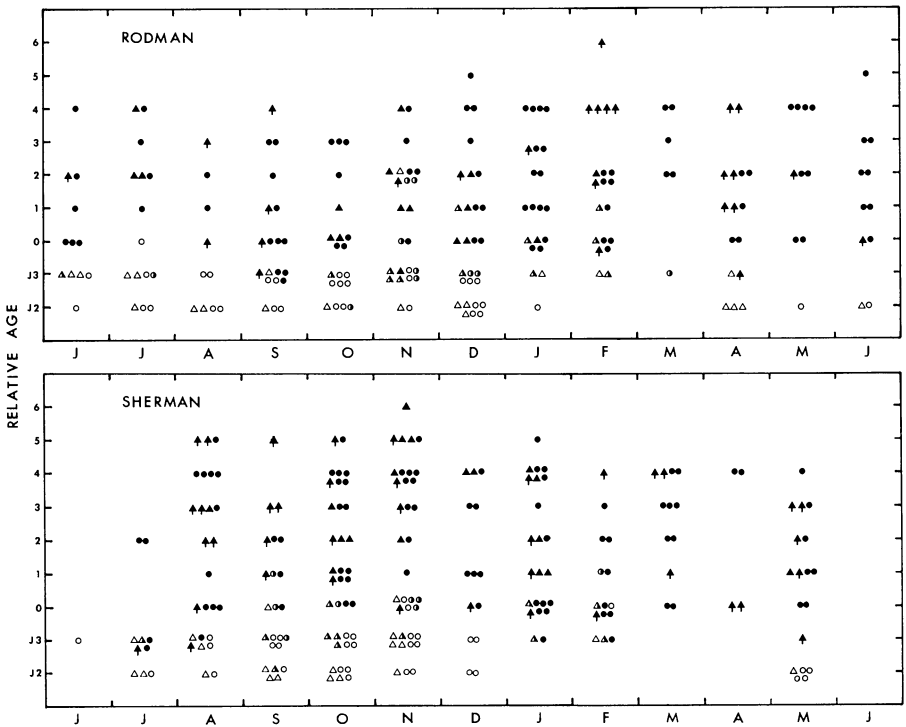


FIG. 18. Relationship of fertility to age and season in sacrificed males (circles) and females (triangles) of *P. semispinosus*. Symbols as in Figure 15.

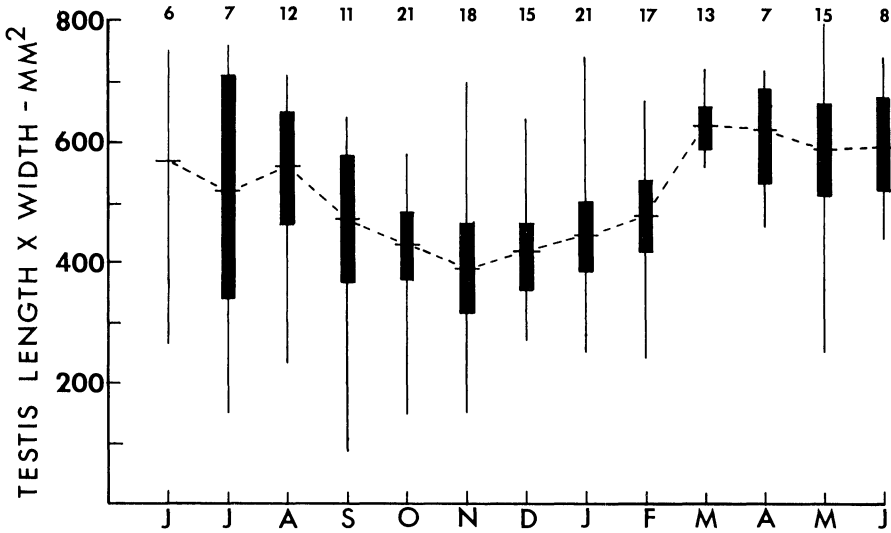


FIG. 19. Testis size in sacrificed *P. semispinosus* adults 220 mm+ in body length. Rodman and Sherman samples are combined. Symbols as in Figure 14.

Annual productivity: Based on the observed pregnancy rates of 15 recaptured individuals, each female *P. semispinosus* is capable of producing 4.68 litters per year (Table 11). One adult female that was followed for 12 months produced five litters (in June, August, October, February, and May). Rates of litter production were similar for females in both populations.

The observed productivity can be checked by using the method of Emlen and Davis (1948). In the year, 67 of 126 preserved females (53.1 per cent) 195 mm or more in body length were visibly pregnant. Substituting this value into the formula $F = I \times T/G$, where F = frequency of pregnancy, I = per cent visibly pregnant, T = length of time during which specimens were collected, and G = gestation period, we get $F = 0.531 \times 365/51$. Gestation period in *P. semispinosus* has recently been determined by Tesh (1970a). F , the number of litters in one year, in this case is 3.80, which is slightly lower than the observed value.

Since several captured females were pregnant and lactating, it is probable that this species undergoes a post-partum estrus. Average litter size, based on 51 pregnant females, was 2.49. Thus assuming no litter mortality (see below), an adult female spiny rat could produce, on the average, about 11.6 young per year (Table 11).

In *P. semispinosus*, litter size does not increase with an increase in female's age because litter size was not correlated with body length ($P > .05$ using the corner test of association). Number of young is apparently controlled by the number of ova that implant, rather than by the resorption of embryos. Of 51 pregnant females, only three had resorbing embryos (one of one, one of two, and two of two embryos, respectively). This represents a

postimplantation loss of only 3.1 per cent. Also indicating that resorption of embryos does not commonly occur is the fact that litter size was not negatively correlated with size of embryo. Table 13 compares the number of corpora lutea with the number of embryos or uterine swellings for each ovary and corresponding uterine horn. In all instances, corpora lutea outnumbered embryos by a factor of 1.6 to 2.9.

TABLE 13

CORPORA LUTEA VS. EMBRYOS IN *Proechimys semispinosus* AT RODMAN AND SHERMAN

Site	Ovary & uterine horn	N	Mean no. corpora lutea per ovary	Mean no. embryos per uterine horn
Rodman	Right	17	3.76 ± 0.29	1.29 ± 0.39
	Left	17	3.11 ± 0.87	0.76 ± 0.46
Sherman	Right	17	2.88 ± 1.17	1.35 ± 0.57
	Left	16	2.68 ± 0.63	1.62 ± 0.42

Means are given ± 95% confidence intervals.

In both populations there was a tendency for implantation to occur more frequently in one uterine horn (Table 13). At Rodman significantly more embryos implanted in the right horn than the left, presumably owing to the significantly greater production of ova from the right ovary ($P < .001$). At Sherman, the difference in mean number of embryos per uterine horn was not statistically significant ($P > .40$). Unilateral pregnancies occurred in 10 of 23 females (42.5 per cent) at Rodman; in eight of the 10 females, embryos were in the right horn. At Sherman unilateral pregnancies were found in 11 of 28 females (39.3 per cent), and in eight of these the embryos were in the left horn. In at least five of the unilateral pregnancies, the ovary on the side lacking embryos contained no corpora lutea, indicating that that ovary had been inactive when conception occurred. Perhaps ovaries in some female spiny rats alternate in activity as in the porcupine (*Erethizon dorsatum*) (Mossman and Judas, 1949).

Age at sexual maturity: Based on observed pelage changes of recaptured juveniles and subadults, spiny rats attain adult size and pelage, and hence sexual maturity, at about six months of age. Eight females, first marked as weanlings or early juveniles, were followed through their first pregnancy. Their estimated age at first pregnancy averaged 9.2 months (range 6 to 12 months). Three additional pregnant subadults (body lengths 195 to 197 mm) were probably close to six months old. Data from the histological examination of ovaries indicated that most females less than 195 mm in body length had not ovulated, whereas most females larger than this had done so. Females between 170 and 195 mm in body length usually contained maturing follicles while smaller (younger) individuals contained only primary follicles.

Few females above 200 mm in body length (tooth wear index of 1) failed to show signs of recent reproductive activity when collected (Fig. 18).

Males become sexually mature at a slightly larger size than females and are probably sexually mature when six to seven months old. Nearly all males with a body length of 210 mm or greater (tooth wear index 0 to 6) contained large numbers of spermatozoa in the seminiferous tubules and cauda epididymides; males smaller than this seldom did (Fig. 18). Minimum testis size for which a male could be considered fertile was 195 mm². Males of body length 195–205 mm were beginning active spermiogenesis but usually lacked sperm in their cauda epididymides. Seminiferous tubules of most males 175–195 mm in body length contained spermatogonia and primary spermatocytes, many of which were meiotically active. Individuals less than 175 mm long contained only spermatogonia in the seminiferous tubules.

LIFE TABLES

The dynamics of any population are best summarized in the form of a *life table* that also includes fecundity data. In such a table measures of age-specific survivorship and fecundity are presented which, when their products are summed, indicate whether the population is increasing, decreasing, or stationary. Although present data on survivorship leave much to be desired, age at sexual maturity and natality rates are fairly accurately known so that I have attempted to construct a provisional life table for each species following the example of Caughley (1966).

Using the data from the adjusted survivorship curves (Fig. 12) and observed natality rates, I computed life tables for females of each species assuming that sex ratios are 1:1 at birth. These computations are given in Table 14. In two species, *O. capito* and *P. semispinosus*, natality rates are probably fairly constant once females attain sexual maturity. In *L. adspersus*, however, breeding is seasonal and only those females born early in the season mature quickly enough to raise a litter before the season ends. Among adults, only two of 24 were known to have produced two litters in the 1967 breeding season. Therefore, the major reproductive contribution in this species is made by females reproducing for the first time in the season after that in which they were born (Table 14).

