Reproduction, Growth and Development in Two Contiguously Allopatric Rodent Species, Genus *Scotinomys*

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INTRODUCTION

A systematic synopsis of *Scotinomys* in 1972 (Hooper, 1972) summarized the information on morphology, ecology and distribution of the genus. The known populations were found to represent two species, *S. xerampelinus* and *S. teguina,* the latter polytypic. The species were shown to be allopatric, but there was evidence that where their ranges abutted they might be locally sympatric. Relationships of the populations in those areas were not understood. The data then available suggested that the two species were insectivorous, diurnal, communicated by high frequency sounds, and that they contrasted in several anatomical and behavioral traits.

That systematic synopsis posed questions and set the basis for subsequent research. In areas of contiguous sympatry, are the species occupying different microenvironments? Do they compete, and if so, for what resources? How do interspecific anatomical and behavioral differences (e.g., in aggressiveness, thermoregulation, voice (Fig. 1), size of eye, and number of mammary glands), relate to altitudinal segregation of the species, reproductive strategies, and possible interspecific competition? Information on some of the interspecific differences is detailed elsewhere: temperature regulation (Hill and Hooper, 1971); orbital region and size of eye (Hooper, 1975); karyotypes and accessory reproductive glands (Carleton, Hooper, and Honacki, 1975); and high frequency vocalization (Anderson and Hooper, ms.).

Fig. 1. *Scotinomys teguina* vocalizing.

The present report is concerned principally with four aspects of the biology of *Scotinomys:* reproduction, postnatal growth and development, behavior and food habits, and distribution and habitats. Secondly, it discusses factors and selection pressures which possibly were involved in the evolution of different reproductive regimes, behaviors, and ecologies of the species.

MATERIALS AND METHODS

The animals used in the laboratory were obtained in Sherman live traps baited with peanut butter and rolled oats, and then shipped by air to facilities in the University of Michigan Museum of Zoology. They are from the following Middle American localities. *Scotinomys teguina.* Costa Rica: Cartago, Tapantí, 1200 m, May 1969, 1; Volcán Irazú, 2850-2940 m, June 1969, 15; March 1971, 6; August 1972, 13; Puntarenas, Monte Verde, 1430 m, May 1969, 8. Nicaragua: Matagalpa, 9 km N Matagalpa, Santa Mariá, de Ostuma, 1300-1400 m, May 1969, 5. Panamá: Chirquî, Rîo Chirquî Viejo, 1800 m, May 1969, 1. *S. xerampelinus.* Costa Rica: Cartago, Volcán Irazú and Volcán Turrialba, 2700-3000 m, April 1969, 13; August 1972, 19.

The animals were housed in polycarbonate cages (Maryland Plastics Inc.) of two sizes: 26.7 cm x 48.3 cm x 15.5 cm for mated pairs and 21 cm x 28 cm x 16 cm for single individuals. White pine shavings covered the cage bottom to a depth of 4 cm, and cotton batting and small metal cans were provided for nesting materials. The lab diet consisted of Purina Cat Chow pellets supplied ad libitum together with a daily feeding, usually in early morning, of approxi-

mately ten large mealworms (*Tenebrio*) per individual. The meal-worms were dusted with a mineral-vitamin powder (Pervinal Nutritional Supplement, Thayer Laboratories, Inc.) prior to distribution to the mice. Dusted larvae were consumed as avidly as those not dusted, and pupal and adult stages were eaten as readily as larvae. Gravid females or those nursing young received an additional ration of mealworms in late afternoon. Females with nursing young and recently-weaned young also were given wheat germ. This food was used by the young mainly during the period in transition from mother's milk to the hard diet of mealworms supplemented by cat chow. Water was furnished ad libitum. The animal room was maintained on a 12:12-hour light/dark cycle and at a temperature of approximately 20° C. Relative humidity, not controlled, varied from 40 to 70 percent.

Mice usually were not paired until they reached adult proportions (about three months). Newly paired individuals were watched closely for indications of incompatibility because protracted fighting typically resulted in loss of fur on the rump and nape of neck and sometimes death of the subordinate individual. Severe antagonism, more frequently observed in *xerampelinus*, seemed to result when a female resisted continual mounting attempts by a male. Allowing the male to remain in the cage with the female prior to parturition and during lactation did not adversely affect the rearing of a litter: numerous litters were successfully raised both when the male parent was allowed to remain and when he was removed. Young were routinely weaned at one month of age. Young of a litter were kept together in one large cage until three months of age.

Data on growth and development of the animals were collected over the four-year period September 1969 to July 1973. Weight, total length, and lengths of tail, hind foot, and ear were measured on day of birth and subsequently at weekly intervals to three months of age. Body length was calculated from total length and tail length. Weight to nearest 0.01 gram was obtained with a Mettler P1200 analytical balance.

Young were restrained in a small cardboard box while being weighed. Standard length measurements were taken with a flexible plastic rule calibrated in mm. Total length and tail length were rounded to the nearest mm, while hind foot and ear lengths were recorded to the nearest 0.5 mm. The young, when being measured, were held in hand (appressed to the plastic rule, the end of the tail at 0 mm). Though their uncooperativeness contributed error to the length measurements, especially total length, we assume that the errors tend to cancel out. We rejected anesthesia because it typically resulted in death of the young animal. Newborn individuals were examined at 10X magnification with a binocular microscope. Subsequent developmental features were observed with the unaided eye. The animals were checked once or twice each week for the following

developmental events: opening of eyes, unfolding of pinnae, freeing
of digits, opening of external auditory meatus, eruption of incisors,
emergence of pelage, locomotor ability, and perforation of the vulva.

Females in late stages of pregnancy were checked twice daily
(morning and late afternoon). Recorded date of birth is that day on
which the litter was discovered, although it may have occurred in the
late evening of the previous day. When there was evidence that one
or more young had been eaten by the parent(s), those litters were
not included in our analysis of litter size and sex ratios. Since the sex
of young less than one week of age was sometimes difficult to
determine accurately, those litters in which a young died within the
first week were eliminated from the analysis of sex ratios. In
estimating length of gestation, intervals between births were recorded
only for those females continuously paired with a male, and extraor-
dinarily long interbirth intervals were omitted.

Stomach contents and proportions of the hindgut were exam-
ined to gain information on food habits of wild-caught *Scotinomys*.
Contents of the stomachs were removed and stored in 70% alcohol.
Later, they were teased apart in a petri dish and examined at 10X to
45X magnifications. The food was categorized as insect (orders and
families if possible), seed, berry, or fibrous plant material, and the
percent volume of each category was estimated. The 130 stomachs
examined (67 *teguina* and 63 *xerampelinus)* are from localities as
follows. *S. teguina.* Costa Rica: Alajuela, Volcán Poas, 20; Cartago,
Moravia, 7: Volcán Irazú, 21; Puntarenas, Monte Verde, 3; San José,
Cerro de la Muerte, 11. Panamá: Chiriquí, Río Chiriquí Viejo, 5. *S.
xerampelinus.* Costa Rica: Cartago, Volcán Irazú, 31; San José, Cerro
de la Muerte, 32.

For study of the remainder of the alimentary tract, adult
wild-caught specimens, initially fixed in 10% formalin and stored in
70% alcohol were used. The collecting localities and number of
specimens examined are as follows: *S. teguina.* Costa Rica: Cartago,
Moravia, 9; Puntarenas, Monte Verde, 1. *S. xerampelinus.* Costa Rica:
Cartago, Volcán Irazú, 10. The hindguts (small intestine, large intes-
tine, and caecum) were removed intact, pinned out (taut but not
stretched) and measured to the nearest mm.

Activity patterns of the species in the laboratory were moni-
tored in small mazes, each 36.8 × 34.3 × 6.4 cm. Three treadles in
each maze activated microswitches connected to an Esterline-Angus
event recorder (Model AW). The treadles were placed at strategic
locations (at nest box, in food and water area, and a third in a long
runway) to ensure that most bouts of activity would be monitored;
the animals could not avoid crossing a treadle when moving from one
section of the maze to another. The mazes were housed in a Hot-Pac
environmental chamber under a constant temperature (20° C) and
humidity (50%). The daylight period (0530 to 1930 hrs) was
simulated by two bright overhead fluorescent lamps, and that of

night hours (1930 to 0530 hrs) by an incandescent bulb, its output approximately that of 10 watts at 60 volts. Each animal was allowed three to five days to adjust before its activity was recorded. Activity records for most of the animals span seven or more consecutive days.

DISTRIBUTION AND HABITATS

The two known species of *Scotinomys* inhabit the mountains of Middle America. *S. teguina,* with four geographic races (Hooper, 1972), is distributed from the state of Chiapas, Mexico, southeastward to western Panamá (Fig. 2). *S. xerampelinus* is restricted to Costa Rica and western Panamá (Fig. 3). The species live in temperate or subtropical climates where there is moisture and cloud cover for much of the year. Both are now highly discontinuously distributed, due probably to changes in climate in Pleistocene time or later and certainly to activities of man, who has usurped the animals' habitat for agricultural and other purposes.

Though both species inhabit cool, moist, montane environments,
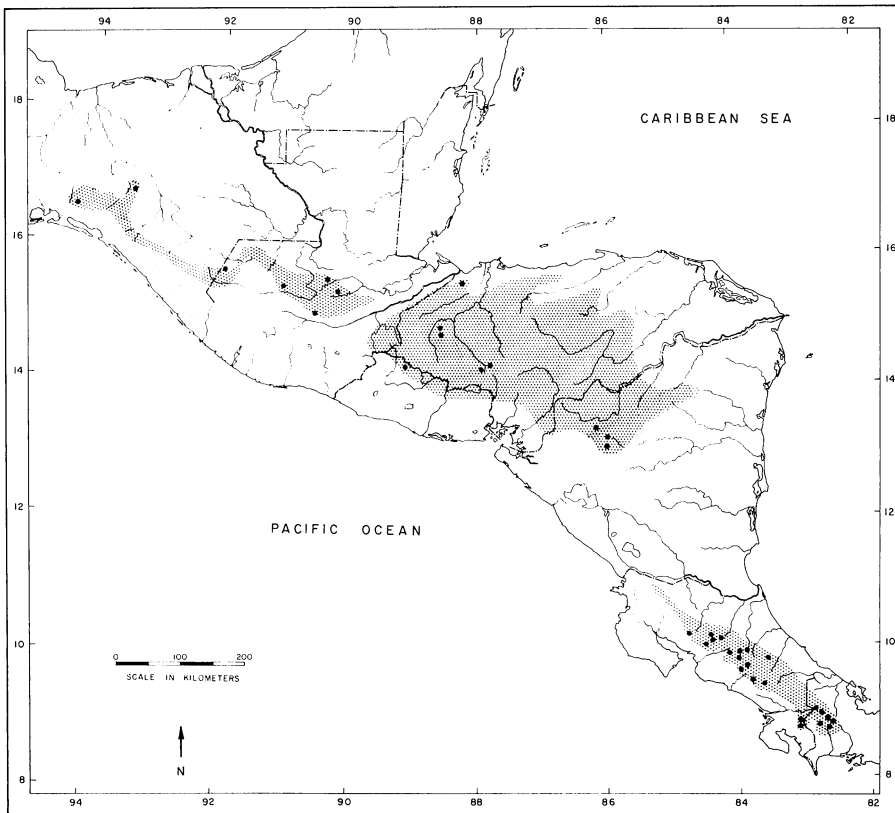
Fig. 2. Part of Middle America showing distribution of *S. teguina.*
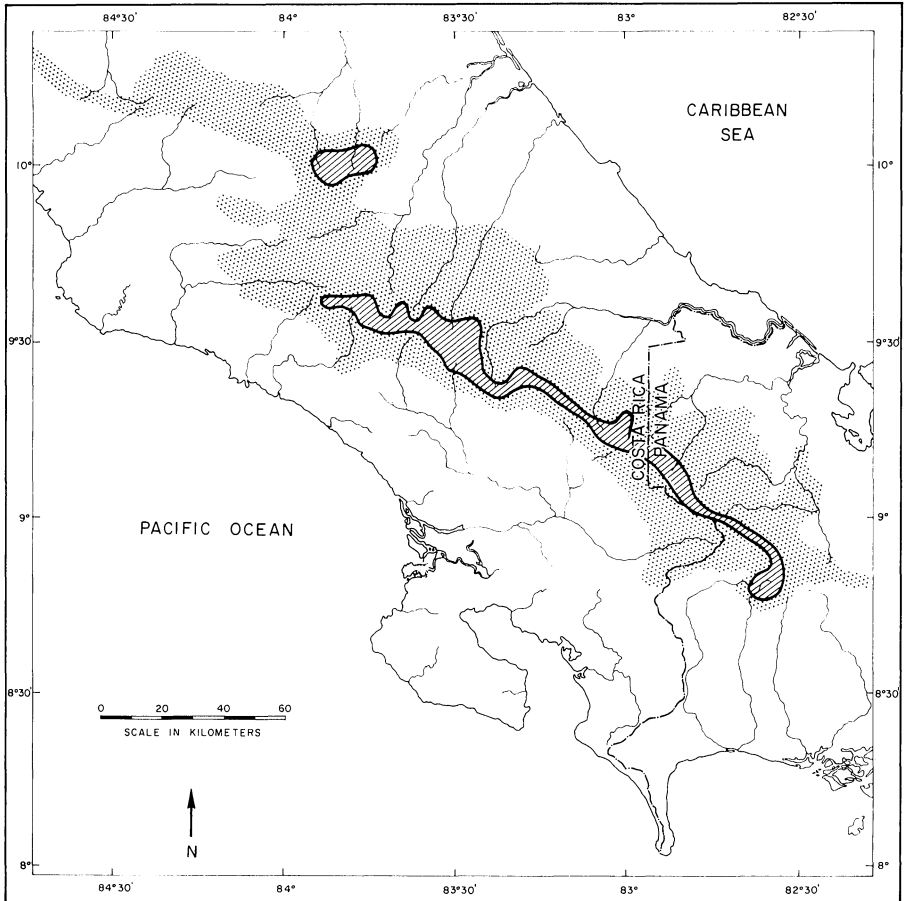
Fig. 3. Part of Costa Rica and Panamá showing geographic ranges of *S. teguina* (stippled) and *S. xerampelinus* (hatched lines).

they are for the most part segregated altitudinally and by vegetation zones. The following synopses are based on known occurrences of the species expressed in terms of vegetation types or life zones as described by Carr (1950), Wagner (1964), Stuart (1966), Myers (1969), and especially Tosi (1969) and Sawyer and Lindsey (1971).