The life table for females of *P. semispinosus* was constructed under the assumption that the populations were stationary (see Survivorship). Thus its computed R_0 approximates 1.00. In *L. adspersus* and *O. capito*, on the other hand, R_0 was calculated using estimated mortality and natality rates. In the former species, R_0 is less than 1.00 and greater than 1.00 in the latter (Table 14). If taken at face value, these estimates of net reproductive rates indicate that the population of *L. adspersus* is declining while those of *O. capito* are increasing. However, considering the limited data upon which those tables are based, the results are in reasonable agreement with the expected value, and it may be doubted that the populations are really declining or increasing.

Mean age at death (e_x of the "0" age interval) differs among the three species (Table 14). At birth, individuals of *P. semispinosus* have the greatest life expectancy (10.3 months) and those of *O. capito* the shortest (2.9 months).

MOVEMENT PATTERNS AND HOME RANGE SIZE

Movement patterns and sizes of home ranges of the species were determined by two different methods. In characterizing the movement patterns, which are sometimes used as an index of home range size (Davis, 1953; Brant, 1962), two statistics, D, the average distance between recapture sites, and M, the longest distance between two capture sites, were calculated for individuals recaptured six or more times in successively different traps. These

TABLE 14
LIFE AND FECUNDITY TABLES FOR FEMALES OF *Liomys adspersus*, *Oryzomys capito*, AND *Proechimys semispinosus*

Age (mos)	l_x	d_x	m_x	$l_x m_x$	q_x	e_x
<i>L. adspersus</i>						
0	1.072	0.066	0.000	0.000	0.061	8.074
1	1.009	0.067	0.000	0.000	0.066	7.547
2	0.942	0.066	0.000	0.000	0.070	7.040
3	0.876	0.066	0.000	0.000	0.075	6.542
4	0.810	0.067	0.139	0.113	0.082	6.034
5	0.743	0.067	0.000	0.000	0.090	5.533
6	0.677	0.067	0.000	0.000	0.098	5.024
7	0.610	0.066	0.000	0.000	0.108	4.521
8	0.544	0.066	0.000	0.000	0.121	4.008
9	0.477	0.067	0.000	0.000	0.140	3.501
10	0.411	0.066	1.600	0.658	0.160	2.983
11	0.354	0.067	0.000	0.000	0.194	2.458
12	0.278	0.066	0.133	0.037	0.237	1.930
13	0.212	0.066	0.000	0.000	0.311	1.375
14	0.146	0.067	0.000	0.000	0.458	0.771
15	0.079		0.000	0.000		
$R_0 = 0.808$						
<i>O. capito</i>						
0	1.000	0.282	0.000	0.000	0.282	2.889
1	0.718	0.210	0.000	0.000	0.292	2.827
2	0.508	0.146	0.000	0.000	0.287	2.788
3	0.362	0.104	0.990	0.358	0.287	2.711
4	0.258	0.073	0.990	0.255	0.282	2.603
5	0.185	0.054	0.990	0.183	0.291	2.432
6	0.131	0.037	0.990	0.130	0.292	2.229
7	0.094	0.027	0.990	0.093	0.287	1.910
8	0.067	0.018	0.990	0.066	0.268	1.478
9	0.049	0.016	0.990	0.049	0.326	0.837
10	0.033		0.990	0.033		
$R_0 = 1.167$						

TABLE 14 (cont.)

Age (mos)	l_x	d_x	m_x	$l_x m_x$	q_x	e_x
<i>P. semispinosus</i>						
0	1.000	0.180	0.000	0.000	0.180	10.297
2	0.820	0.150	0.000	0.000	0.182	10.338
4	0.670	0.100	0.000	0.000	0.149	10.428
6	0.570	0.100	0.000	0.000	0.175	10.083
8	0.470	0.080	0.390	0.183	0.170	10.015
10	0.390	0.070	0.390	0.152	0.179	9.864
12	0.320	0.050	0.390	0.125	0.156	9.803
14	0.270	0.045	0.390	0.105	0.166	9.433
16	0.225	0.040	0.390	0.088	0.177	9.120
18	0.185	0.030	0.390	0.072	0.162	8.877
20	0.155	0.025	0.390	0.060	0.161	8.400
22	0.130	0.023	0.390	0.051	0.176	7.823
24	0.107	0.018	0.390	0.042	0.168	7.290
26	0.089	0.015	0.390	0.035	0.168	6.562
28	0.074	0.012	0.390	0.029	0.162	5.689
30	0.062	0.011	0.390	0.024	0.177	4.597
32	0.051	0.008	0.390	0.020	0.156	3.373
34	0.043	0.008	0.390	0.017	0.186	1.814
36	0.035		0.390	0.014		
$R_0 = 1.017$						

Symbols: l_x = age-specific survivorship; d_x = number dying in interval x , $x + 1$; m_x = age-specific fecundity; q_x = age-specific mortality rate; e_x = age-specific life expectancy.

statistics were then averaged for each sex, species, and population and compared intra- and interspecifically using the Wilcoxon two-sample test. For each species no significant differences were found between the movements of immature and mature individuals of the same sex so that age classes have been combined in Table 15.

Seasonal changes in movement patterns were studied by calculating the mean monthly distances between different successive capture sites of males and females separately. In this analysis, captures occurring repeatedly at the same distance were disregarded to prevent the masking of longer movements, which had a low probability of occurrence, by shorter movements.

Home range size of each resident captured four or more times in at least three different traps was calculated by the exclusive boundary strip method of Stickel (1954). Data from individuals captured only in peripheral traps were discarded as were obvious forays beyond "normal" home range boundaries. Since available information indicated that juveniles and sub-adult ranges were not appreciably smaller than those of adults, data from all age classes were combined, but adults provided the bulk of the data in Table 16. Differences in home range sizes within and between species were tested for by the Wilcoxon two-sample test.

TABLE 15

MOVEMENT PATTERNS IN *Liomys adspersus*, *Oryzomys capito*, AND *Proechimys semispinosus*

Species	Locality	Sex	N	No. movements	Avg. D	Avg. M
<i>L. adspersus</i>	Rodman	M	8	61	43.0	95.9
		F	22	228	30.3	45.3
<i>O. capito</i>	Rodman	M	13	162	56.9	121.1
		F	4	52	41.3	80.0
	Sherman	M	18	205	49.4	103.4
		F	5	42	37.2	66.8
<i>P. semispinosus</i>	Rodman	M	14	155	46.1	94.3
		F	4	31	37.2	63.1
	Sherman	M	11	110	39.4	77.2
		F	12	116	38.3	62.2

D, average distance (in m) between captures; M, average longest distance (in m) between captures.

L. adspersus.—Both Avg. D and Avg. M were significantly greater for males than females (Table 15), and males made significantly longer movements in the dry season than in the wet season ($P < .05$). The average distance between captures of males in the wet season was 39.9 m and in the dry season 51.6 m (Fig. 20). The high value for September was caused by one individual that shifted its home range 160 m in that month. Longer movements of males in the dry season are probably associated with breeding activity. Corresponding changes in the movements of females were not detected. Their average distance between captures in the wet season was 31.9 m and in the dry season 32.0 m.

Home ranges of spiny pocket mice averaged 0.56 ha and were the smallest of the three species. There were no significant differences between the size of male and female ranges (Table 16).

O. capito.—At Rodman both Avg. D and Avg. M were greater in males than females, but only the male Avg. M was significantly greater at Sherman ($P < .05$; Table 15). Comparing the same sex in the Rodman and Sherman populations, males at Rodman had a greater Avg. D and Avg. M than males at Sherman; those statistics were similar for females in both populations. No seasonal differences in movements were found within sexes at both locations (Fig. 20).

Home ranges of rice rats averaged 1.33 ha and were the largest of the three species; male ranges were larger than female ranges (Table 15). The ranges of Rodman males were larger than those at Sherman, but females at both locations had comparably-sized home ranges.

P. semispinosus.—There were no significant differences in Avg. D and Avg. M between sexes in each population, within the same sex between populations, or between seasons ($P > .05$; Table 15 and Fig. 20).

TABLE 16
HOME RANGE AND TRAP UTILIZATION IN *Liomys adspersus*, *Oryzomys capito* AND
Proechimys semispinosus

Species	Location	Sex	N	Home Range Size m ²	Size hectares	Number of traps entered per individual
<i>L. adspersus</i>	Rodman	M	18	5660.2 ± 1425.5	0.57 ± 0.14	4.6 ± 0.67 (8.5)
		F	28	5549.7 ± 1697.9	0.55 ± 0.17	4.0 ± 0.05 (15.8)
<i>O. capito</i>	Rodman	M	16	18017.6 ± 3860.4	1.80 ± 0.39	9.3 ± 2.21 (13.1)
		F	6	12070.3 ± 6772.5	1.21 ± 0.68	7.1 ± 3.48 (14.8)
	Sherman	M	22	14254.3 ± 2693.4	1.43 ± 0.27	7.9 ± 1.47 (11.6)
<i>P. semispinosus</i>	Rodman	F	8	8613.3 ± 1255.2	0.86 ± 0.13	5.3 ± 0.75 (11.1)
		M	18	11445.3 ± 2667.4	1.14 ± 0.27	6.6 ± 1.41 (11.9)
	Sherman	M	14	6562.5 ± 1919.5	0.66 ± 0.19	4.8 ± 1.18 (7.8)
		F	6	9994.4 ± 1534.3	1.00 ± 0.15	6.2 ± 0.96 (11.2)
		F	17	7486.2 ± 1158.6	0.75 ± 0.12	5.1 ± 0.68 (12.0)

Means are given ± 95% confidence intervals. Mean number of captures per individual indicated in parentheses.

Rodman male spiny rats had larger ranges than females, but there was no significant difference between ranges of the two sexes at Sherman (Table 15). Ranges of Rodman males were larger than those of Sherman males, but those of females of the two areas were alike.

Ranges of most individuals remained quite stable for periods of up to one year in *L. adspersus* and *P. semispinosus*. Three *P. semispinosus* (two at Rodman, one at Sherman) and two *O. capito* (both at Sherman) were known to shift their ranges up to 50 m away from the grids. At Rodman only six individuals were known to move from one part of the grid to another. Three adult male spiny pocket mice shifted their areas of activity 90 m, 150 m, and 160 m in March, October, and September, respectively. Two adult male rice rats moved 200 m and 145 m in September and February, respectively. One juvenile female spiny rat moved 120 m in October; this may represent a dispersal movement from its place of birth. At Sherman one male spiny rat shifted its home range 145 m in July. Since few individuals evidenced marked changes in areas of activities within the grids, seasonal shifts, if they occur, must have carried animals beyond the range of the traps and thus were not detected.

In this study the use of distances between successive captures as an index of home range size proved to be valid for each species. Significant correlations between Avg. D and home range area were found after the data were transformed to logarithms. Correlation coefficients for *L. adspersus*, *O. capito*, and *P. semispinosus*, respectively, were: 0.733, 0.646, and 0.399 ($P < .05$ in all cases). Wolfe (1968) found average distance between successive captures in *Peromyscus leucopus* to be positively correlated with home range area after two, four, and six captures.

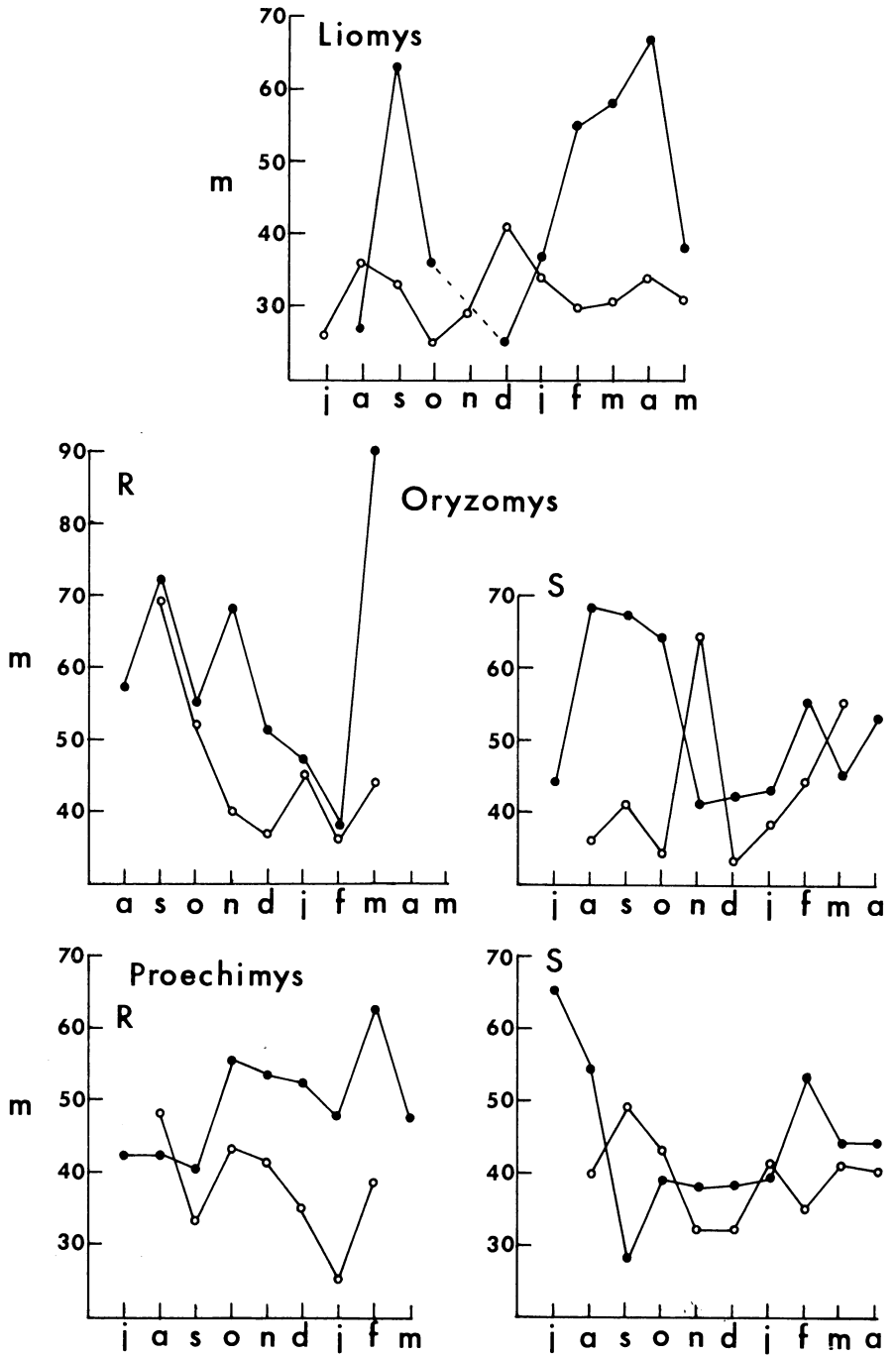


FIG. 20. Average distance (in m) between captures in males (solid circles) and females (open circles) in three species of rodents. See text for explanation.

SPATIAL RELATIONSHIPS OF HOME RANGES

Home ranges can be distributed in one of three patterns—clumped, uniform, or random—and the pattern that obtains within species offers some insight into intra-specific social interactions. A clumped pattern suggests that positive interactions are occurring between individuals, a uniform pattern suggests that negative interactions are occurring, and a random pattern suggests that neither positive nor negative interactions predominate. The spatial arrangements of home ranges within each species were studied with the aid of a computer program designed to compare the observed location of individual captures with a randomized distribution of those captures, following the methods of Metzgar (1968) and Metzgar and Hill (1971). Resident animals only were considered in this analysis. The ratio, observed range overlap to expected range overlap, termed the “index of range overlap,” yields a value of 1 when ranges are randomly distributed, a value greater than 1 when ranges overlap extensively, and a value less than 1 when range overlap is minimal. The significance of deviations from the expected frequency distributions for all traps and for just those capturing two or more individuals was tested by Chi-square or, when sample sizes were small, by the Kolmogorov-Smirnov one-sample test.

Results of the analyses showed that in all species home ranges were oriented randomly with respect to members of the same or opposite sex. A detailed account of the results is presented elsewhere (Fleming, 1969). Indices of range overlap based on only those traps capturing two or more individuals revealed only one case of significant deviation from random expectation (Table 17). *O. capito* males and females at Sherman showed a clumped distribution; at Rodman there was a similar but nonsignificant tendency in this species. These two lines of evidence suggest that most individuals of each species are neither strongly attracted nor repelled by other individuals of the same or opposite sex when establishing their home ranges.

For *L. adspersus* there is additional information supporting the contention that home ranges overlap. Spiny pocket mice nest in burrows, and I saw many individuals ducking into holes. Multiple use of the same burrow by individuals of the same and/or opposite sex was noted on several occasions. While as many as five individuals used the same burrow at various times, two was the usual number of pocket mice known to be using the same burrow in the same month. Two such burrows, excavated in June 1967, proved to be fairly short tunnels which probably served as temporary refuges. Although there is no evidence to show that several individuals were utilizing the same nest site, the fact that several individuals were utilizing the same refuge holes indicates that their home ranges must overlap. Prior knowledge of the location of the holes was indicated by the behavior of the mice when released. In no instance did a mouse obviously “stumble” onto a hole and disappear into it. On the contrary, individuals usually dashed quickly to the hole or else wandered about briefly until they found a path

TABLE 17
HOME RANGE OVERLAP IN *Liomys adspersus*, *Oryzomys capito*, AND *Proechimys semispinosus*
AT RODMAN (R) AND SHERMAN (S)

Species	Location	Sex	Index of Home Range Overlap	χ^2 or D (df)
<i>L. adspersus</i>	R	M	1.14	5.48 (7)
	R	F	1.07	6.31 (9)
	R	M & F	1.10	8.85 (11)
<i>O. capito</i>	R	M	1.34	3.05 (2)
	R	F	0.63	0.257
	R	M & F	1.24	3.18 (2)
	S	M	1.18	1.46 (6)
	S	F	1.36	0.198
	S	M & F	1.28	12.85* (6)
<i>P. semispinosus</i>	R	M	0.92	2.28 (3)
	R	F	0.41	0.609
	R	M & F	1.04	0.51 (3)
	S	M	1.47	4.71 (6)
	S	F	0.88	0.79 (6)
	S	M & F	1.12	5.06 (7)

Significant deviations from a value of 1.00 indicate either clumping (> 1.00) or repulsion (< 1.00) of home ranges. Statistical significance; * = $P < .05$.

that led them directly to the hole. On several occasions rice rats were seen to use the same burrows as spiny pocket mice.

DISCUSSION

Liomys adspersus, *Oryzomys capito*, and *Proechimys semispinosus* live in the same habitat under the same environmental conditions but differ in many ecological and biological parameters. The main difference, one which influences many other parameters, is the fact that *L. adspersus* breeds seasonally whereas *O. capito* and *P. semispinosus* breed year-round. This difference and others may result from the different evolutionary histories of the species.

Despite their obvious biological differences, do these species share ecological characteristics that are "tropical" in nature, ones which are also seen in other "tropical" rodents and not in "temperate" rodents? Ecological differences between the three species and other temperate and tropical rodents will be discussed here. Data concerning the ecology of other temperate and tropical rodents are summarized in Tables 19, 20, and 21.