   S. teguina ranges altitudinally from 1000-1100 m in Honduras and Guatemala to 2940 m on Volcán Irazú, Costa Rica. They occur in vegetation zones described as hardwood cloud forest in Honduras (Carr, 1950), broadleaf montane cloud forest in Guatemala (Stuart, 1966), and montane and lower montane rain forest in western Panamá (Meyers, 1969). In Costa Rica, for which we have more complete information, the species is recorded from forest zones classified by Holdridge and Tosi (Tosi, 1969) as premontane rain, lower montane wet, lower montane rain, montane wet and possibly into the lower edge of montane rain forest. Its principal zones of

occurrence are lower montane rain forest (and adjoining margins of premontane rain forest) and montane wet forest. These forests are mostly evergreen. The trees tend to be medium in height (20-30 m), with compact crowns and small coriaceous leaves and with moderate to very heavy loads of epiphytes, especially on the tree crowns and branches. The understory is composed mainly of broadleaf evergreen shrubs, tree seedlings, and ferns and herbs. Fallen tree trunks and branches (logs) are of medium to high densities. The forests are mixed, with no one species usually dominant. Oaks (*Quercus*) occur in all zones, and in some areas various species of the genus are predominant. *Eugenia* is also common. Other genera represented include *Cornus, Persea, Clusia, Drimys, Didymopanax,* and *Weinmannia.* The animals occur under logs, moss, or ferns within the forest, and in grass or forbs in clearings.

S. xerampelinus ranges altitudinally from approximately 2150 m in the vicinity of Volcan Chirqui, Panama to 3300 m on Cerro de la Muerte, Costa Rica. It is restricted to forests, meadows and grasslands in the upper parts of high mountains characterized by two vegetation or life zones: montane rain forest and páramo. Montane rain forest is predominantly evergreen with many species of oak dominating the overstory. Canopy trees are thick, short-trunked, and 25-30 m in height. Understory trees have small irregular crowns and trunks. Leaves of the canopy and understory are small and leathery. Tree ferns and bamboo are common in the shrub layer. The sparse ground layer consists of seedlings, herbs, ferns and bamboo. Fallen trees and branches and cavities at bases of trees are abundant on the forest floor. There are epiphytes on all parts of the trees, forming especially heavy mats on crown branches. Genera represented include *Quercus, Miconia, Vaccinium, Weinmannia, Didymopanax,* and *Garrya.* Above 3000 m the montane forest gives way to a low growth of stunted trees, shrubs, herbs and grasses. This formation, the páramo, includes marshes, meadows, expanses of bunch grass or bamboo and thickets of shrubs and stunted trees. Genera represented in the Costa Rican páramo include *Escallonia, Weinmannia, Clethra, Pernettya, Vaccinium, Myrtus, Chusquea, Arctostaphylos, Castilleja* and *Senecio.* This zone is perennially wind-swept, cool, and draped in clouds or rain. *S. xerampelinus* lives on the ground both in the forests and in the meadows and thickets of shrubs and stunted trees on the páramos.

In a broad sense, the two species are allopatric, with *S. xerampelinus* found in the highlands and *S. teguina* ranging lower into subtropical areas. The distributional pattern is more complex than this, however, for the two have been found together at several localities. A more descriptive distributional picture is one of contiguous allopatry with a narrow band or local pockets of sympatry. The following examples serve to illustrate this point.

In the mountains around Volcán Chiriquî, Panamá, Enders and

students (1939) collected *xerampelinus* at high elevations, up to 3200 m, in lower montane rain forest and páramo. They obtained one specimen at a locality where examples of *teguina* were trapped. This was on Finca Lerida at Casita Alta, a cabin at approximately 2150 m in a steep-sided valley (the Velo) which heads on one of the craters. Because of cold air drainage, conditions in the valley (e.g., at 2150 m) are much like those higher in the mountains. The specimen of *xerampelinus* was trapped on an abandoned planting of fruit trees in the valley. *S. teguina* was found in grass and bushes on a ridge between the Velo and another valley (Enders, in litt). At lower trapping sites (approximately 1700, 1525, 1250, 1150 and 1000 m), only *teguina* were captured, in zones we believe to have been lower montane or premontane wet forest.

Several instances of sympatry have been recorded along Highway No. 8 on Volcán Irazú, Costa Rica, where field parties from the University of Michigan Museum of Zoology have worked over a period of 13 years. The highway ascends the southwestern flanks of Volcán Irazú (Fig 4) and, at approximately 2800 m, winds around to the southeastern and eastern sides, thus passing from the montane wet forest zone into the margin of montane rain forest. This latter section of road was studied most intensely.

In 1962, both species were obtained at 2850 m elevation in and near a small canyon located 0.2 km north of San Juan Chicoa; the mouth of the canyon is at San Juan Chicoa. Examples of *teguina*
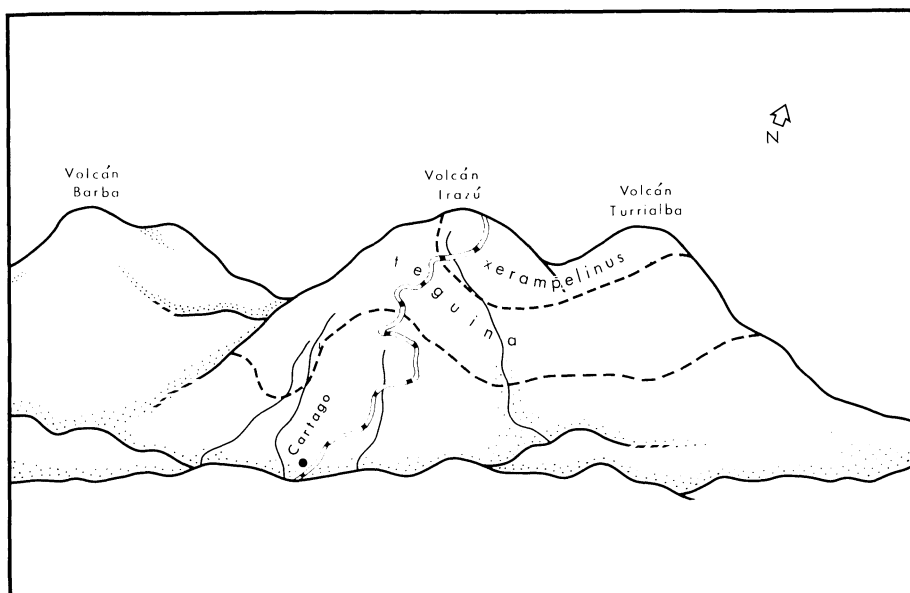
Fig. 4. Schematic profile view of southeastern slopes of Volcán Irazú and adjoining V. Turrialba, Costa Rica showing vertical distribution of *S. teguina* and *S. xerampelinus*. Approximate position of highway 8 on Irazú is indicated.

were caught on the dry brush-and-tree covered slopes of the canyon, and those of *xerampelinus* in fencerows of grass and shrubs in adjoining moist pastureland. Efforts in four subsequent years to locate *xerampelinus* in this area have been unsuccessful; only *teguina* were taken in the canyon and in similar habitats at two other localities east of the canyon (0.5 and 2.5 km by road NE San Juan Chicoa). During the intervening years, the region above the canyon has been heavily cleared for growing vegetable crops rather than grazing cattle.

Three other areas of local sympatry were discovered further east along Highway No. 8 in 1969, 1972, and 1975. These are situated at 4.5, 5.2, and 5.7 km (by road) NE San Juan Chicoa at elevations of 2860, 2900 and 2920 m, respectively, at the edge of the montane rain forest zone. At 4.5 km NE, specimens of *teguina* occurred in runways under shrub-covered logs left in open pasture; one example of *xerampelinus* was trapped 40 m away in a brush pile overgrown with grass and located in a lush pasture where many large trees remained standing. At the second site (5.2 km NE) both species were trapped in grass hummocks along fence rows near houses and barns of a dairy farm. The habitat at 5.7 km NE San Juan Chicoa consisted of cleared pasture land where many old logs remained, but only a few trees were left standing. Six specimens of *xerampelinus* and three of *teguina* were collected there; in fact, one of each species was taken at the same live-trap set in a runway under exposed roots at the base of a tree. Slightly further upslope at elevations of 2950 and 3000 m, *xerampelinus* but no *teguina* were found. Thus, on the southern flanks of Irazu', a belt of contact and local sympatry occurred approximately between 2850 m and 2930 m at the junction of the montane wet and montane rain forest zones.

Another area of contact, observed in 1975, adjoins the Pan American Highway, elevation 2590 m, 4 km NE El Copey (de Dota) in the Cordillera de Talamanca. This locality was on a mountain ridge between the Rio Macho drainage to the north and Rio Pirris system to the south. Dense, drenched forests (montane rain?) of northern slopes merged with slightly drier areas (lower montane rain?) to the south. The northern slopes were being cleared of trees. Traps were set in entanglements of raspberry and other brush overgrowing felled trees, and in runways through grass and shrubs at the border of the forest. Specimens of *teguina* and *xerampelinus* were caught in both situations. No difference in microhabitat was evident at this area of sympatry. Only *xerampelinus* occurred at upslope localities (2730, 2800, and 2920 m) along the same highway.

The interaction of prevailing climatic patterns and topography affects the local distribution of the two species. On Volcán Irazú, for instance, the contact zone on the south-facing slopes is around 2850 to 2930 m, as documented above. This altitude is the highest recorded for *teguina*. Around the volcano to the east, where the

slopes are bathed by moisture-laden winds and cloud, there is the more lush and epiphyte-draped vegetation of the montane rain zone. Here the contact belt is lower; *xerampelinus* has been taken as low as 2350 m at Finca Coliblanco (Fig. 4); on that side, no *teguina* have been found above that elevation. The low temperatures obtaining in the geographic range of *xerampelinus* may be inimical for *teguina* (Hill and Hooper, 1971).

ACTIVITY PATTERNS AND FOOD HABITS

Activity

In the laboratory both species are almost wholly diurnal. This is evident both in observations in the lab colony and in activity records of individuals monitored by an event recorder. Subjective observations of the colony suggest that the greatest amount of activity occurred in morning (7-11 am). In that period most individuals were outside of their nest cans and called frequently. In the afternoon, fewer animals were noticeable, although some were active throughout the afternoon. The presence of an investigator in the lab did not inhibit activity except when he made a noise or stood close to the cages. The diurnal habits of *Scotinomys* strikingly contrasted with the nocturnal activity of *Peromyscus* and *Reithrodontomys* also maintained in the colony.

Quantitative records of individuals kept in an environmental chamber corroborated our subjective impressions. In mean number of minutes active per hour, individuals of both *S. teguina* and *S. xerampelinus* exhibited high levels of activity from morning to early afternoon (0600 to 1300 hrs), but showed a marked decline later in the afternoon (Fig. 5). Approximately 87 percent of the daily activity of both species was confined to the daylight period; forays at night were sporadic and generally brief. No significant differences between the two species were noted in amount of activity (Table 1); however, the species partitioned that activity somewhat differently. In most tests of *xerampelinus* (15 of 19), a bimodal pattern was apparent. The individuals were active for long intervals in the morning, then quiescent in mid- to late afternoon before a second peak of activity in early evening. This later spurt of activity was regular in length and occurrence in some animals, irregular in others. In 10 of 15 animals, it was mostly in the dark period. In *teguina* there was no clear-cut bimodality in activity profiles. Instead, the typical pattern (11 of 13 trials) consisted of long spans of activity in the morning (not significantly different from *xerampelinus*, (Table 1), followed by many short bursts, progressively shortening through the afternoon. Short bursts predominated in *teguina*, and there were
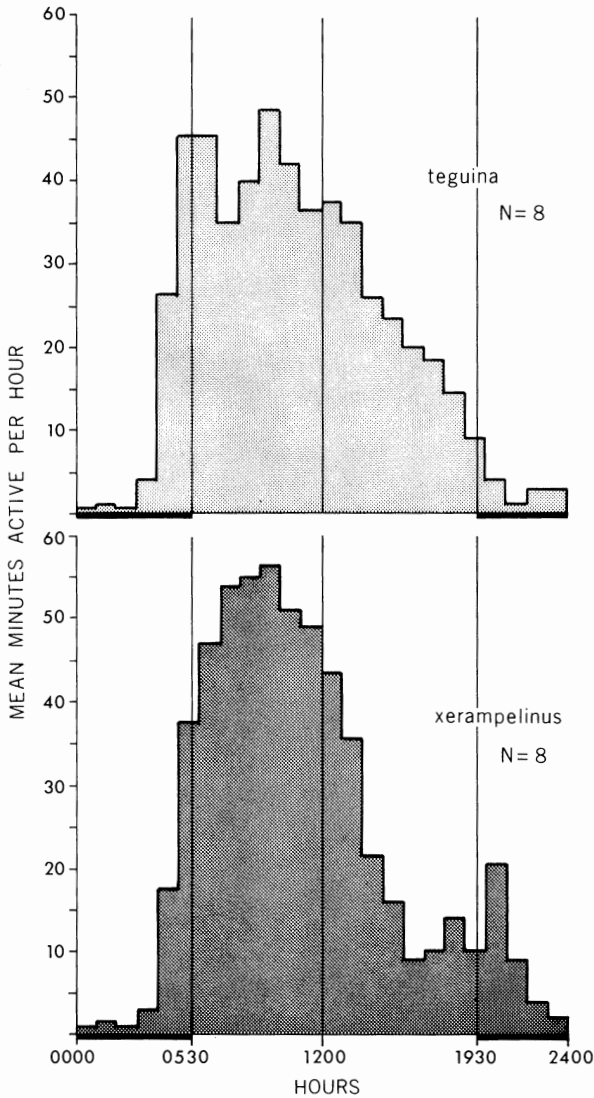
Fig. 5. Activity relative to daylight (0530-1930 hrs) of the two species of *Scotinomys* in the laboratory.

more of them (Fig. 6). Mean number of bouts per day (13 individuals of each species monitored for seven days) was 7.4 (range 3.6-12.6) in *teguina* and 3.9 (2.2-5.8) in *xerampelinus*. The difference is highly significant ($t = 4.25$, $P < .001$).