POPULATION FLUCTUATIONS

Fluctuations in densities of the three species paralleled each other in both forests. In the first half of the wet season, densities of each species increased. Since breeding was not occurring in *L. adspersus*, the slight increase

in its density seen from June (?) to September had to result from immigration. Some of the immigrants captured only in one session must have been transients. Natality and immigration both contributed to the density increases in the *O. capito* and *P. semispinosus* populations. Contrary to the case in *L. adspersus*, few of the immigrant *O. capito* and *P. semispinosus* were transients as most established residences on the grids.

In the latter part of the wet season densities began to decline and continued to do so in *O. capito* and *P. semispinosus* until the end of the study (Fig. 8). Whether these declines had a common cause or were just a coincidence is not known. They probably were the result of several interacting factors, including food shortage, predation, and emigration.

Seasonal changes in the abundance of conspicuous fruits and seeds of palms and other plants were measured in an attempt to determine whether changes in rodent densities could be related to changes in food availability. Palms were sampled by counting the number of ripe bundles of nuts that would fall within two meters of the 10 grid lines, mangos by counting the number of fresh fruits that had fallen within two meters of each grid line prior to or during a trapping session, and figs and hog plums (*Spondias mombin*) by counting the number of fallen fruits per square meter under trees fruiting near each grid line. Numbers of palm bundles or fruits were converted to grams to obtain a crude estimate of the fruit biomass available to terrestrial mammals each month. *Liomys*, *Oryzomys*, and *Proechimys* are known to feed on some or all of the fruits sampled in this study (Enders, 1935; Fleming, 1970a).

Results of this sampling program indicate that fruit availability varies seasonally in both forests (Table 18). Palm nuts are available from the end of the dry season (March and April) to the middle of the rainy season (September). The mango season begins in March, when unripe fruits are falling, peaks in April and May, and ends in June. At the height of its season in 1967, mangos were abundant and many appeared to be untouched by mammals. Hog plums, more common at Sherman than at Rodman, were ripe from July to September. Fig trees were also more common at Sherman and fruited rather sporadically in eight of 12 months (Table 18). Other species that fruited during the year at Rodman were custard apple (*Annona reticulata*), in July and August, and two unidentified trees that shed seeds eaten by *Liomys* in February and June; other species fruiting at Sherman included: *Protium panamensis* (?) and *Virola* sp., two uncommon species, in May and June; *Gustavia superba*, which fruited in the rainy season and whose fruits appeared to be eaten by agoutis and pacas; and *Inga* sp., whose legumes fell primarily in April.

The general picture that emerges from the fruit sampling is that fruit is available from the last half of the dry season to the first half of the rainy season (March to September). Except for the figs at Sherman, few kinds of fruit were available at the height of the rainy season and in the first half of the dry season (October to February). These results are in general agreement

TABLE 18
 AMOUNTS OF FRUIT PRODUCED BY SEVERAL TREE SPECIES ON THE RODMAN (R) AND
 SHERMAN (S) GRIDS

Month	Location	<i>Scheelea</i>	<i>Bactris</i>	<i>Astrocaryum</i>	Corozo	<i>Ficus</i>	<i>Mangifera</i>	<i>Spondias</i>
			Estimated weight of crop in grams					
June	R	8,800,000	33,580	107,744	2 trees	0	0	0
	S	1,375,000	5,340	177/m ² (2) ^a	41,114	0	0	0
July	R	9,325,000	43,970	96,100	0	15/m ² (2) ^a	0	0
	S	1,375,000	0	642	0	0	0	0
August	R	2,474,000	22,160	43,680	0	0	0	0
	S	275,000	0	0	13/m ² (3)	48/m ² (5)	0	0
September	R	2,200,000	13,850	8,736	0	8/m ² (3)	0	0
	S	0	0	0	87/m ² (2)	57/m ² (8)	0	0
October	R	0	6,230	2,912	0	0	0	0
	S	0	0	0	3/m ² (1)	0	0	0
November	R	0	0	8,736	0	0	0	0
	S	0	0	0	3/m ² (1)	0	0	0
December	R	0	0	5,824	0	0	0	0
	S	0	0	0	15/m ² (7)	0	0	0
January	R	0	0	0	0	0	0	0
	S	0	0	0	0	0	0	0
February	R	0	0	0	0	0	0	0
	S	0	0	0	13/m ² (1)	0	0	0
March	R	0	26,600	0	0	0	0	0
	S	0	3,140	0	0	0	0	0
April	R	6,600,000	36,000	26,200	0	0	0	0
	S	275,000	10,050	0	13/m ² (1)	0	34,690	0
May	R	4,675,000	38,000	26,200	0	0	0	0
	S	550,000	10,990	0	0	0	84,367	0
June	R	6,000,000	29,100	26,200	3 trees	0	0	0
	S	0	0	0	0	0	0	0

^a Number of trees sampled indicated in parentheses.

with the observations of other workers in Panama and Costa Rica (Kaufmann, 1962; Janzen, 1967; Smythe, 1970).

Fruit levels were low when rodent densities were declining which suggests a shortage of food could have adversely affected each species. However, no starving or obviously underweight individuals were caught at any time during the study. A covariance analysis of the relationship between body length and weight in *P. semispinosus* showed no significant changes in slope ($P > .05$) when sacrificed samples from the periods August-September, October-November, December-January, February-March, and April-June were compared; data from Rodman and Sherman were analyzed separately. It was not possible to conduct a similar analysis for *L. adspersus* (the assumption of homogeneity of variance was violated) but inspection of the data revealed no obvious changes in body length-weight relationship during the year. For two species, therefore, direct evidence of the adverse effects of a possible food shortage is lacking.

While seasonal changes in the abundance of fruits and seeds may not have directly affected population levels of the three rodents, they may have had an indirect effect by causing mammalian predators to apply increased pressure on prey populations. At least two known predators, the tayra (*Eira barbara*) and common opossum (*Didelphis marsupialis*), eat fruit when available (Enders, 1935; Kaufmann, 1962; Fleming, unpublished) but probably have to concentrate on animal food when fruit levels are low. Trap disturbance, primarily by *D. marsupialis*, was most common in the period of low fruit levels, suggesting that the scarcity of fruit was affecting the behavior of this species.

No obviously diseased animals were captured, suggesting that disease was not a cause of the declines. Of the three species, only *P. semispinosus* was parasitized by bot flies (*Cuterebra*). Males and females of various ages were parasitized by larvae usually located in the shoulder regions. Numbers of bot-infested individuals captured at Rodman were two in September and one in October and at Sherman, two in September, two in January, one in February, five in March, and one in April. Eight individuals were infested with one bot, two with two, one with three, and two with five. The effects of this parasitism, which appeared to be most prevalent in the dry season at Sherman, on the spiny rat populations is not known, but, as suggested for *Peromyscus leucopus* by Wecker (1962), heavily infested individuals might be more susceptible to predation. One young adult female that had previously been a trap-repeater was carrying five bots on its left shoulder in March and was quite weak; it disappeared after March.

Emigration could have been a factor in the density declines, but little evidence was gathered with which to assess its importance. As mentioned earlier, five individuals (three *P. semispinosus* and two *O. capito*) were known to shift their home ranges up to 50 m off the grids. Two additional *O. capito* (one at Rodman and one at Sherman) were trapped up to 400 m from the site of their last grid capture, but both were considered to be

TABLE 19
REPRODUCTIVE AND DEMOGRAPHIC PARAMETERS OF ARCTIC AND TEMPERATE
NORTH AMERICAN RODENTS

Family and Species	Locality and Habitat	Period of Obs.	Density ^a	Length of Breed. Season (mo)
Heteromyidae				
<i>Dipodomys ordii</i>	New Mexico: mesquite assoc. (33°)	1940	1.7-3.0	3.5 (A)
<i>D. merriami</i>	California: creosote bush, etc. (34°)	1956-58	1.8-3.7	6.0
<i>D. heermanni</i>	California: chaparral, hills (38°)	1938-42	9.9-17.3	10.0+
<i>D. agilis</i>	California: coastal sage scrub (34°)	1957-59		7.0
<i>D. spectabilis</i>	New Mexico: herb. plant growth (36°)	1951-53	1.0-2.2	9.0
<i>Perognathus formosus</i>	Nevada: desert (36°)	1962-66		3.0
Muridae				
<i>Oryzomys palustris</i>	Gulf of Mex.: sedge-grass assoc. (29.5°)	1957-60	Variable	<12.0
<i>Sigmodon hispidus</i>	Oklahoma: grasses and forbs (36°)	1959-61		<12.0
	Tennessee: old field (36°)	1958-60		7.0
	Georgia: shrub field (34°)	1944-54		
<i>Reithrodontomys fulvescens</i>	Texas: grassland, pine-grass ecotone (31.5°)	1955-63	avg. = 7.4	5.0+
<i>R. humilis</i>	Tennessee: old field (36°)	1958-60		=7.0
<i>R. megalotis</i>	California: annual forbs, etc. (38°)	1951-52	1.2-29.6	7.0
<i>Peromyscus leucopus</i>	Michigan: oak-hickory forest (42°)	1949-51	1.2-7.2	
	Michigan: oak-hickory forest (42°)	1936-38	7.6-25.8	7.5
<i>P. maniculatus</i>	Michigan: hemlock-hardw. for. (46.5°)	1940-42	10.5-27.2	6.0
	Minnesota: fields & pastures (44°)	1954-55		6.0
	Michigan: blue-grass assoc. (42°)	1938-39	5.2-22.8	7.0
	Michigan: old field (42°)	1940-42		7.0
	California: chaparral edge (38°)	1943-45		7.0
<i>P. truei</i>	California: chaparral edge (38°)	1943-45		7.0
<i>P. californicus</i>	California: chaparral edge (38°)	1943-45		7.0
<i>Ochrotomys nuttalli</i>	Texas: pine-oak forest (31.5°)	1955-57	5.4	<10.0
<i>Neotoma albigula</i>	Arizona: <i>Opuntia</i> , desert (32°)	1932-38	11.8	8.0
<i>N. floridana</i>	Kansas: decid. forest (39°)	1948-54		8.0
<i>N. fuscipes</i>	California: creek bott., chaparral (38°)	1939-49		5.0+
<i>Clethrionomys gapperi</i>	Michigan: hemlock-hardw. for. (46.5°)	1940-42	1.7-10.9	5.0
<i>Microtus pennsylvanicus</i>	Minnesota: cultivated fields (44°)	1954-55		12.0
	Michigan: old field & marsh (42°)	1957-58	18.0-63.0	
<i>M. ochrogaster</i>	Kansas: annual grass (39°)	1950-52	62.2-360.0	12.0
<i>M. californicus</i>	California: annual grass (38°)	1962-64	27.2-640+	<12.0
<i>Synaptomys cooperi</i>	New Jersey: bogs in pine barrens (39.5°)	1953-55	5.7-12.4	10.0
<i>Lemmus trimucronatus</i>	Northwest Terr.: heath sedge, etc. (65°)	1959-62	Variable	2.5+
<i>Dicrostonyx groenlandicus</i>	Northwest Terr.: heath sedge, etc. (65°)	1959-62	Variable	2.5+

Degrees north latitude are given in parentheses

^a Lowest and highest densities (animals/ha) recorded in study

^b No. ♀ offspring per ♀ per year; assumes 1:1 sex ratio at birth

^c Per cent of population surviving at least 1 year

^d Data from sources in Asdell (1964)

TABLE 19 (cont.)

No. litters/year	Avg. litter size	Reprod. ^b potent.	Prob. ^c surviv.	Age Sex. Mat.	Authority
3.0	3.0 (A)	4.5+		ca. 2 mo	Blair (1943)
2.0	3.1 (A)	3.1	16.0		Chew and Butterworth (1964)
3.0	3 (2-5)	4.5	5.0	2 mo	Fitch (1948)
1.0	2.6	1.3		6 mo	MacMillen (1964)
1.55	2.75	2.13	ca. 20.0		Holdenreid (1957)
1.5	5.38	4.0	64.0		French et al. (1967); Duke (1957)
5.0	4.3	12.0	0.0	40-45 dys	Negus et al. (1961)
4.0	5.9	11.8	0.0		Goertz (1965)
	5.4-7.7		0.0		Dunaway and Kaye (1961)
	5.2		0.0	2 ± mo	Odum (1955)
2.0	4-5 (A)	4.0			Packard (1968)
	3.7		5.0		Dunaway (1968)
			0.0		Brant (1962)
			0.0		Snyder (1956)
3.76	4.26	8.0	3.0	2.5-3.0 mo	Burt (1940)
3.0	5.3 (A)	8.0	25.0		Manville (1949)
6.71	4.5	15.1	5.0		Beer and MacLeod (1966)
4.0	4.0	8.0	0.0	9.5 wks	Blair (1940)
4.0	3.64	7.3	5.0	4.5-9.0 wks.	Howard (1949)
4.0	5.0	10.0	0.0		McCabe and Blanchard (1950)
3.4	3.43	5.8	20.0		McCabe and Blanchard (1950)
3.2	1.91	3.1	50.0		McCabe and Blanchard (1950)
3.0	2-3	3.7	0.0	4-8 wks	McCarley (1958)
6.0?	1.95	5.9	0.0		Vorhies and Taylor (1940)
3.0	2.0	3.0		5-6 mos	Rainey (1956)
2.0	2.0	2.1	20.0	6 mos	Lindsdale and Tevis (1951)
6.0?	3-5	12.0	3.0	4 mos	Manville (1949)
10.7	5.7	31.3	0.0	1 mo	Beer and MacLeod (1961)
			0.0		Getz (1960)
4.0	3.18	6.4	5.0	6 wks	Martin (1956)
	4.2 (A)		0.0	2-3 wks	Krebs (1966); Greenwald (1956)
6.0?	3.0	9.0	10.0		Connor (1959)
2.8	ca. 7.0	9.8	0.0	3-4 wks	Krebs (1964)
2.9	ca. 6.0	8.7	0.0	4-5 wks	Krebs (1964)

transients when caught on the grids. Other individuals undoubtedly emigrated from the grids and were never trapped again.

Though population levels of each species fluctuated during the year, the populations can still be considered "stationary" (female $R_0 = 1.00$) if densities and age composition are similar at points in time one year apart. In constructing the life table for *P. semispinosus*, I assumed its populations were stationary and indicated the same may be true for *L. adspersus* and *O. capito* though both had an R_0 less than 1.00 (Table 14). Data suggesting that the Rodman *O. capito* and *P. semispinosus* populations are stationary were obtained when that grid was retrapped in December 1967 by Manuel Correa of the Middle America Research Unit. In 1100 trap nights, 11 *O. capito* and 33 *P. semispinosus* were captured and preserved, and these numbers compare favorably with population levels in December 1966 (19 *O. capito* and 35 *P. semispinosus*). Age structures at both times were also similar (Fig. 13). Only eight *L. adspersus* were trapped in December 1967 presumably because most of the population living on the grid had been removed in June 1967.

The results of one other study have shown that densities of *O. capito* populations fluctuate seasonally in Panama. Enders (1935), working on Barro Colorado Island, found this species abundant at times and scarce at others. Rice rats were commonly collected under logs and rocks in the forest and in a woodpile and under the cook's house in the rainy season, but appeared to scatter throughout the forest in the dry season. On the causes of these concentrations, Enders stated (p. 451) "Food may be a factor, but rain with the consequent filling of their holes by water is probably more important." Although I saw individual rice rats duck into burrows (that were also used by *L. adspersus*), the only nests of this species I found were located above ground, which makes me question Enders' explanation of these concentrations. Fluctuations in the spiny rat population similar to those seen in this study were not mentioned by Enders (1935).

In the Neotropical Region, seasonal or annual population fluctuations have also been reported for *O. capito* and *Proechimys guyannensis* near Belem, Brazil (unpubl., Belem Virus Lab. 1963 Report), for *Rattus rattus* on an island in Lake Valencia, Venezuela (Gomez N, 1960), and for *Akodon arviculoides*, *A. nigrita*, and *Thomasomys sublineatus* near Rio de Janeiro, Brazil (Davis, 1945a). Density in the Venezuelan *R. rattus* population was highest in the wet season (June to November) and lowest in the dry season (January to March), as in the three species of the present study. Population levels of *O. capito* and *P. guyannensis* near Belem increased six- and two-fold, respectively, in 79 weeks and were highest in the 1963 dry season (August to October). Levels of *Akodon arviculoides*, *A. nigrita*, and *Thomasomys sublineatus* in subtropical Brazil decreased sharply for unknown reasons in the period of maximum rains (October to March); levels increased again in April.

Stable population levels have been noted in rodent populations in some

tropical areas, but outbreaks are also known to occur. In Malaya between 1948 and 1950, there were no violent numerical fluctuations or seasonal changes in age structure in populations of several species of *Rattus* (Harrison, 1955). On Ponape Island in the tropical Pacific, densities of *Rattus exulans* and *R. rattus* were "high" throughout the year, but age structure varied seasonally (Strecker, 1962). Outbreaks of rodents, or *ratadas*, have been reported in *Oryzomys xantheolus* in Peru (Gilmore, 1947) and *Holochilus brasiliensis* (= *H. sciureus*) in British Guiana (Twig, 1962). Hershkovitz (1962) reviews other reports of *ratadas* and concludes that ". . . fluctuations in populations may be as drastic in tropical and south temperate latitudes as in Arctic and north temperate areas."

Numerous population studies of temperate North American rodents have indicated that seasonal changes in density and age structure are common. Populations of many species (e.g., *Peromyscus leucopus*, *P. maniculatus*, *Reithrodontomys megalotis*, *Ochrotomys nuttalli*, *Sigmodon hispidus*, *Microtus ochrogaster*, *M. pennsylvanicus*, and *Synaptomys cooperi*) have annual peaks in the fall (except for *O. nuttalli* [Linzey, 1968], sources of data are found in Table 19). Some heteromyid rodents (e.g., *Dipodomys heermanni* and *D. merriami*) reach population peaks in summer while cricetines of the southern and western United States (e.g., *Peromyscus polionotus*, *P. maniculatus*, *P. truei*, *P. californicus*, *Ochrotomys nuttalli*, and *Reithrodontomys fulvescens*) peak in winter or spring (data for *P. polionotus* from Davenport [1964]; other sources listed in Table 19). Geographic variation in timing of population peaks in *P. maniculatus* and *O. nuttalli* are indicated by available data.

Whenever breeding and/or survivorship vary seasonally, fluctuations in density and age structure will obviously occur. Available data for both tropical and temperate rodents indicate that population changes are found whenever environmental variables fluctuate seasonally. More data are needed for tropical species before generalizations about the timing and intensity of their fluctuations can be made.

One generalization that has been made about tropical species is that their densities are usually low (many species in an area but few of any one kind). Results from this study indicate that in the Panama Canal Zone, at least, this may not be true. Densities of *L. adspersus* (6–11 per ha), *O. capito* (0–4 per ha), and *P. semispinosus* (0.4–6 per ha) compare favorably with densities of temperate North American forest-dwelling species (Table 19). In the United States, grassland species (particularly microtines) usually have much higher densities than forest species. Whether this situation obtains in the tropics is not presently known.