Knowledge of activity of wild populations is derived from hearing their vocalizations and from trapping records. Their distinctive calls were heard throughout the day, but were more frequent before midday. In four successive days of trapping on Volcán Irazú, Costa Rica in February 1975, time of capture of individuals was as follows:

TABLE 1

Mean hours of activity in *Scotinomys*; 13 individuals of
each species monitored for 7 days in the laboratory.

Period	Hours Active (means and extremes)			
	teguina	*xerampelinus*	*t*	P
Daylight	7.5 (4.7-12.1)	8.0 (5.8-10.8)	0.774	.446
Night	1.1 (0.2-2.2)	1.3 (0.6-2.1)	0.636	.530
24 hours	8.6 (5.1-12.5)	9.3 (6.4-11.4)	1.001	.323
First active period of day	4.4 (1.1-9.4)	5.8 (2.3-9.1)	1.630	.113
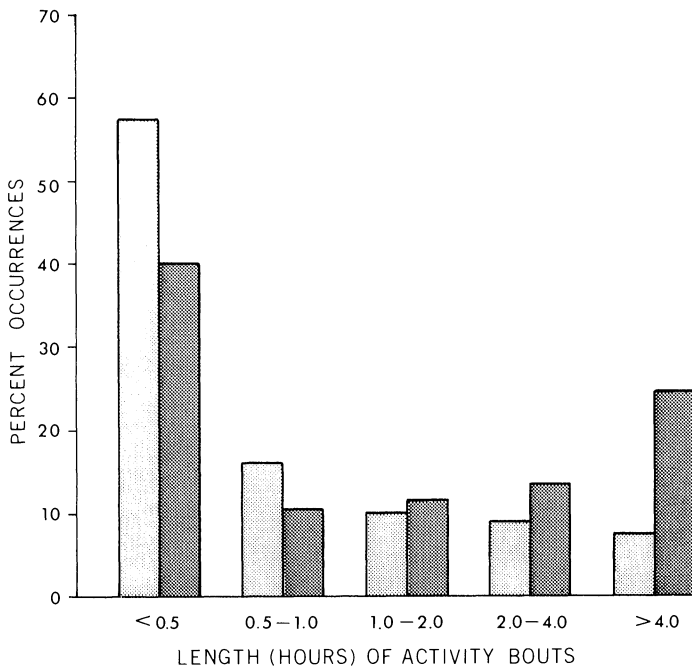
Fig. 6. Frequencies of activity bouts of different lengths in *teguina* (light
bars) and *xerampelinus* (dark bars). Frequencies for each species represent
summations for 91 days of monitored activity (13 individuals, seven days each).

S. teguina 0600-1200 hrs, 8; 1200-1800 hrs, 11; 1800-0600 hrs, 4. *S.
xerampelinus* 0600-1200 hrs, 7; 1200-1800 hrs, 9; 1800-0600 hrs, 5.
Although the long intervals afford no insight to individual activity
patterns, these results confirm that the species are predominantly

diurnal. Several of the individuals caught in the 1800-0600 hrs period obviously had spent little time in the traps.

Food Habits

Observation of food preferences of laboratory animals and examination of the stomach contents of wild-caught individuals indicate that both species of *Scotinomys* feed predominantly on insects.

In our attempts to maintain a vigorous, healthy laboratory colony, many different food items were offered with varying degrees of acceptance and success in promoting breeding. The animals ate all kinds of insects (crickets, grasshoppers, beetles, moths and potato grubs) offered, and accepted snails, but not earthworms or raw hamburger. They ate blueberries, strawberries, and raspberries and refused lettuce, moss, and several types of grasses. They preferred sunflower seeds to kernels of corn, crushed oats, or wheat grains; they ate only the germinal segment of corn and wheat grains.

Qualitative observations of prey-capture in the laboratory clearly suggested that *teguina* was more adept at feeding upon mobile forms (e.g., crickets) than was *xerampelinus*. When a cricket was placed in the cage, *teguina* seemed visually to track the prey and pounce upon it; if the cricket escaped, the mouse usually pursued it. A *xerampelinus* in a similar situation initially appeared oblivious of the cricket. Often, it would run over the cricket, stop, raise its nose and sniff, and only then detect the prey. *S. teguina*, thus, seemed to rely more on visual cues in locating and capturing insects; whereas, *xerampelinus* utilized olfaction as its primary sensory mode for locating prey. These observations are more relevant to the significant differences in eye size in the two species (Hooper, 1975) and also to their food habits in the wild as related below.

Fragments of insects were discovered in each stomach of both species, and comprised the most important foodstuff by percent volume (Table 2). Seeds, berries and fibrous plant material were encountered, but their total bulk accounted for a minor part of the diet, and some of the plant material may have been in the gut of the insect prey. Of the insects present, Coleoptera predominated. In both species of *Scotinomys*, examples of Carabidae (ground beetles) occurred most often, followed by approximately equal amounts of Staphylinidae (rove beetles) and Scarabaeidae (scarab beetles). Members of all three families are mainly terrestrial in their habits, as are the *Scotinomys*. Other families of beetles represented include Tenebrionidae, Hydrophilidae, and Leptinidae. The samples reported in Tables 2 and 3 represent different areas of capture (see Materials and Methods) and both wet and dry seasons.

The species differed in the kind and life-stage of insect consumed. *S. teguina* ingested more hemipterans (mostly adults) whereas

TABLE 2

Stomach contents of field-caught *Scotinomys teguina* (N = 67)
and *S. xerampelinus* (N = 63).

Food	Percent occurrence		Percent volume	
	teguina	*xeramp.*	*teguina*	*xeramp.*
Seed	98.5	90.4	9.6	5.4
Berry	49.2	31.7	2.2	1.7
Fibrous plant material	86.5	66.7	8.8	7.8
Insecta	100.0	100.0	79.4	85.1
Coleoptera	100.0	98.4	64.8	73.2
Hemiptera	50.7	7.9		
Homoptera	7.5	3.2		
Diptera	7.5	26.9	14.6	11.9
Hymenoptera	23.9	14.3		
Odonata	1.5	4.7		
Orthoptera	1.5	0.0		

TABLE 3

Incidence of adult and larval insects in stomachs of *Scotinomys
teguina* (N = 67) and *S. xerampelinus* (N = 63).

Insects	Percent occurrence		Percent insect volume	
	teguina	*xeramp.*	*teguina*	*xeramp.*
Adult				
Coleoptera	95.5	42.8	50.5	11.0
Other Insecta	61.2	9.5	13.6	1.2
Larvae				
Coleoptera	52.2	95.2	31.1	75.0
Other Insecta	11.9	36.5	4.8	12.8

S. xerampelinus ate more dipterans (mainly larvae). Adult parts of
insects were more frequent in *teguina* and larval forms were more
abundant in *xerampelinus* (Table 3). Of all insect remains identified,
adult parts comprised 64 percent by volume in *teguina* compared
with 12 percent in *xerampelinus*. For larval stages, the opposite
relationship obtained, 36 percent by volume in *teguina* versus 88
percent in *xerampelinus*. These differences are highly significant
(Mann-Whitney U-test, P < .0001). The adult-larval ratios contrast as
much, or more, in sympatry as in allopatry (Table 4), indicating that
the concentration on adult insects by *teguina* and on larvae by
xerampelinus does not solely reflect relative abundances of those life
stages at different habitats or elevations.

The data in Table 4 suggest some shift in diet of the two species where their ranges overlap. The samples of *teguina* collected in sympatry with *xerampelinus* (compared with those obtained in allopatry) show a larger average volume of insect matter, of which larvae constitute a greater percentage. The differences in mean volumes of insect and vegetable matter are barely statistically significant (Mann Whitney U = 77.5, P = .059); those in proportions of larval and adult stages are not statistically significant (M-W U = 111.0, P = .551). In the sympatric examples of *xerampelinus* (compared with allopatric samples), there is a smaller average volume of insects and, of those, a larger proportion of larvae (Table 4). however, statistical tests of those samples indicate no significant differences either in volumes of insect and vegtable food (M-W U = 123.0, P = .139) or in mean percentages of adult and larval stages (M-W U = 126.0, P = .086).

The digestive tracts of both species are closely similar in gross anatomical structure including dentitions (Hooper, 1972), anatomy of the stomach (Carleton, 1973), and absolute and relative lengths of the hindgut segments (Table 5). Mean length of the small intestine in females of both species exceeds that recorded for males: 364 mm (♀♀) versus 327 mm (♂♂) in *teguina* and 342 mm versus 327 mm in *xerampelinus*. This disparity in small intestine length between the sexes is highly significant in *teguina* (P < .001), but not in *xerampelinus* (P = .42). The diminutive caecum, totaling only 3.9% of the total hindgut length, is typical among rodent species which are primarily insectivorous (Vorontsov, 1967).

BEHAVIOR IN THE LABORATORY

Voice

Both species of *Scotinomys* have a repertoire of vocalizations which contain both sonic and ultrasonic components. Mentioned below are those which are audible to the human ear.

Young.—Sounds emitted by young of both species consist mainly of clicking or sucking noises and harsh and soft squeaks. Simple clicks, heard in young up to five to seven days old, appeared to be produced by the lips and tongue as they attempted to suckle; the jaws move in synchrony with the sounds. During the nesting period, the young issue soft, almost mewing, squeaks which seem indicative of mild discomfort. Typically, this low-intensity squeaking emanated from the nest when the female entered or departed and when the young were trying to locate a nipple. A harsh, sharp squeak is uttered in circumstances of annoyance or disturbance. This noise, first given by young approximately a week before the eyes

TABLE 4

Stomach contents of *S. teguina* and *S. xerampelinus* obtained
in areas of allopatry and sympatry on Volcán Irazú and
Cerro de la Muerte, Costa Rica in February 1975.

Species	N	Percent total volume		Percent insect volume	
		Vegetable Matter	Insects	Adults	Larvae
teguina					
allopatry	18	23.8	76.2	68.6	31.4
sympatry	14	18.8	81.2	62.6	37.4
xerampelinus					
allopatry	32	16.2	83.2	13.3	86.7
sympatry	11	27.6	72.4	1.6	98.4

TABLE 5

Absolute and proportional lengths of regions of the hindgut
in *Scotinomys* (N = 10 for each species).

Regions	*teguina*		*xerampelinus*	
	Mean and range (mm)	Percent of hindgut	Mean and range (mm)	Percent of hindgut
Small intestine	336.4 (300-370)	81.3	336.1 (300-378)	80.6
Large intestine	61.4 (48-73)	14.8	64.8 (56-75)	15.5
Caecum	16.4 (12-19)	3.9	16.2 (12-20)	3.9
Total	414.2 (369-457)		417.1 (377-461)	

opened, is quite like that produced by adults in similar situations. It was elicited from young when they were being weighed and measured, and was frequently heard during sibling squabbles. When uttering the sound the young assumed a defensive posture and generally oriented toward the source of disturbance, e.g., human finger or fellow sibling, rather than retreated from it.

One sound apparently was peculiar to the young of *teguina*: five to ten piping notes uttered in rapid succession in a fairly regular cadence, though slightly faster early in the sequence. Each note of the series has a soft, dulcet quality unlike the sound of the usual squeaks. The young were stationary when uttering it. The vocalization seemed to function as a distress signal, for example, in five to

12 day-old young which were alone and separated from nest and mother, or which had been removed for measurements. Isolated *xerampelinus* responded with soft squeaks in those situations. Females retrieved young which uttered this distress call; however, silent individuals were sometimes retrieved as well. The call is reminiscent of the long adult song, described below, except that each pulse is simpler and lower in intensity and the entire call is much shorter.