SURVIVORSHIP

If the survivorship curves in Fig. 12 accurately reflect rates of mortality in *L. adspersus* and *O. capito*, these two species have mortality patterns that differ significantly from each other. The curve for *L. adspersus* indicates

TABLE 20
REPRODUCTIVE AND DEMOGRAPHIC PARAMETERS OF TROPICAL RODENTS

Family and Species	Locality and Habitat	Period of Obs.	Density ^a	Length of Breed. Season (mo)
Heteromyidae				
<i>Liomys adspersus</i>	Panama: dry trop. forest (9°N)	1966-67	5.4-11.0	6.0
Muridae				
<i>Oryzomys capito</i>	Panama: wet & dry forests (9°N)	1966-67	0.34-4.3	12.0
<i>Oryzomys capito</i>	Brazil: second. & virgin for. (1.5°S)	1962-63		12.0
<i>Akodon arviculoides</i>	Brazil: second. & virgin for. (22°S)	1942-43		8.0
<i>Rattus rattus</i>	Venezuela: dry trop. for. (10°N)	1956-58	1.5-6.1	12.0
<i>Rattus rattus</i>	Ponape island (7°N)	1955-58		12.0
<i>R. exulans</i>	Ponape island (7°N)	1955-58		12.0
	Malaya: forest (3°N)	1948-50		12.0
<i>R. rattus jalorensis</i>	Malaya: forest & oil palm pl. (3°N)	1948-50		12.0
<i>R. rattus argiventer</i>	Malaya: wasteland (3°)	1948-50		12.0
<i>R. mulleri</i>	Malaya: forest (3°N)	1948-50		12.0
<i>R. whiteheadi</i>	Malaya: forest (3°N)	1948-50		12.0
<i>R. rajah</i>	Malaya: forest (3°N)	1948-50		12.0
<i>R. diardi</i>	Malaya: town (3°N)	1948-50		12.0
<i>R. bowersi</i>	Malaya: forest (3°N)	1948-50		12.0
<i>R. sabanus</i>	Malaya: forest (3°N)	1948-50		12.0
<i>R. canus</i>	Malaya: forest (3°N)	1948-50		12.0
<i>Chiropodomys gliroides</i>	Malaya: forest (3°N)	1948-50		12.0
Echimyidae				
<i>Proechimys semispinosus</i>	Panama: wet & dry for. (9°N)	1966-67	0.4-5.6	12.0
<i>P. guyannensis</i>	Brazil: second. & virgin for. (1.5°S)	1962-63		12.0
<i>P. iheringi</i>	Brazil: second. forest (22°S)	1942-43		12.0
<i>P. dimidiatus</i>	Brazil: virgin forest (22°S)	1942-43		12.0

Degrees latitude are given in parentheses

* Calculated by the method of Emlen and Davis (1948)

^a Lowest and highest densities (animals/ha) recorded in study

^b No. ♀ offspring per ♀ per year; assumes 1:1 sex ratio at birth

^c Per cent of population surviving at least 1 year

TABLE 20 (cont.)

No. litters/yr.	Avg. litter size	Reprod. ^b potent.	Prob. ^c surviv.	Age Sex. Mat.	Authority
1.44	3.2	2.25	28.0	ca 3 mos	Present study
6.1	3.9 3.1 3-5	11.9	ca. 3.0 3.0? 0.0 5.0?	40-45 dys	Present study Belem Virus Lab. Reports, 1962-3 Davis (1945a, 1947) Gomez (1960)
3.2	3.8	6.1			Storer (1962)
3.9	2.5	4.9	36.0		Storer (1962)
4.35*	4.2	12.8	8.0		Harrison (1951, 1955, 1956)
3.48*	3.2-5.3	7.5	34.5		Harrison (1951, 1955, 1956)
1.13*	5.5	3.1	26.0		Harrison (1951, 1955, 1956)
2.34*	3.8	4.6	22.5		Harrison (1951, 1955, 1956)
4.70*	3.0	7.0	9.6		Harrison (1951, 1955, 1956)
1.74*	3.3	2.9	28.0		Harrison (1951, 1955, 1956)
4.58*	5.2	11.9	9.6		Harrison (1951, 1955, 1956)
1.74*	4	3.5	26.0		Harrison (1951, 1955, 1956)
2.44*	3.1	3.8	13.5		Harrison (1951, 1955, 1956)
2.78*	3	4.2	19.0		Harrison (1951, 1955, 1956)
2.26*	2.2	2.5	34.5		Harrison (1951, 1955, 1956)
4.7	2.5 2 1-2 2.7	5.8	36.0	ca 6 mos	Present study Belem Virus Lab. Reports, 1962-3 Davis (1945a, 1947) Davis (1945a, 1947)

that a constant number of animals die per unit time, regardless of the number remaining. The curve for *O. capito* indicates that a constant fraction of the number alive die at each age. These two survivorship curves resemble types II and III of Slobodkin (1961). The survivorship curve for *P. semispinosus* was drawn assuming that mortality was age-constant. Based on the observed survival rates of marked and sacrificed individuals, this assumption seems reasonable.

Mortality rates, the q_x column in Table 14, also differ between the species. Early mortality in *L. adspersus* was apparently low, and the rate steadily increased with increasing age. The mortality rates of *O. capito* and *P. semispinosus* were constant owing to the nature of those species' survivorship curves. With better data on survivorship early and late in life, perhaps each of the q_x curves would resemble a "U" (high mortality early and late in life) that has been reported for several mammals by Caughley (1966).

The scanty data available on survivorship in tropical rodents are summarized in Table 20. Few *O. capito* and *Proechimys guyannensis* in forests near Belem were recaptured for more than one year, but most animals were several months old when first marked and mortality owing to handling was high (unpubl., Belem Virus Lab. 1963 Report). Average lifespan of *Rattus rattus* on Zorro Island, Venezuela, was about five months though a few rats lived 15 months (Gomez N, 1960). Juvenile survivorship varied seasonably as found in *P. semispinosus* in Panama. Young born in the dry season survived through the wet season, whereas few born in the wet season survived through the dry season. Annual survivorship of several species of Malayan and Polynesian rats is similar to that of *L. adspersus* and *P. semispinosus* (Table 20).

In temperate North America, many cricetines and microtines live less than one year (Table 19), and an annual population turnover is probably the rule. Semiannual turnovers probably occur in *Microtus pennsylvanicus* and *Sigmodon hispidus* (Getz, 1960; Odum, 1955). An annual turnover occurs in populations of *Akodon azarae* in the grasslands around Buenos Aires, Argentina (Pearson, 1967). Lifespans covering more than one year occur in species of *Neotoma* (Finley, 1958; Linsdale and Tevis, 1951; and Rainey, 1956), in *Peromyscus californicus* (McCabe and Blanchard, 1950), in *P. maniculatus* (Manville, 1949), in *Dipodomys merriami* (Chew and Butterworth, 1964), in *D. spectabilis* (Holdenreid, 1957), and in *Perognathus formosus* (French et al., 1967). Most species having a high annual survivorship are characterized by relatively low reproductive rates (Table 19).

Data available on survivorship in temperate and tropical rodents suggest that similarly-sized species from both regions have comparable annual probabilities of survival. For example, few individuals of *Peromyscus leucopus* or *Oryzomys capito*, temperate and tropical ecological counterparts, survive one year (Fleming, 1970b) whereas lifespans of two or three years are not uncommon for individuals of *Neotoma floridana* (Fitch and Rainey, 1956) and *Proechimys semispinosus*. The relationship between body size and survivorship apparently breaks down in rodents that become seasonally dormant.

Lifespans of three to five years occur in *Perognathus longimembris*, a 6–8 g desert-dwelling heteromyid (French et al., 1967), and, judging from their low reproductive rates (Brown, 1967), individuals of *Zapus princeps*, a species that hibernates for eight months of the year, have relatively long lifespans.

REPRODUCTION

The three species differ considerably regarding their reproductive rates, defined as the number of litters produced per month of breeding, and patterns and, hence, in their potential rates of population growth. *L. adspersus* breeds seasonally at a rate of about 0.24 litters per month whereas *O. capito* and *P. semispinosus* breed year-round at rates of 0.51 and 0.39 litters per month, respectively. With respect to age at sexual maturity, an important parameter in terms of its consequence for population growth (Cole, 1954), the species also differ significantly. Females of *O. capito* begin to breed at less than two months of age while females of *P. semispinosus* are six to nine months old before they produce their first litter. Although some females of *L. adspersus* attain sexual maturity at about three months of age, most probably do not produce their first litter until nearly one year old. Thus, the two year-round breeders appear to have potentially higher population growth rates than the seasonal breeder.

Although *O. capito* and *P. semispinosus* breed throughout the year, their reproductive rates differ significantly owing to the longer gestation period of the latter species. As determined by the birth of six litters under laboratory conditions, length of gestation in *O. capito* is 28.2 days, and young are altricial at birth. This gestation period, based upon the interval from the day a male was confined with a female to the day a litter was born, is maximal. With better data, gestation in *O. capito* may prove to be similar to the value of 25 days in *O. palustris* (Svihla, 1931). In contrast, spiny rats have a long gestation period (51 days) and are precocial at birth (Tesch, 1970a). The smaller litter size of *P. semispinosus* has probably resulted from the increased size and advanced development of the young at birth, a trend also seen in heteromyid rodents (Eisenberg and Isaac (1963)). Kangaroo rats (*Dipodomys*) produce young that are more precocial than those of spiny pocket mice (*Liomys*), and gestation periods are longer and litters smaller in *Dipodomys*. As a result of its smaller litter size and longer gestation period, *P. semispinosus* produces fewer young per unit time than *O. capito*.

Despite the fact that the three species are existing under the same climatic regime, they display two different reproductive patterns, seasonal and aseasonal. Presumably these patterns are the products of natural selection, and each is the most advantageous one available to individuals of each species. At our present knowledge, it is not clear why the spiny pocket mouse should find a seasonal pattern more advantageous than an aseasonal one, but presumably the ultimate factor is related to producing young under optimal conditions, whether these are the availability of food or dry nest sites. Since this spiny pocket mouse is abundant in the savannas of western

Panama (Handley, 1966), it is probably faced with a food source such as grass seeds that is only seasonally available throughout a large part of its range. Of interest in this respect is the fact that *Heteromys desmarestianus*, the wet forest counterpart of *L. adspersus* along the Caribbean slope in Panama, apparently breeds year-round (Fleming, 1970a). How the "optimal conditions" for the production of young differ (if indeed they do) between *H. desmarestianus* and *L. adspersus* is not known. Perhaps suitable food is more evenly distributed throughout the year in the wet forests although I have no conclusive evidence of this.

The proximate factor(s) responsible for timing of breeding in *L. adspersus* is currently unknown but could conceivably include changes in photoperiod or rainfall, although the former factor is usually discounted as a cue to breeding in tropical vertebrates (Moreau, 1950; Skutch, 1950; Miller, 1963). Both males and females attain breeding condition by October and first conceptions probably occur in November, at the height of the rainy season when day-length is decreasing. Since seasonally-breeding Panamanian bats are also becoming reproductively active at this time (Fleming and Hooper, unpublished), the same environmental factor(s) apparently synchronize breeding in several species of Panamanian mammals. Experimental work is needed to elucidate the nature of such a cue(s).

The differences in reproductive patterns of the species are, in part, the result of their separate evolutionary histories. Most rodents of the family Heteromyidae are polyestrous seasonal breeders, with the availability of food, rainfall, and the onset of winter (in the United States) serving as ultimate or proximate selective factors (Asdell, 1964; Eisenberg, 1963). Most cricetines breed throughout the year in warmer parts of their ranges if temperatures are not too high (Walker, 1964). Little is known about the reproductive biology of most echimyid rodents, but in species of the genera *Proechimys*, *Cercomys*, *Echimyus*, *Hoplomys*, and *Diplomys*, the trend is to have small litters (avg. = 2-3) of precocial young (Walker, 1964; Tesh, 1970a, b). Females in species other than *P. semispinosus* are probably also polyestrous. Davis (1945a) reported that *Proechimys dimidiatus* and probably *P. iheringi* breed throughout the year in subtropical Brazil. Thus, in light of the different evolutionary histories of the species in this study, it should not be surprising to see different reproductive patterns in animals living under the same climatic conditions, especially when food availability probably undergoes significant fluctuations during the year.

Although spiny rats produce young throughout the year, there was a tendency at Rodman, at least, for more females to be pregnant in the first half of the year than in the last half. Whether this represents a significant trend towards concentrating births into a restricted portion of the year cannot be determined at this time. However, if current data concerning disappearance rates reflect real differences in survival rates that vary with the season in which young are born, a restricted breeding season might be selectively advantageous under present environmental conditions. Females

producing young only in the dry and early wet seasons will perhaps produce more offspring that reach maturity than those extending their reproductive efforts over the entire year. With these considerations in mind, one wonders why females at Sherman do not show a higher proportion of pregnancies in January through June. This aspect of the biology of *P. semispinosus* certainly deserves further study.

Reproductive rates and patterns of *L. adspersus* and *O. capito* may differ from those of their temperate North American relatives (e.g., *Liomys pictus*, and *Oryzomys palustris*). The biology of *L. pictus* is poorly known, but age at sexual maturity and litter size are probably similar to those parameters in *L. adspersus*. However, *L. pictus* may breed throughout the year (Hall and Kelson, 1959), which, if true, represents a significant difference from *L. adspersus*. *A priori*, the reverse might be expected to be true.

Oryzomys palustris, a temperate relative of *O. capito*, is not restricted to the temperate zone but ranges as far south as the Panama Canal Zone where it is apparently rare (Handley, 1966). Age at sexual maturity is probably similar in both species. Litter size may be similar, but this parameter varies widely in *O. palustris* (Negus et al., 1961). Hamilton (1946) reported that *O. palustris* in Virginia can produce nine litters per year whereas *O. capito* probably produces around six per year. These data suggest that the reproductive rate of *O. capito* is lower than that of *O. palustris*.

Except for the fact that *P. semispinosus* breeds throughout the year, the reproductive biology of the spiny rat is similar to that of North American wood rats (*Neotoma*). Both are approximately the same size, attain sexual maturity at comparable ages (Tables 19 and 20), and have small litters. However, young of *Neotoma* are altricial while those of *Proechimys* are precocial.

Since many tropical rodents live under conditions that tend to promote year-round breeding whereas temperate and arctic species are exposed to conditions favoring seasonal breeding, it is of interest to determine whether species from northern latitudes display the same reproductive effort in their limited breeding seasons as do tropical species. While several criteria can be used to determine reproductive effort (see Williams, 1966), I will use reproductive rate, the number of litters produced per month of breeding, in the following comparisons, which utilize data from Tables 19, 20, and 21.

When their reproductive efforts (rates) are compared, arctic and temperate murids (cricetines and microtines) produce a significantly greater number of litters per month of breeding than tropical murids ($P < .001$; Table 22). Among the northern murids, microtines (7 species; $x = 0.90$) have a greater reproductive rate than cricetines (7 species; $x = 0.52$) ($.05 > P > .01$). Northern murids also breed at a faster rate than temperate heteromyids ($.05 > P > .02$). *Liomys adspersus*, the only tropical heteromyid for which reproductive data exist, breeds at a lower rate than most temperate heteromyids (Table 22). Although rates of breeding in temperate

TABLE 21
REPRODUCTIVE DATA FOR NORTH AMERICAN RODENTS

Family & Species	Length of Breeding Season (mo)	Avg. Litter Size	No. Litters per yr	Latitude	Authority
Heteromyidae					
<i>Perognathus parvus</i>	4.0	5.2	2	48	
<i>P. fasciatus</i>	5.0	4-6	1	42	
<i>P. flavus</i>	9.0	3-6	2?	34	
<i>P. longimembris</i>	3.0+	5	2	39	
<i>Dipodomys spectabilis</i>	6.0	1.8	3	34	
Muridae					
<i>Onychomys leucogaster</i>	7.0	4	5.1	40	
<i>Neotoma mexicana</i>	4.0?	2-4	1	39	
<i>N. micropus</i>	6.0	2	2+	34	
<i>Microtus operarius</i>	3.0?	6	2+	64	
<i>M. miurus</i>	3.0	8.23		71	Hoffmann (1958)
<i>M. oeconomus</i>	3.0	7.5		71?	Hoffmann (1958)
<i>M. montanus</i>	5.0	6.5		39	Hoffmann (1958)
<i>M. oregoni</i>	8.0	3.0		49	Hoffmann (1958)
Zapodidae					
<i>Zapus hudsonius</i>	4.5	5.5	2	42	Whitaker (1963)
<i>Z. princeps</i>	<4.0	4.8-6.7	1	41	Brown (1967)
<i>Napeozapus insignis</i>	4.0	4.5	1-2	42	

Data are from sources listed in Asdell (1964) unless otherwise noted.

and tropical murids differ significantly, the total number of litters produced per season or year by these two groups is not significantly different ($.20 > P > .10$); temperate murids, however, do produce significantly more litters per year than temperate heteromyids ($.01 > P > .001$). Finally, there are no significant differences in litter size between temperate and tropical murids and heteromyids ($P > .40$). The three species of North American zapodids for which there are sufficient data resemble temperate heteromyids in their low reproductive rate and large litter size (Table 22).

It therefore appears that among murid rodents, at least, northern species are making a greater reproductive effort during their breeding season than are tropical species, which produce the same number of litters per year as northern species but over a longer breeding season. This difference suggests there are latitudinal gradients in the reproductive efforts of some rodents, presumably resulting from geographic variations in the selective pressures molding reproductive rates and patterns. Since the reproductive efforts of temperate murids also differ from those of heteromyids and zapodids, the

TABLE 22
COMPARISON OF REPRODUCTIVE PARAMETERS OF TEMPERATE AND TROPICAL RODENTS

Parameter	Temperate Species			Tropical Species	
	Murids (24 spp.)	Heteromyids (11 spp.)	Zapodids (3 spp.)	Murids (14 spp.)	Heteromyids (1 sp.)
No. litters per month	0.63 ± 0.12	0.40 ± 0.15	0.36	0.26 ± 0.02	0.24
No. litters per year or season	4.06 ± 0.85	2.00 ± 0.49	1.50	3.19 ± 0.80	1.44
Avg. litter size	4.06 ± 0.62	3.76 ± 0.84	5.27	3.71 ± 0.51	3.2

Data taken from Tables 19, 20, and 21. Means are given ± 95% confidence intervals.

latter two groups apparently have utilized different means (i.e., lower reproductive rates combined with periods of dormancy) than murids in adapting to the challenge of a seasonally fluctuating environment.

HOME RANGE SIZES AND DISTRIBUTIONS

A summary of the home range data shows that populations of *Liomys adspersus*, *Oryzomys capito*, and *Proechimys semispinosus* consist of individuals possessing discrete home ranges that are usually distributed randomly with respect to other members of the same species. Males tend to have larger home ranges than females, and significant differences in range size exist between species.

The many factors known to affect home range size include size of species, sex, age, food habits, habitat quality, population density, and season of year (Blair, 1953). Effects of some of these factors are evident in the three species of this study. On the basis of body size *P. semispinosus* should have the largest home ranges, since this species is at least twice as large as *O. capito* and *L. adspersus*; however, *O. capito* had home ranges that were considerably larger than those of *P. semispinosus*. The disparity between size of body and home range is further seen when *O. capito* and *L. adspersus* are compared. Though body sizes are similar, ranges of *O. capito* averaged about twice as large as those of *L. adspersus*.