Adult.—Adult vocalizations consisted of squeaks of various intensity and quality and a sustained call or "song". In both species the squeaks, louder and sharper in adults than in young, were produced in various agonistic encounters. Relatively quiet squeaking occurred during hassles over morsels of food. More intense "chits" were given in both inter- and intrasexual aggressive interactions. A harsh, raspy note was sounded by females when they resisted their mate's attempts to mount. In those altercations, the female assumed a belligerent, defensive posture by rising on the haunches with forelimbs retracted, fur raised, and mouth opened widely exposing the incisors. A chorus of high-pitched, barely audible squeaks was sometimes heard in both species when animals were initially paired. These vocalizations were given only within the nest; it was not determined which of the sexes produced them.

The most elaborate sequence of sounds in the species' repertoire is the "song". We label it so because of its length, complexity, and obvious analogy to bird and insect sound patterns. The songs of both species carry well in the field and can be recognized. A major part is above 20 kilohertz with only a fraction within human hearing. Frequencies in the song range from 43 to 14 kHz in *teguina* (Fig. 7) and from about 30 to 12 kHz in *xerampelinus* (Anderson and Hooper, ms). The song of *teguina* is a quick sequence of 52 to 129 beats or pulses of sound (Table 6), somewhat resembling the trill of an insect. Initially, the sequence is so rapid that individual beats are obscured. As the song progresses, pauses between the pulses gradually lengthen (Fig. 7) as do the pulses themselves and, consequently, the end of a song is attenuated, each beat sounding crisply in a staccato manner. A progressive increase in volume is apparent so that later beats of sound are much louder than earlier ones, and they sweep to lower frequencies. As a result, the end segment of a song is more easily detected by the human ear. A full song may last seven to ten seconds, but may be abruptly terminated if the animal is suddenly disturbed. Populations of *teguina* differ in song. Individuals from Nicaragua averaged 75.6 beats per song, compared with 106.3 beats in mice from Costa Rica (t = 9.280, P < .0001).

The song of *xerampelinus* differs from that of *teguina* in the following aspects. It is significantly shorter in number of beats (t = 14.18, P < .001), consisting of 26 to 42 pulses and lasting two to four seconds. The cadence of beats is more regular; there is not the extreme attenuation of the call as in *teguina*, and instead of a gradual
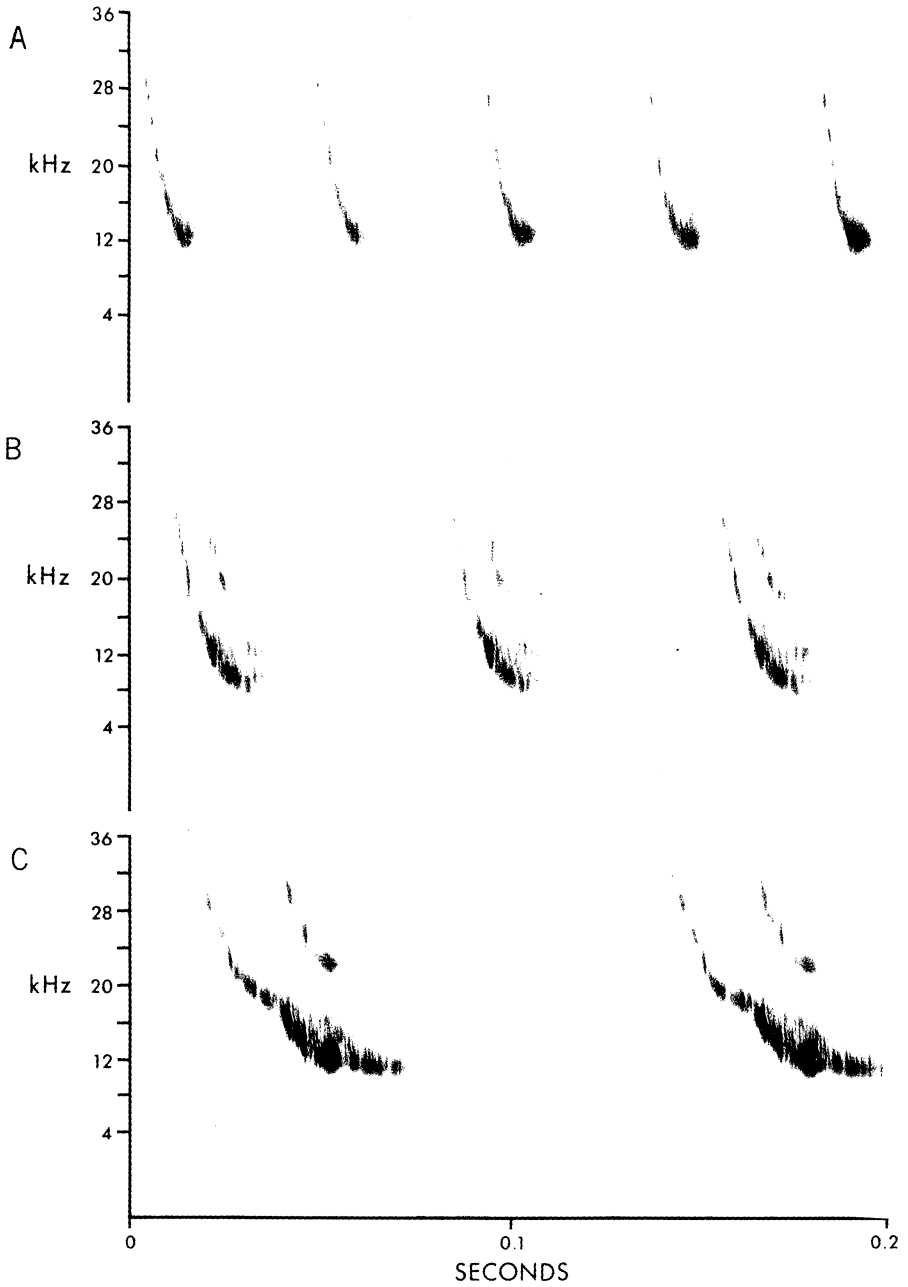
Fig. 7. Sonagrams of early (A), middle (B) and late (C) parts of a "song", 115 total pulses of *teguina*, no. 107, from Volcán Irazú, 2800 m, Costa Rica. Frequencies above 25 kHz, mostly outside the tolerance of the Uher tape recorder, are incompletely registered.

TABLE 6

Number of pulses of sound in "song" of *Scotinomys*

Species and locality	N	$\overline{X}$	2SE	Range
S. teguina				
Nicaragua				
522♂	8	67.1	3.3	60-74
529♂	15	80.2	6.1	52-93
All Nicaragua	23	75.6	4.8	52-93
Costa Rica				
107♂	28	107.4	5.3	79-129
1022♂	1	79	-	-
1024♂	1	91	-	-
1025♂	5	107.8	7.9	98-119
1035♀	1	83	-	-
1043♀	3	102.3	12.3	93-114
1045♂	9	110.8	7.9	87-126
All Costa Rica	48	106.3	3.9	79-129
All *teguina*	71	96.4	4.6	52-129
S. xerampelinus				
Costa Rica				
220♂	8	37.4	1.4	36-42
813♂	4	30.2	3.8	26-35
818♂	2	32.0	-	-
828♂	6	33.2	5.2	26-41
All *xerampelinus*	20	34.2	2.1	26-42

increase, a nearly even volume is maintained throughout the call. In general, the song of *xerampelinus*, as heard by the human ear, resembles the early part of that of *teguina*, rather than simply being a compressed version of it.

Males of both species called much more frequently than females, often while perched on nest cans or food trays. Characteristically, an animal would rise on its haunches, assuming a bipedal stance, and point its snout upward as it vocalized (Fig. 1). Calls also were given from an all-fours position.

Various stimuli and behavioral states appeared to increase the frequency or enhance the predictability of calling. Both in the laboratory and in the field, the song of one individual seemed to elicit responses from others. As in a chain reaction, a single call would be followed by another, then by two more, and finally a chorus of simultaneous calls. Pairing elicited calling. Males, even those which had been previously silent, began to call shortly (one to five minutes) after being paired with a female. Much naso-anal contact, mainly initiated by the male, was observed between songs and, associated therewith, the calls generally increased in intensity. Cotton swabs, rubbed against a female's venter and then placed in the cage of an isolated male, often instigated vocalizations. Olfactory cues

again seemed important as the male periodically visited and sniffed the cotton swab between songs. In interspecific dominance experiments involving male-female pairs, one male would vocalize with greater frequency than the other. These instances present some idea of the usual contexts in which songs were heard; however, an animal oftentimes would suddenly interrupt its current activity and sing without perceptible external stimulus.

A few females of each species were observed calling. To the unaided ear, their song resembled that of males. In most instances, the female was alone in a cage. For example, lone females which had just given birth gave calls. The song in this situation might function to attract a mate during her postpartum estrus. Horner and Taylor (1968) also noted that female *Onychomys torridus* vocalized sparingly, and in at least one instance the calling female was known to be in postpartum estrus.

Sight and Smell

The species differ in size of eyes. Both the eyeball and the lens are absolutely and proportionally larger in *teguina* (Hooper, 1975). What these different eye-sizes mean in terms of function and selective advantages to the animal is unknown. Subjective laboratory observations indicate that *teguina*, with larger eyes than *xerampelinus*, is more responsive to visual cues, relies strongly on sight in locating prey, is more aggressive, and is quicker in movement. The larger eye-size of *teguina*, thus, may be related to food detection and capture and, as well, to avoidance of predators (Hooper, 1975). There have been no rigorous tests of these hypotheses on these animals.

Midventral sebaceous glands occur in both species. These are situated beneath an area of dusky-white fur and their size varies with age and sex. They are evident in some old females, and are largest in males, sometimes covering an area 15-20 mm long by 4-7 mm wide. Enlargement of the gland and intensification of the fur coloration are associated with swelling of the scrotal region and probably sexual maturity. The gland functions in scent-marking. Males were frequently seen dragging their venters over articles in their cages, and in the activity mazes a thick, waxy exudate accumulated on the edges of the recording treadles as males passed over them. The musky odor, readily detectable by humans, is much more pronounced and the gland apparently larger in *xerampelinus*.

Interspecific Behavior

Matings.—Twelve interspecific matings (10 *xerampelinus* ♂ X *teguina* ♀ and 2 *xerampelinus* ♀ X *teguina* ♂) were attempted. Animals selected for the matings had produced young in captivity. There were no fertile matings in the pairings, which lasted for periods of 2 to 14 months. The individuals behaved normally, much as when matched

with members of their own species. There were vocalizations, naso-anal contacts and mountings. Complete copulations were not observed, although these easily could have escaped detection. Subsequent to the interspecific crosses, four of the females were remated to males of their own species and successfully conceived and raised litters.

Behavior.—To acquire knowledge of basic behavioral patterns of the two species and to explore the possibility of agonistic behavior between them, two series of experiments were initiated. These involved encounters both between and within sexes and species. The animals in these test series were on the same 12:12 light cycle maintained in the laboratory colony.

In the first series, the encounters took place in an apparatus consisting of two interconnected plastic cages provided midway with a glass partition. Single animals were placed in each cage for a period of 24 hours, after which the partition was removed and the individuals allowed to interact. Combinations of individuals were then observed for periods of 30 minutes to two hours as follows: ♂-♂ *teguina,* 6; ♂-♂ *xerampelinus,* 8; ♀-♀ *teguina,* 3; ♀-♀ *xerampelinus,* 3; ♂ *teguina-♂ xerampelinus,* 1.

The second group of experiments was conducted in 1.2 m X 2.7 m arenas, each subdivided lengthwise by a removable plywood partition into two equal compartments. Each arena was enclosed by wood and black plastic to a height of 1.5 m, and the floor was covered with wood shavings and crisscrossed by willow branches. Nest boxes, water bottles, and food containers were positioned similarly in each compartment. Heterosexual conspecific pairs were introduced into each compartment, allowed ten days for habituation, then formally observed for two days with the partition in place, and finally observed two additional days after removal of the partition. The entire sequence of a test required 14 days. Eventually, 44 different individuals (11 of each sex of each species) were run through this procedure representing the following number of replicates of possible species combinations: *teguina-teguina,* 2; *xerampelinus-xerampelinus,* 2; *teguina-xerampelinus,* 10.

In the observation periods, the animals were coded for 24 behavioral states designated, for example, as groom, run, stereotyped pacing, mark substrate, nasal-nasal contact, nasal-anal contact, fight, chase, vocalize. Dominance is here defined on the basis of a persistent submissive mannerism (typically running away or cowering) in one animal in the presence of another. Results of these two sets of tests lead to the following conclusions:

1. Behaviors of each species include an array of communications. These include self- and reciprocal-grooming, nasal-oral-anal contacts, tail and ear positioning, probable scent marking, and other postures and motions conveying information.

2. Males of both species display complex agonistic behaviors including threatening crouches, vocalizing, aggressive chasing, scuffling and biting.
3. Dominance was evident in adults of each species. In the 18 within-species male-female arena pairings, males dominated the females. Many of the contacts may have been a part of mating behavior. There was also dominance (as defined above) in each of four male-male intraspecific pairing (two of each species). Three of the four dominant males also vocalized more after the partition was removed, spent more time on "foreign" soil and gained more weight than the subordinates.
4. The results of the interspecific pairings were equivocal. In three of ten pairings the *teguina* male was dominant; in two, the *xerampelinus* male dominated; and in seven the results were inconclusive because few or no contacts between the males were observed in the observation periods.
5. Judging from all paired encounters in the two schedules of experiments, interspecific behavioral interactions (including dominance) closely resemble intraspecific ones. No special set of behaviors were evident in confrontations between individuals of the different species.
6. Spacing between individuals and infrequent encounters within each sex in the experimental arenas suggest considerable individual independence, and possible periods of mutual avoidance, both within and between the species.

These are observations of laboratory animals. It is unknown what parts of the behavioral repertoire seen in the laboratory obtain in individuals in their native environments.

REPRODUCTION

Seasonality in Breeding

In our laboratory colonies, litters were produced by both species in all months; there was no obvious concentration of births at any particular part of the year (Fig. 8). Many females regularly delivered litters at approximately one-month intervals until either the male was removed or one of the pair died. For example, one *teguina* female (No. 10B) produced eight consecutive litters at intervals of 32, 31, 29, 29, 30, 31, and 28 days; another (No. 38) delivered seven successive litters with intervening periods of 29, 31, 31, 30, 31, and 31 days. This steady succession of births was more common in *teguina*, and this species produced many more litters than did *xerampelinus*, though initial breeding stocks of both species were approximately equal (Fig. 8). The maximum number of litters born to any one female was 12 for *teguina* and 15 for *xerampelinus*; in
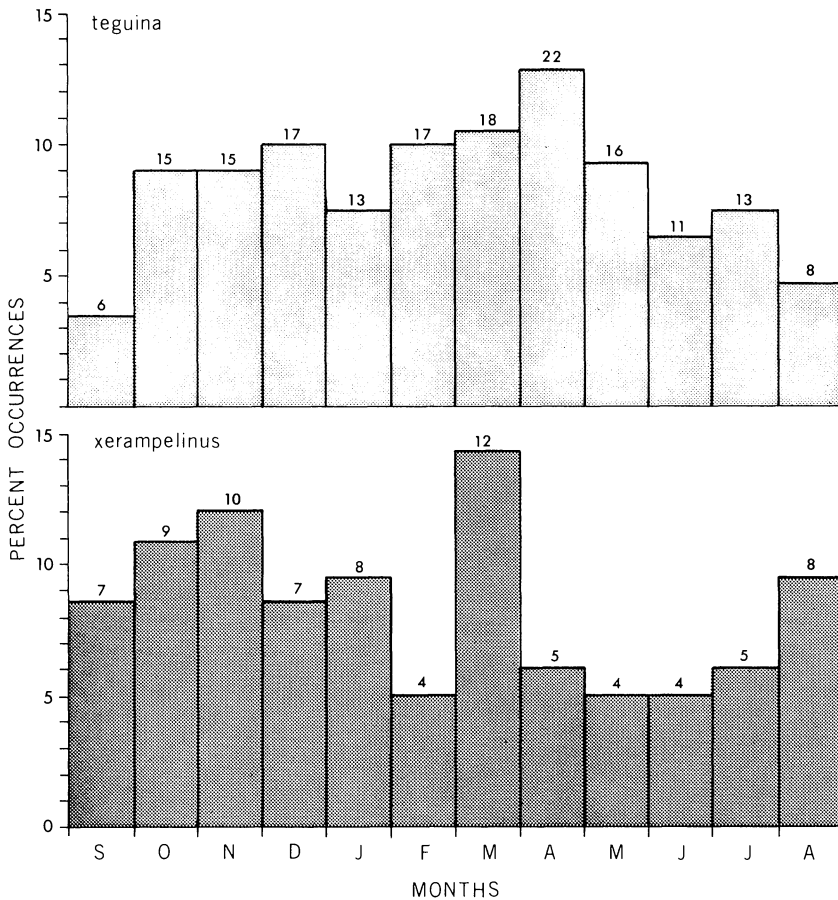
Fig.8. Frequency distribution of litters produced by month in the laboratory in *S. teguina* (N = 171) and *S. xerampelinus* (N = 83). Absolute number of litters born per month is indicated above bars.

those particular instances, the animals were not continously paired as no effort was made to achieve fecundity records. Both males and females remained reproductively potent well over one year and even over two years of age. Animals approaching age three years and older showed signs of senility and reduced reproductive capacity. One lab-born individual of *teguina* died at four years eight months. A wild-caught *teguina* which survived four years ten months in the laboratory must have been about five years old. The oldest *xerampelinus* was four years.

Our information on seasonality in field populations is scanty and spans only part of the year, namely the dry season and early part of the rainy season. Pregnant females are recorded for the following months: *S. teguina*– January, February, April, May, June, July and August; *S. xerampelinus*– January, February, May, June, July and August. The absence of breeding records for September

to December results from lack of trapping effort rather than a documented cessation of reproduction. Thus, there are records of pregnancies in both species for every month (excepting March for *xerampelinus*) for which information is available.

Gestation

The length of gestation, as estimated by the mean interval between births, approximates one month in both species (Table 7). There is, however, a statistically significant two-day difference (t = 4.59, P < .0001) in average duration of pregnancy between the two species (30.8 days in *teguina* versus 33.1 days in *xerampelinus*).

That the mean interbirth span closely approximates the actual gestation period is supported by (1) the shortest recorded interval between initial pair formation and birth of a litter, (2) the period between an observed copulation and subsequent birth of a litter, and (3) instances of postpartum conception and subsequent removal of the male. For all pairings of animals in the laboratory (over 100 for each species), the shortest elapsed period until the birth of the first litter was 30 days for *teguina* and 32 days for *xerampelinus*. Though copulation and conception can seldom be expected to occur on the first day of pairing, the shortest span determined for each species closely matches the calculated mean interval between births. Copulations that were judged to be complete were observed only twice in *teguina*. In both of those the interval to parturition was 31 days. We have no comparable observations on *xerampelinus*. In *teguina*, there were two occurrences in which the male was separated from his mate shortly after the female gave birth. A subsequent litter was born 31 days later. Similarly, one *xerampelinus* female produced a second litter 30 days after the male was removed. These minimum lengths of gestation closely match the figures determined from interbirth intervals. Further, they indicate a postpartum estrus in both species.

There is evidence that a lactation-induced prolongation of the interbirth period occurs in *xerampelinus*, but not in *teguina*. Such a

TABLE 7

Comparison of species of *Scotinomys* in length of gestation as indicated by interval (in days) between births of consecutive litters.

Interbirth	*teguina*		*xerampelinus*		t	P
	N	$\overline{X}$ and Range	N	$\overline{X}$ and Range		
Young weaned	32	31.1(29–36)	17	34.3(29–38)	5.385	<.001
Young died	16	30.8(27–36)	10	31.9(30–38)	1.181	.248
All samples	50	30.8(27–36)	27	33.1(29–38)	4.590	<.001

prolongation is deduced from comparing two types of interbirth intervals: one in which the young died within one week after parturition, and the other in which the young were successfully weaned. If the stimulus of suckling young does in fact prolong this interval, then interbirth intervals wherein the young died during their first week should be shorter than those in which the young were normally weaned. An examination of those instances revealed significant differences for *xerampelinus* (t = 2.37, P = .025) but not *teguina* (t = .059, P = .55) (Table 7). Additional support for lactation-lengthened gestation period derives from the significant positive correlation between length of the interbirth interval and number of nursing young in *xerampelinus* (r = .4556, P < .05), but not in *teguina* (r = .056, P < .20). These calculations provide strong circumstantial evidence that some mechanism, probably related to suckling and lactation, exists in *xerampelinus* that increases time between births. Since there is evidence of a postpartum estrus, these stimuli probably delay implantation of the embryos, rather than simply delay estrus. It is important to note that interbirth intervals in which the young died do not differ significantly in the two species (Table 7). Hence, this interbirth interval is probably a better estimate of actual gestation length in non-lactating *xerampelinus*.

Litter Size

Based on all litters born in the laboratory, the two species differ slightly in mean litter size (Table 8). This difference is statistically significant (t = 3.63, P < .0005; Mann-Whitney U = 4650.0, P < .0005). There is a wider range in litter size in *teguina* (1-5) than in *xerampelinus* (2-4), and the variances differ significantly (F = 1.59, P < .01) due to the dissimilar distributions in litter size. Most litters of *xerampelinus* consisted of three or four young, while those of *teguina* more frequently contained two or three (Fig. 9).

Mean litter sizes vary geographically in the samples of *teguina* (Table 8). They are alike for the two low-elevation stocks—Santa Mariá de Ostuma, Nicaragua, 1300 m and Monte Verde, Costa Rica, 1430 m. Each differs significantly (P < .01) from the highland population—Volcán Irazú, Costa Rica, 2800-2940 m. The difference in mean litter size between the low and highland examples of *teguina* is almost as pronounced as that between the low-elevation stock of *teguina* and that of *xerampelinus* (Table 8). The highland sample of *teguina* is not significantly different (t = 1.50, P = .13) from that of *xerampelinus* obtained from sites at 2800-3000 m on Volcán Irazú and 2700 m on Volcán Turrialba, Costa Rica.

In *teguina*, mean litter size increases in the first three litters. Early litters, especially a female's first, tend to be smaller than later ones (Fig. 10). Five of the six litters of only one young were first litters. In *xerampelinus*, mean size of the first litter is near the
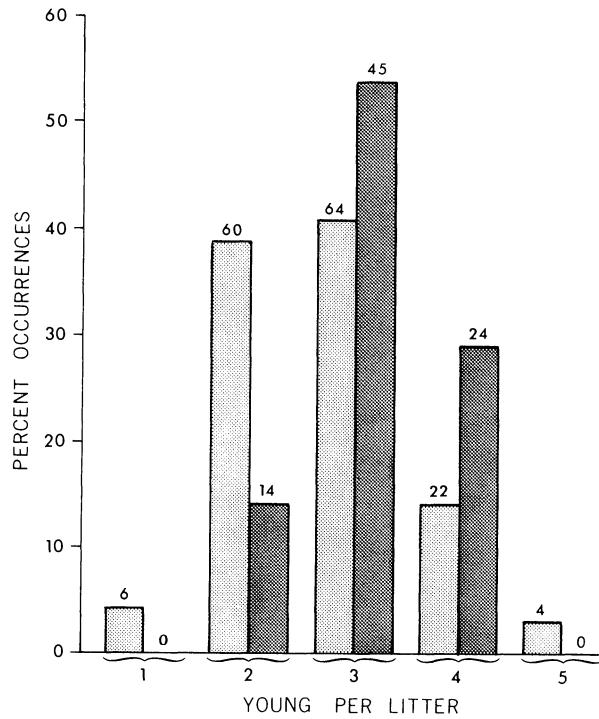
Fig. 9. Frequency distribution of laboratory-born litters of *S. teguina* (pale bars; N = 156) and *S. xerampelinus* (dark bars; N = 83). Figure above bars refers to absolute number of a given litter size observed.

TABLE 8

Litter sizes of *Scotinomys*

Species and locality	N	$\overline{X}$	1SD	Range
Conceived in laboratory				
teguina				
Santa María de Ostuma, Nicaragua, 1300 m	38	2.55	.795	1-4
Monte Verde, Costa Rica, 1430 m	25	2.28	.678	1-4
Volcán Irazú, Costa Rica, 2800-2940 m	90	2.94	.852	1-5
teguina				
All localities	156	2.73	.845	1-5
xerampelinus				
All localities	83	3.12	.669	2-4
Conceived in wild				
teguina	21	2.28	.643	1-3
xerampelinus	9	2.67	.707	2-4
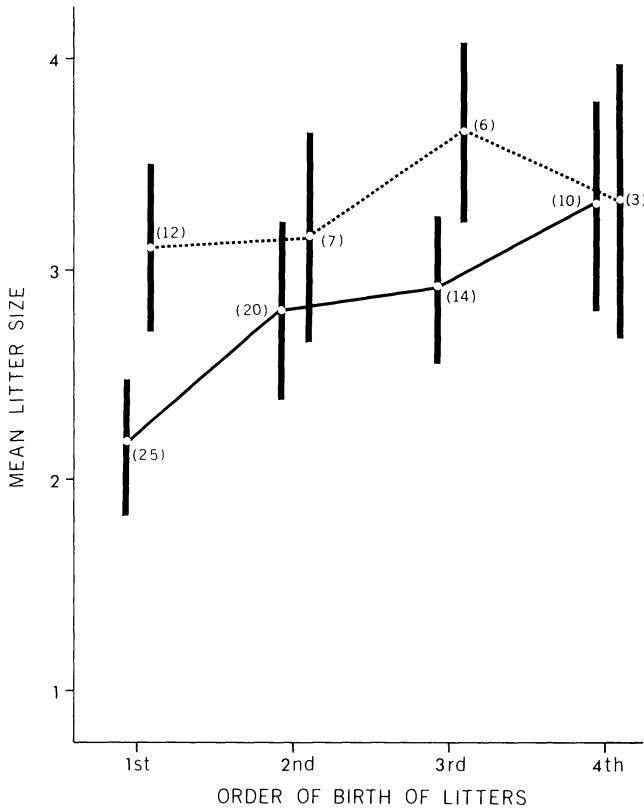
Fig. 10. Variation in litter size with respect to the first four litters born to laboratory-reared *teguina* (solid line) and *xerampelinus* (broken line). Sample sizes, means and two standard errors of each mean are indicated.

average for the species, and there is no clear-cut trend of increased litter size with age of female. In this regard, mean size of first litters differs significantly between species ($t = 3.45$, $P < .002$), while mean size of each second, third, and fourth order birth does not; however, samples of *xerampelinus* at these latter points are small.