Differences in range size seen between species may result in part from differences in kinds and availabilities of foods eaten. Although details of their food habits are not well known, each species is known to concentrate on different food sources. *L. adspersus* consumes seeds, palm nuts, and some insects, *O. capito* probably is omnivorous, and *P. semispinosus* may be mostly frugivorous (Fleming, 1970a). Differences in home range size imply that concentrations of preferred foods may be quite different for each species. McNab (1963) has pointed out that "hunters" generally have larger home ranges than "croppers." Of the three species, *O. capito* is most likely a

"hunter" while *L. adspersus* and *P. semispinosus* are most likely "croppers" as they can concentrate on seasonally "dense" food sources such as seeds, palm nuts, and fallen fruits.

Stickel (1960), Brant (1962), Lidicker (1966), and Krebs (1966) among others, have noted that movements of animals living in sparse populations are longer than those of animals living in dense populations. In the three species studied here, average home range size is inversely related to average population density, i.e., spiny pocket mice had smaller ranges than rice rats. Within species, male *O. capito* and *P. semispinosus* had larger ranges at Rodman than at Sherman. Throughout most of the year population levels of these species were higher at Sherman than at Rodman, but differences in habitat quality may also be involved. However, since females in both populations had similarly-sized ranges, home range size in these males may be density dependent.

Prior to attaining sexual maturity, some rodents disperse from their place of birth to establish a new home range (Howard, 1949; DeLong, 1967). No differences were found in the movements of immature and mature individuals of any of the three species, but this does not preclude the possibility that juveniles disperse from their birthplaces and establish their own home ranges before entering traps. Evidence for such a possibility is the fact that in each species only about 33 per cent (range, 15–40 per cent) of the immature individuals marked on the grids failed to establish home ranges there. This value may be high because some immatures that were not recaptured may have already had home ranges that barely entered the grids. Dispersal movements, if they exist, may occur just after weaning because in many cases small juveniles of all species established residence on the grids. Once established, these individuals never shifted their home ranges.

Intraspecific behavioral interactions have long been considered important in the regulation of small mammal populations, but until recently little work has been done to demonstrate their effect. Sadleir (1965) and Healy (1967) have shown that adult male aggression in *Peromyscus maniculatus* negatively affects juvenile recruitment success and keeps population levels low in the summer. Metzgar (1968), working with *Peromyscus leucopus*, showed that females maintain home ranges that are exclusive of other females and that remain stable in the face of fluctuating population levels. Success of female immigrants in establishing home ranges is dependent on the density of female residents so that a behavioral mechanism operates to limit the density of female woodmice.

A random or clumped distribution of home ranges with respect to members of the same and opposite sexes, as seen in *L. adspersus*, *O. capito*, and *P. semispinosus*, implies that behavioral interactions may not be an important source of population regulation in these species. Within each species, no individuals displayed exclusive home ranges that could limit the number of individuals residing in an area. While no overt evidence of territoriality was seen from the distribution of home ranges, the possibility that nest sites

or food caches are defended still exists. No information bearing on this possibility was gained in this study.

The spatial distribution of *L. adspersus* ranges differs somewhat from that of other species of heteromyids. Ranges of male *Liomys salvini* at Cerros de Palomas, Costa Rica, were larger than those of females, and both sexes tended to segregate in different parts of the study area (MacPherson, 1967). Ranges of that species averaged three times smaller than those of *L. adspersus* (0.15 ha vs. 0.56 ha). In southern Mexico, male and female ranges of *Liomys irroratus* are spatially segregated in the rainy season (Wagner, 1961). Females with ranges that are exclusive of other females have been reported in *Perognathus penicillatus* and *Dipodomys agilis* (Blair, 1943; MacMillen, 1964). Ranges that overlap among members of the same sex are found in *Perognathus longimembris*, *Dipodomys ordii*, *D. merriami*, and *D. spectabilis* (Blair, 1943; Chew and Butterworth, 1964; Holdenreid, 1957). The fact that some heteromyids possess mutually exclusive ranges is not surprising owing to the asocial behavior of most adults (Eisenberg, 1963).

There are few reports of home ranges in other species of tropical rodents. At Belem, Brazil, ranges of *Proechimys guyannensis* (males = 1.40 ha; females = 0.15 ha) were larger than those of *O. capito* (males = 0.69 ha; females = 0.08 ha) (unpubl., Belem Virus Lab. 1963 Report); this is just the opposite of results in this study. In subtropical Brazil, movements of recaptured *Akodon arviculoides*, *A. nigrita*, and *Thomasomys sublineatus* indicated that individuals inhabited restricted areas that were probably less than 100 m in diameter; the longest movement recorded for any individual was 375 m (in *A. arviculoides*) (Davis, 1945b). Harrison (1958) believed that individuals of several species of Malayan rats did not maintain discrete ranges but that they wandered randomly. He expressed the distribution of these movements as *standard diameters* whose values ranged from 70 to 136 m in different species. Ranges of male *Rattus exulans* on Ponape Island were greater than ranges of females, and size of ranges in both sexes was inversely proportional to population density (Jackson and Strecker, 1962).

Generalizations about the home range concept based on results of numerous studies of temperate mammals are found in Blair (1953), Brown (1962), and Sanderson (1966). I can think of no theoretical reasons why the concept of home range as applied to temperate rodents should not apply to tropical rodents. Available data indicate that many rodents, regardless of habitat, remain in discrete areas most of their lives.

CONCLUSIONS

Several points have emerged from this study. The first is that a strongly seasonal rainfall pattern in a tropical environment can have a significant effect on the biology of the rodents living there. Most of the breeding activity of *L. adspersus* was confined to the dry season, and at Rodman the proportion of pregnant to nonpregnant *P. semispinosus* was higher in the first (drier) half of the year than in the last (wetter) half. Population levels

of each species fluctuated seasonally and were highest in the rainy season, lowest in the dry season. Finally, survivorship in young *P. semispinosus* born in the dry half of the year was higher than in young born in the wet half.

A second point is that the biology of each species strongly reflects its phylogenetic history. That is, although living under the same environmental conditions, each species has biological characteristics more closely resembling those of related species and genera than they do each other. Different evolutionary histories can explain in part the interspecific differences in reproductive rate, litter size, and condition of young at birth.

Thirdly, two populations of *O. capito* and *P. semispinosus* living in different habitats 56 km apart were demographically similar. Population fluctuations were nearly synchronous, and reproductive rates were similar in each population. However, the distribution of births in *P. semispinosus* was spread more evenly throughout the year at Sherman, and average lifespan was apparently greater there than at Rodman. Population levels of both species were generally higher at Sherman than at Rodman. In view of the fact that the demographic properties of populations of species separated by a distance of one km or less sometimes differ widely (DeLong, 1967; Krebs, 1966; Newson, 1963), the similarities seen in the two populations of *O. capito* and *P. semispinosus* are striking.

The fourth point—that reproductive rates of *L. adpersus* and *O. capito* are lower than those of temperate North American relatives—needs further documentation. Little is known about the rate of litter production in temperate species of *Liomys* or *Oryzomys palustris*. To gain this information, studies of marked and released individuals are needed. Data gained in this manner are obviously superior to the calculation of reproductive rates from a knowledge of length of breeding season and gestation period and by assuming a postpartum estrus does or does not occur.

Finally, both similarities and differences were found when the population ecologies of temperate and tropical rodents were compared. Population densities of rodents in the Panama Canal Zone compare favorably with densities of temperate forest-dwelling rodents. Whereas annual survivorship of similarly-sized temperate or tropical species is usually comparable, reproductive rates of temperate murids tend to be higher than those of tropical murids. This difference suggests that there exist latitudinal gradients in the selective pressures molding reproductive rates as well as patterns. Investigations of intraspecific variation in the demographic parameters of a single species such as *Sigmodon hispidus* that ranges in both temperate and tropical regions would help to elucidate the relationship of seasonality to reproductive rates and survivorship in rodents.

SUMMARY

Five populations of three species of rodents, *Liomys adpersus* (family Heteromyidae), *Oryzomys capito* (family Muridae), and *Proechimys semispinosus* (family Echimyidae), were studied for one year in two forests in the

Panama Canal Zone, Central America. A basic objective was to discern whether these tropical rodents have lower, more stable population levels, lower reproductive rates, and higher survivorship rates than relatives or ecologic counterparts in temperate regions.

The two study sites, located at opposite ends of the Canal Zone, consisted of a dry tropical forest on the Pacific slope and a moist tropical forest on the Atlantic slope. *L. adpersus* was found only in the Pacific forest while *O. capito* and *P. semispinosus* occurred in both forests. Nearly 580 individuals of the three species were captured over 3,000 times on live-trap grids, and an additional 784 individuals were sacrificed and preserved for detailed laboratory study.

Population densities in each species fluctuated seasonally; peak levels occurred at the height of the rainy season (October to December). Densities of *L. adpersus* (5–11 per ha) were greater throughout the year than those of the other two species. Breeding occurred year-round in *O. capito* and *P. semispinosus* but was restricted to the period December to May (mostly dry season) in *L. adpersus*. Each adult female of *L. adpersus*, *O. capito*, and *P. semispinosus* can produce, on the average, about 4.5, 23.7, and 11.6 offspring per year, respectively. In *L. adpersus*, *O. capito*, and *P. semispinosus*, the probability of surviving one year is 0.28, <0.05, and 0.36, respectively. Survivorship in *P. semispinosus* varied seasonally; young born in the dry season lived longer than those born in the wet season.

In each species, individuals had discrete home ranges that were randomly distributed with respect to members of the same or opposite sex. Ranges averaged larger in males and were largest in *O. capito* (avg. = 1.32 ha) and smallest in *L. adpersus* (avg. = 0.55 ha).

Temperate and tropical rodent populations are compared with respect to population densities, annual survivorship rates, and reproductive rates. In regard to these parameters, rodents in the Panama Canal Zone have population densities comparable to those of temperate forest-dwelling species; survivorship rates of similarly-sized rodents, whether temperate or tropical, are usually similar; and the reproductive rates of temperate murids are higher than those of tropical murids.

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