Information on litter size derived from embryo counts of wild-caught individuals is too scanty to provide meaningful comparisons (Table 8). Though *xerampelinus* averages larger than *teguina* in mean number of embryos (2.67 versus 2.28) the difference is not statistically significant ($t = 1.443$, $P = .16$).

Sex ratios of the newly-born young are provided in Table 9. In neither species does the overall proportion of males to females deviate significantly from the expected one to one ratio. There is a trend, especially in *teguina*, of fewer males with increase in litter size, but only litters of two in *xerampelinus* and of five in *teguina* depart significantly from a 50/50 proportion of males and females ($P < .05$, Chi-square test).

Care of Young

Nesting habits of the two species in the laboratory contrast markedly. Nests are constructed principally or entirely by females. Those of *teguina* are more elaborate, larger, and better formed. Females of *teguina* were frequently observed carrying tufts of shredded cotton, usually intermixed with wood shavings, into their nests. This behavior was noted both prior to parturition and throughout nursing of a litter. In shredding the cotton and wood shavings, the animal held a wad of nesting material with her forepaws, then, by backward jerking movements of her head, ripped it repeatedly with the incisors. The completed nest of finely teased cotton and wood shavings was resilient and fluffy. Though the nest was usually in the metal can, sometimes it occupied a corner of the cage or almost one-third of the cage. In these large structures, there were two or three nest chambers and at least two entrances to the nest. Female *teguina* frequently performed swift, laterally-directed movements of their forelimbs in a sweeping or clearing motion about their nest entrance or in well-defined runways. This behavior seemed to function to clear nest entrances and pathways. That part of the cage not occupied by the nest was often riddled with distinct, well-trodden paths.

In *xerampelinus*, females did not carry, manipulate, rework, and shred the cotton and wood shavings to the extent seen in *teguina*, and they did not engage in the clearing activity. Cotton placed in their cages more often was ignored and gradually trampled and matted. females made less use of the cans as nesting chambers, and when they did, a wad of unworked cotton usually plugged the entrance. Commonly, the nest of *xerampelinus* consisted of a shallow depression rounded out in the cage litter by the female's body and covered over with cotton and wood shavings. There were no large, well constructed nests as seen in *teguina*.

TABLE 9

Neonatal sex ratios according to size of litter in species of *Scotinomys*.

| Size of litter | *teguina* | | *xerampelinus* | |
	No. of litters	Percent males	No. of litters	Percent males
2	31	54.8	9	77.8
3	36	46.3	23	46.4
4	12	43.8	9	50.0
5	6	30.0	-	-
Total	85	46.0	41	52.0

Female *teguina* with nursing young aggressively defended their nests and resisted attempts to remove the young. When the nest was opened, the female frequently pulled the infants to another part of the nest or hastily attempted to repair holes in it. We often used a long prod to keep the adult away and avoid being bitten. Female *xerampelinus*, in contrast, never exhibited these defensive attitudes. When we disturbed the nest, the female typically moved away from the young, offering no resistance. In every aspect of behavior in the laboratory, *xerampelinus* was more tractable and docile than *teguina*. Differences in temperament were observed within *teguina*. Stocks from Nicaragua, Panamá, and Monte Verde (Costa Rica) were more excitable and pugnacious than those from Volcán Irazú (Costa Rica). The latter approached, but did not match, *xerampelinus* in tractability and temperament.

The male played a lesser role in care of nests and young. In both species, there were no adverse effects when the male was allowed to remain in the cage after birth of a litter. Parturition could sometimes be anticipated when the male was found huddling in the corner away from the nesting can. A few days after birth, he was again tolerated and residing in the nesting chamber with the female and litter. Thereafter, when the female left to procure food and water, the male often remained in the nest and when observed was huddling over the young. In neither species, however, did the male retrieve a young from outside the nest. Male *teguina* exhibited some paternal care and cooperation with the mate. He cleared runways around the nest and participated in nest construction, performing like a female in transporting and shredding cotton and wood shavings, although not with the same frequency and intensity. This behavior was not observed in male *xerampelinus*.

Teat-clinging is highly developed in young *teguina*, but not in young *xerampelinus*. The clinging response is present in newborn *teguina* even though their incisors have not yet erupted, and it persists until shortly after the young have opened their eyes (12–15 days). The incisors of nestling *teguina* are not modified to insure a firmer grip as in some rodents, for example *Neotoma* (Hamilton, 1953) and *Nyctomys* (Birkenholtz and Wirtz, 1965). When we were measuring the young, it was necessary to forcibly remove young *teguina* from the mother's nipples, whereas young *xerampelinus* became detached from the teats when the mother moved. Disturbance of the nest of *teguina* characteristically caused flight of the female; the young tightly adhered to her nipples as they were dragged around the cage. They usually were not attached when females fed or drank, however. In the few observed instances of a female leaving the nest, she made an effort, often with obvious difficulty, to detach the infant and return it to the nest before she resumed feeding. In several instances, young of *teguina* were raised by a female *xerampelinus* and vice versa. In such crossfostering attempts, the nipple-clinging

behavior was evident only in young *teguina*. A female *xerampelinus* appeared "perplexed" when the adopted young remained attached as she moved about the cage. Furthermore, her efforts to remove the young were awkward and frequently unsuccessful. In the reciprocal trial, young *xerampelinus* displayed no enhanced nipple-clinging ability, although they were being raised by a female *teguina*. Even in mixed litters, the young of *xerampelinus* detached easily while young of *teguina* held on firmly.

In both species, weaning is gradual and commences shortly after the young open their eyes. Though it is difficult to define precisely the age when the young are totally independent of the mother, the following observations provide some indication. Young of *teguina* were first noted outside of the nest on days 16 through 18 (the majority open the eyes at 13 to 15 days). Initially their forays outside the nest were brief and exploratory; they picked up and briefly gnawed on many items—both food particles and non-food substances— and frequently tried to snatch bits of food from the mother's paws or mouth, but did not feed extensively on their own. The female's reaction to food-snatching by the young differed from her behavior towards other conspecifics in a similar situation. While not overtly proffering food to her young, she never denied them or retrieved food morsels which they succeeded in taking; but she would fiercely resist and contest such food-stealing by her mate or other adult conspecifics. Though she continued to nurse during this period, outside the nest she gave less and less attention to the young. By days 18-20 *teguina* were commonly observed feeding on mealworms, drinking from water bottles, and spending much longer intervals outside the nest. Suckling apparently terminates about this time; no young were detected nursing beyond three weeks of age.

Weaning in *xerampelinus* is similar except that the process lags approximately three days behind *teguina*: young were noted outside the nest on days 19 to 22 (eyes open mainly at 16-19 days), were taking solid food and drinking water by days 21 to 24, and apparently ended nursing when three and one-half weeks old. In summary, offspring of *teguina* seem capable of surviving independently of the mother by three weeks of age, and those of *xerampelinus* by three and one-half weeks. At these ages, the animals feed themselves and maintain their weight and growth. Young of both species were routinely removed from their mother at age one month. In the wild, the young may normally associate with the parent (s) longer than indicated by our laboratory determinations of age-at-weaning. The observed tolerance and sociability demonstrated by the female (and her mate) toward the young in instances where litters were allowed to overlap suggest a longer association of parent and offspring.

POSTNATAL GROWTH AND DEVELOPMENT

Selected Developmental Events

Condition of the Neonate.—No striking differences were noted between young of the two species on the day of birth. The eyes are shut tightly, but a faint line marks the future borders of the upper and lower eyelids. Pinnae are closely appressed against the side of the head and are identified by only a slight crease. The digits of the forelimbs and hind limbs are united to the nail; both palmar (5) and plantar (7) tubercles are conspicuous. Neither the upper nor lower incisors have erupted, but the lower incisors are visible beneath the gumline. Mystacial vibrissae are present. The anal orifice is closed. The urogenital papilla is prominent, but to distinguish the sexes externally is sometimes difficult. The sexual difference in distance between anal orifice and urogenital papilla is less pronounced in *Scotinomys* than in some other newborn rodents, for example those of *Peromyscus* and *Reithrodontomys*. Dorsal surfaces of the body and head are darkly pigmented, while the tops of the forefeet and hind feet are grayish-pink. Though no hairs on the dorsum are visible macroscopically, fine, scattered, gray ones are discernible under a dissecting microscope. The venter is pink, entirely devoid of hair, and the abdominal wall is somewhat translucent, revealing the viscera and blood vessels. In young which have nursed, the stomach may be identified by its whitish appearance. Young exhibit no external coordinated movement or locomotion. They are capable of uttering a sharp squeak and a repetitious "clicking" sound as described earlier.

Pigmentation and Pelage.—In *teguina*, on day two, dorsal hairs, concentrated on the back and rump, are longer and more dense and can be discerned with the unaided eye. By day three, the complete dorsal surfaces of the fore- and hind feet are dusky, and ventral hairs are visible macroscopically; the venter is darker on day four, and by day six is densely pigmented. On days three through eight, the skin on the flanks and abdomen of the young has a rugose aspect, and epidermal flakes are commonly seen. Pelage development on the dorsum progresses from head to tail. By day four, the head has usually acquired dense pelage, while hair on the back and rump is relatively sparse, leaving the darkly pigmented skin visible. Typically, juvenile pelage entirely covers the dorsum by day seven. Development of pelage on the venter lags behind; by day seven, while hairs are more numerous and longer, the underlying skin is still visible, and a dense, smooth pelt is not acquired until days nine or ten. Thereafter, appreciable changes in juvenal pelage are in density and length.

Pelage develops in *xerampelinus* much as in *teguina*, but lags by 2-3 days. Dark pigmentation is not seen until day nine, and a full blanket of fur is not present until day 11 or 12. Juvenile and adult pelages are alike in color in both species.
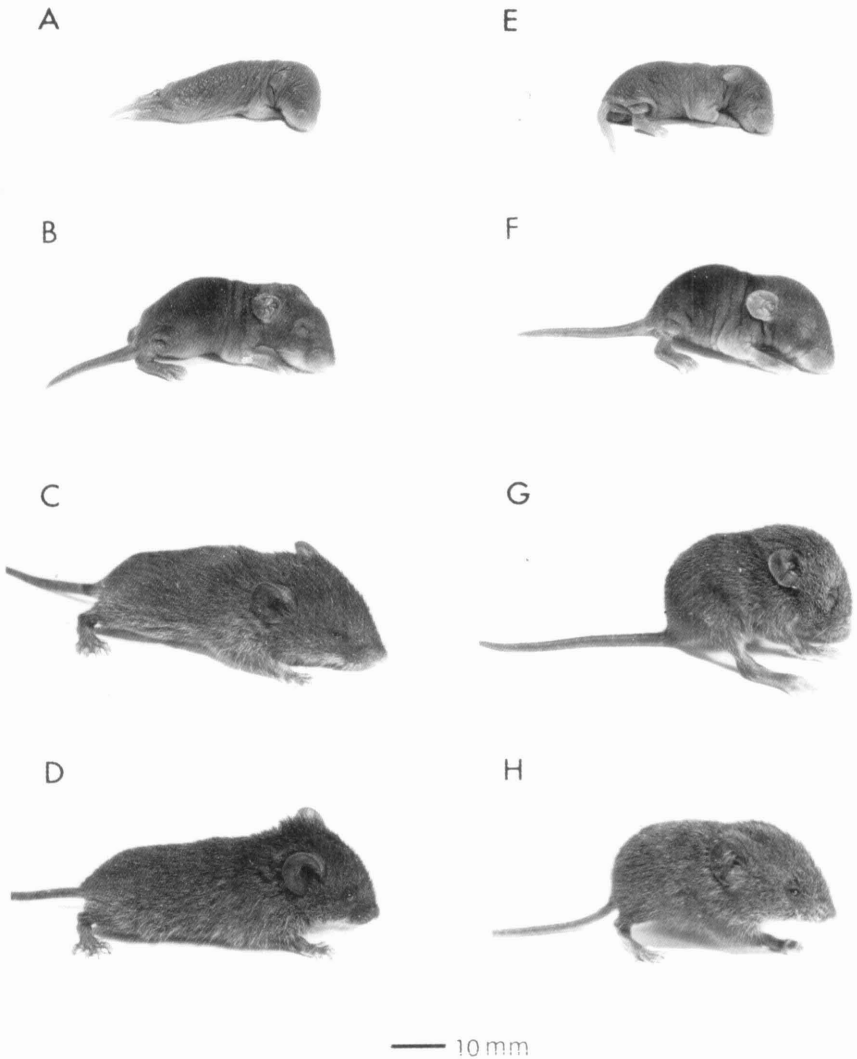
Fig. 11. Photographs of laboratory-raised *teguina* (A-D) and *xerampelinus* (E-H) at birth (A,E), one week (B,F), two weeks (C,G) and three weeks (D, H).

In studying replacement of pelages, we have relied on preserved specimens. Young *S. teguina* were sacrificed at selected intervals (approximately four individuals per stage) and prepared as flat study skins. No sign of molting was evident in young up to four and one-half weeks of age. Evidence of post-juvenal molt appeared at five weeks and lasted through eight weeks. The pattern in hair replacement resembles that described for other cricetine rodents: it begins on the midventer and spreads dorsally, the molt lines typically uniting middorsally, then progressing to the head and tail. By eight weeks, juvenile pelage (and pigment on the flat skins) occurred only on the crown and rump. The subadult pelage is like that of older
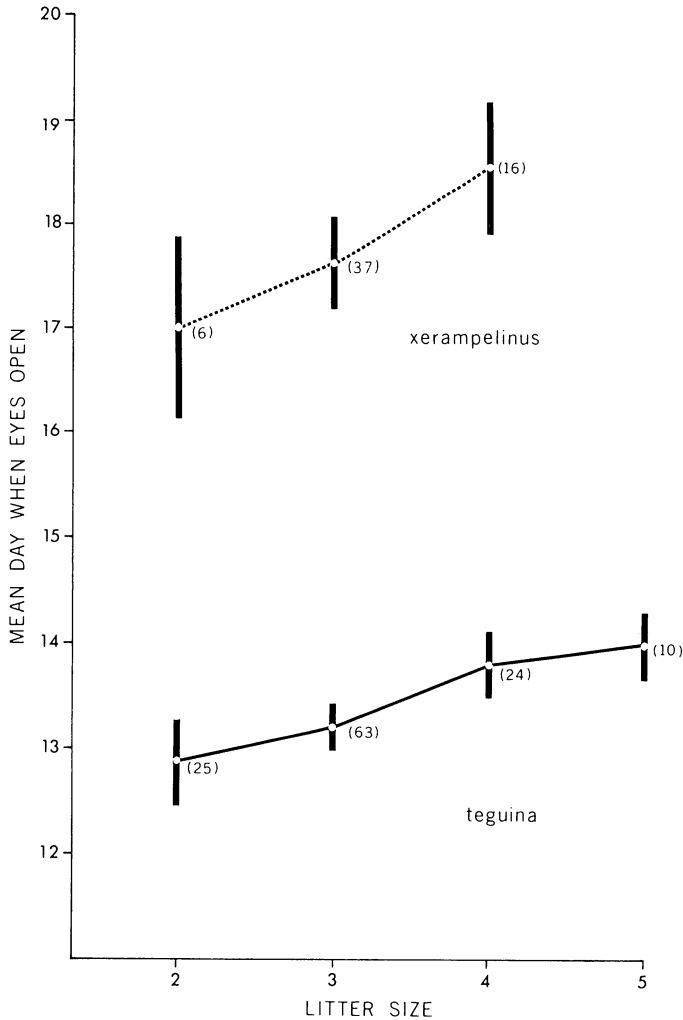
Fig. 12. Relationship of age at eye opening and litter size in *Scotinomys*. Sample sizes and two standard errors of the means are indicated.

animals and lacks the fine, lax texture of the juvenal pelt. No evidence of molting was observed in young sacrificed at ages nine, 11 and 12 weeks. There is some indication of another molt beginning at 16 weeks. We have not traced pelage sequences in *S. xerampelinus*.

Opening of Eyes and Other, Developmental Features.—On the average, the eyes of *teguina* open at 13.3 days while those of *xerampelinus* open at 17.8 (Fig. 11). The difference is significant ($t = 26.56$, $P < .0001$) with only a one-day overlap in the range of eye-opening of the species. Young of *xerampelinus* displayed a wider range than did those of *teguina* (eight versus four days); the corresponding variances differed significantly ($F = 2.01$, $P < .001$). In both species, age at eye opening is associated with size of litter:

young in large litters opened their eyes later than those in small litters (Fig. 12). The delay amounts to no more than one day.

Ages at opening of the external auditory meatus, freeing of the digits and other developmental events were also earlier in *teguina* than in *xerampelinus* (Table 10).

Locomotion.—A young *teguina* at birth characteristically lies in one place, periodically twitching in a spasmodic, uncoordinated manner, and if placed on its back is unable to right itself. By day two it can lift and support itself with the forelimbs, but frequently falls over and cannot right itself. By day five, some can regain an upright position; however, most cannot do so until day seven or eight. When they do succeed, they sit in one place, give distress squeaks, and do not attempt to crawl. By day seven, they progress fairly well, their limbs are sprawled laterally from the body and their venters touch the substrate. They can move quadrupedally, but their gait is clumsy and unsure. Between days eight through ten their limbs assume the normal vertical position, the body is elevated during locomotion, and movements are more directed and rapid. By days 12 through 14 the young can run; when the nest is opened, they quickly scamper and leap about the cage. This frantic escape behavior upon disturbance of the nest begins even before the eyes have opened. By days 16 to 18, young of *teguina* seem to be as competent as adults in most locomotor skills.

In young *xerampelinus* the sequence of locomotor development is as described above, but the rates are slower. For example, whereas 19 of 29 individuals of *teguina* (65%) could right themselves on a flat surface on day seven, none of 17 young *xerampelinus* could do so until day ten or eleven. At day 14, when young *teguina* were running about with their eyes open, young *xerampelinus* still progressed blindly in an ungainly quadrupedal gait with limbs sprawled laterally

TABLE 10

Post-natal timing (in days) of selected developmental events in five litters (approximately 15 individuals) of each species of *Scotinomys.*

	teguina	xerampelinus
Elevation of pinnae	3–4	4–6
Eruption of incisors		
lower	3–5	4–6
upper	4–7	6–8
Freeing of digits		
forefeet	4–6	6–9
hind feet	6–8	7–10
Opening of external		
auditory meatus	11–13	13–16
Opening of eyes	12–15	15–22
Emergence from nest	16–18	19–22

(Fig. 11). They did not develop coordinated locomotion like that of adults until they were 21 to 24 days old, in contrast to 16-18 in *teguina*.

Growth Rates

Weekly changes in weight and several linear measures were traced from birth to three months of age in order to provide information on postnatal growth patterns and rates in the two species. For purposes of analysis, weights and measurements of the sexes were combined, since Student *t*-tests indicated no significant differences between the sexes in weight and length of body at any given age. Adult size is here defined as those dimensions attained at three months of age. This age was selected because it is the approximate age at which growth levels off in these laboratory animals. The size of three months old laboratory-raised animals also agrees well with that of wild-caught specimens judged to be adult (Hooper, 1972:28-30). For instance, a series of 17 field-trapped *teguina* (from Volcán Irazú, Costa Rica) averaged 132.4 mm in total length and 53.7 mm in length of tail, while the corresponding values for lab-reared conspecifics at three months were 133.6 mm and 55.4 mm. Similarly, 19 field-caught *xerampelinus* had a mean total length and mean tail length of 150.6 mm and 72.8 mm respectively compared with 151.0 mm and 74.0 mm for three month old laboratory-raised specimens. In both species, adult size, as here defined, slightly exceeds the dimensions of the animals on achieving reproductive maturity.

Growth curves of both *Scotinomys* species (Figs. 13-15) generally conform in shape to those observed in other muroid rodents. The curves for the several bodily dimensions reach an asymptote at different ages. Those for length of hind foot and length of ear have a strong decrease in slope at approximately three weeks of age and show little increase beyond the fourth week (Fig. 15). Those of total length, length of body, and length of tail level off at five to eight weeks and have a less pronounced inflexion (Figs. 13, 14). All measures of linear growth attain the adult level earlier than weight. The curve for weight slopes gradually, without a prominent bend. A slight abatement in weight gain is apparent in *xerampelinus* between four and five weeks, but not in *teguina* (Fig. 13).

The two species differ in developmental rates. For example, although adult total length of *xerampelinus* exceeds that of *teguina*, young *teguina* keep pace with young *xerampelinus* through three weeks of age (Fig. 13). Conspicuous differences in total length of the two species emerge at five weeks due to the absolutely and relatively longer tail of *xerampelinus* which accounts for its larger total length. The two species are alike in length of body of both newborn and adults and
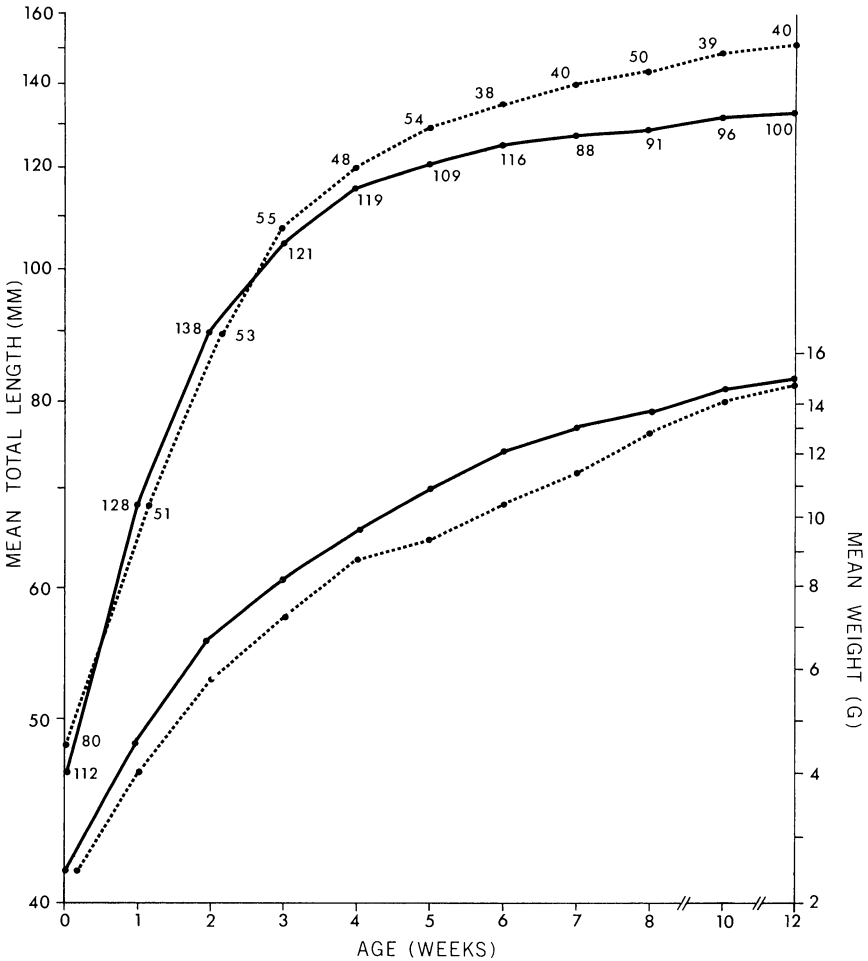
Fig. 13. Semilogarithmic plots of growth in total length and weight in laboratory-reared *teguina* (solid line) and *xerampelinus* (broken line). Sample sizes apply to both measurements.

therefore, comparison of growth in this dimension is a better indicator of differences in actual rates of development. Body length increases faster in *teguina*, the greatest hiatus evident at two through six weeks (Fig. 14). The growth rates may be related to litter size. Young from large litters weighed less than conspecifics of smaller litters at a given age (Fig. 16); disparities in linear measures associated with litter size were not as pronounced.

Growth in the two species may also be interpreted in terms of arithmetic and geometric rates and as a percent of adult size. Geometric growth rates calculated for each weekly interval, using the method of Simpson, Roe and Lewontin (1960: 394), afford a sensitive comparison of changes in rates through time. In all growth variables studied, greater rates of development were observed in
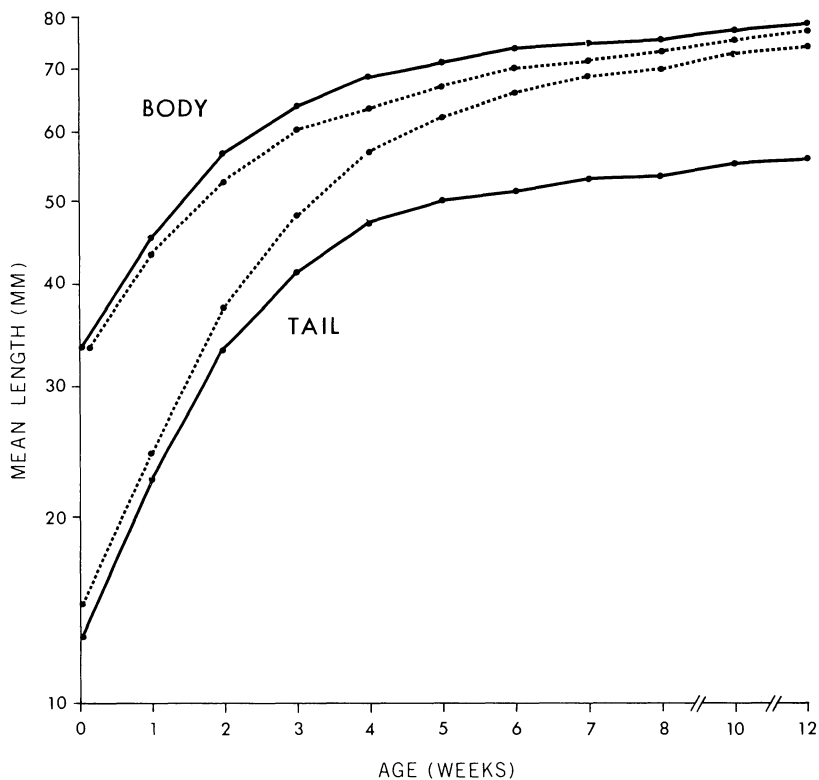
Fig. 14. Semilogarithmic plots of growth in length of body and of tail in *Scotinomys*. Other information as in Fig. 13.

teguina during early growth, and *xerampelinus* maintained higher rates at later ages. This relationship is illustrated by comparison of weekly changes in the geometric growth rate for length of body. The two points at which the declining growth rate curves for length of body intersect (Fig. 17) approximately bracket the time of weaning of both species. For *teguina* this occurs between two and three weeks of age and for *xerampelinus* between weeks three and four. One might expect a retardation in rate of development of the young during transition from mother's milk to solid food. Beyond four weeks, the rate in *xerampelinus* accelerates past that of *teguina* and thereafter consistently remains higher. Growth expressed as a percentage of adult size also reinforces the notion that individuals of *teguina* mature more rapidly (Fig. 18).

Sexual Maturity

The species differ in age at which females attain sexual maturity. Maturity, as estimated by the date of vulval opening, averages 33.8
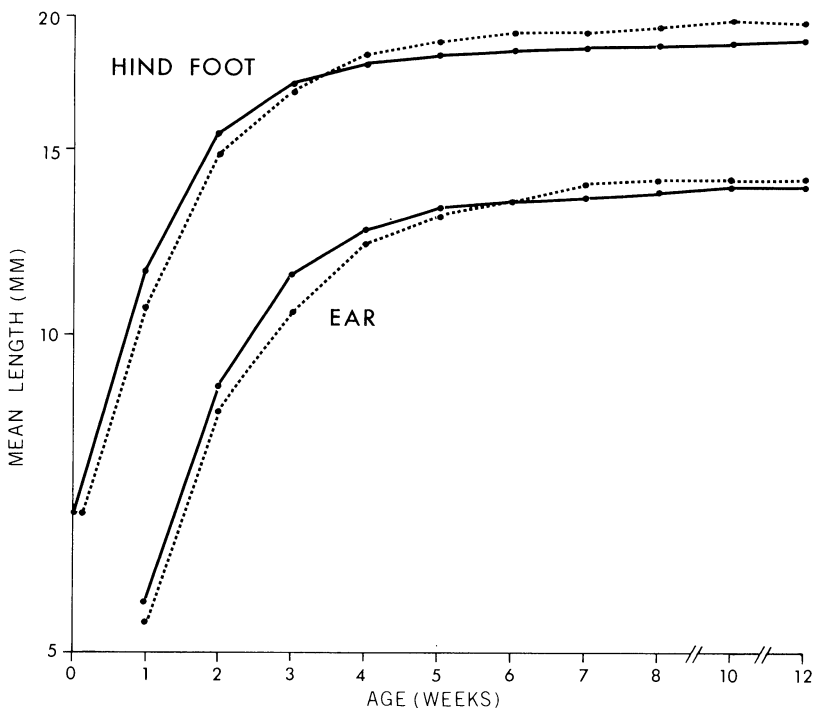
Fig. 15. Semilogarithmic plots of growth in length of hind foot and of ear in *Scotinomys*. Other information as in Fig. 13.

days (range, 28-39) for 41 *teguina* in contrast to 51.8 (range, 44-60) for 15 *xerampelinus*.

There is close correspondence between mean age of vulval opening and earliest known conception in *teguina*, but not in *xerampelinus*. The two youngest *teguina* females to give birth were 67 and 69 days of age. These individuals, paired (with non-siblings) respectively at 35 and 37 days of age, delivered their litters after 32 days. The earliest at which a *xerampelinus* gave birth was 124 days. This individual had been caged continuously with a male since age 67 days and, assuming a gestation length of 31 days, conception occurred when she was 93 days old. Other *xerampelinus* females paired to non-sibling males at two months of age did not produce litters until five, six and eight months old.

It is noteworthy that while female *S. teguina* were housed with their brothers to age 3 months, they seldom became pregnant. In contrast, five-to eight-week old females outcrossed to non-sibling males usually conceived within a short time. Such a reduction in reproductive performance among siblings has been reported and more firmly substantiated for *Peromyscus maniculatus bairdi* (Hill, 1974).

Sexual maturity in male *teguina* was ascertained by detection of spermatozoa in ˙squash preparations of the cauda epididymis and by
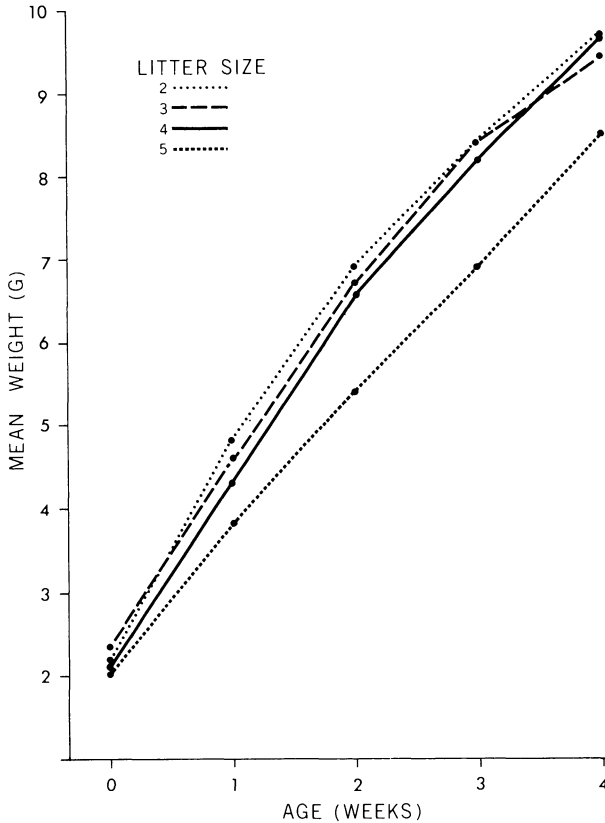
Fig. 16. Gain in weight with respect to size of litter in *teguina*. For litter sizes of 2, 3 and 4, sample size is not less than 20; for litter size of 5, sample size is 15.

examination of the accessory glands and position of the testes. In *teguina* no spermatozoa were seen in the caudae epididymides of animals aged five weeks and younger, and only one of three animals at age six weeks contained sperm in the caudae. The eight males examined of age eight weeks or older were fertile. Puberty in males, thus, came within ages six to eight weeks, a period for which we have no preserved specimens.

The state of the accessory glands in *teguina* also indicated that five-week and most six-week old males are immature. In those animals the preputial glands were relatively small, and the vesiculars were short, thin and apparently empty. The first external indication of descent of the testes occurred at five weeks, but a fully scrotal condition was not seen until six or seven weeks. Thus, males matured on the average approximately seven to ten days later than females.

We have less information on age of sexual maturity in *S. xerampelinus*. Descent of the testes was externally evident at age six
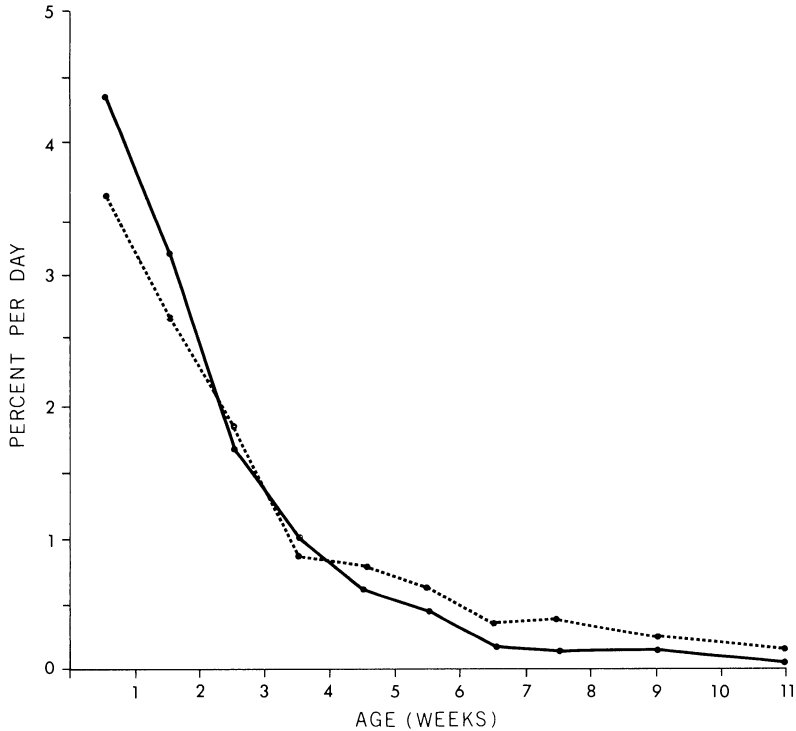
Fig.17. Geometric growth (percent per day) in body length in *teguina* (solid line) and *xerampelinus* (broken line). Sample sizes as in Fig. 13.

weeks, and the fully scrotal state by seven or eight weeks. The midventral gland is also prominent at that time.

DISCUSSION

Evolution of Interspecific Differences

Despite their many morphological resemblances, *Scotinomys teguina* and *S. xerampelinus* diverge markedly in numerous aspects of their behavior and reproductive biology. *S. teguina* builds more elaborate nests; displays some paternal cooperation in nest construction and runway clearance; has smaller litters, the young of which adhere tightly to the female's teats; the female aggressively defends the nest and young, fosters rapid growth of its young, and reaches sexual maturity earlier. The following discussion attempts to identify selective pressures leading to such contrasts in reproductive pattern between two closely related species. Implicit in this discussion is the assumption that differences revealed in our laboratory study reflect actual differences in the biologies of the two species, not different responses to the laboratory. It is hoped that this laboratory informa-
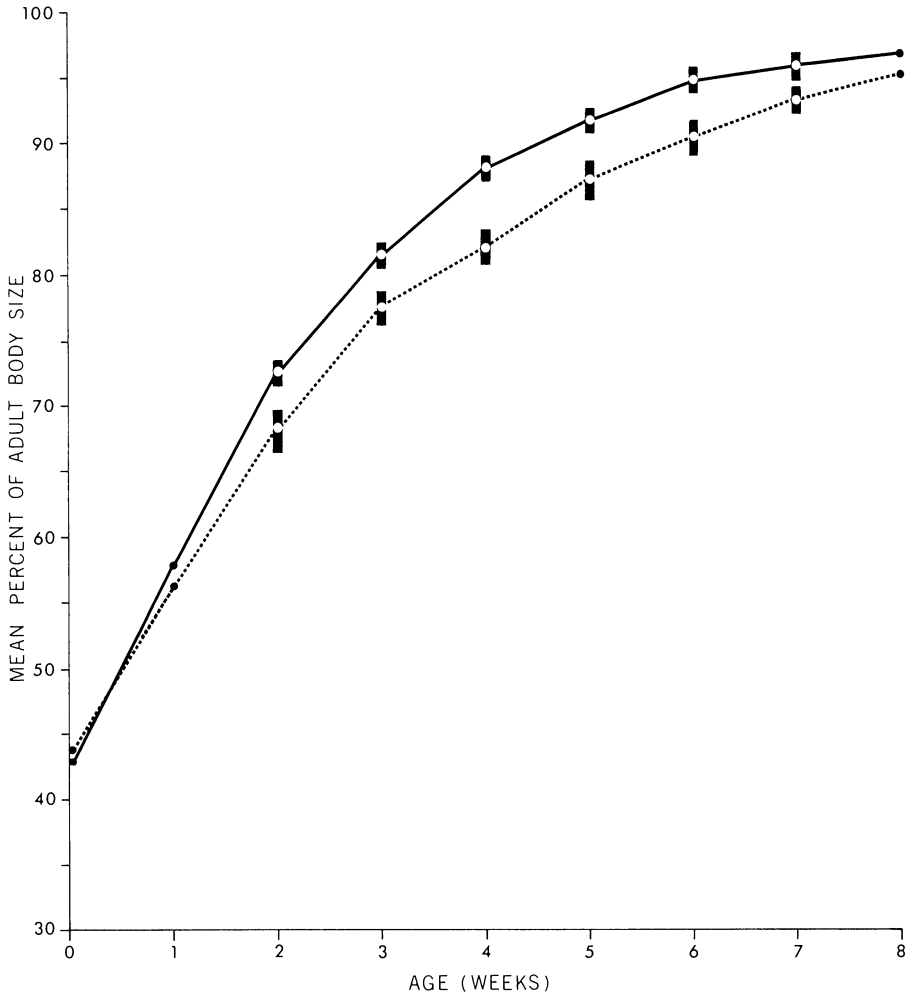
Fig. 18. Growth in body length in terms of adult size (see text) in *teguina* (solid line) and *xerampelinus* (broken line). Sample sizes as in Fig. 13. Vertical bars indicate 95% confidence intervals.

tion provides a firm framework for developing questions to be answered by detailed study in the field.

Interpretations of some of the differences in reproductive strategy may be viewed in terms of the concepts of r- and K- selection developed by MacArthur and Wilson (1967). As elaborated by those authors, r- selection embraces life history phenomena such as early maturity, large clutch size, and minimal parental care, which contribute to a high intrinsic rate of increase (r) of the population. Evolution of such reproductive characteristics may be expected in populations which are below the carrying capacity of the environment and therefore not resource limited. This concept can apply to species which colonize early successional stages or regularly reestab-

lish their populations in a highly seasonal environment. In a population whose size approaches the carrying capacity of the environment (K), i.e., is resource-limited, selection favors individuals exhibiting smaller clutch size with larger young, delayed maturity, and prolonged parental care. Presumably such adaptations confer higher competitive ability in a crowded environment as found, for example, in species inhabiting climax or more stable environments. Unfortunately, field information on the long-term population dynamics of *Scotinomys* is scanty and prohibits evaluation of their life history attributes in terms of these hypotheses. Further, it cannot be determined which of the two species might have had a history of colonizing early successional stages, since both are found today in mature forest as well as grassland and shrubs at the forest's edge. Continued human alteration of the habitat adds further complications and makes identification of the species' original habitat associations speculative.

Aside from the difficulty in obtaining a measure of the relative densities of either species relative to the carrying capacity of the environment, the reproductive characteristics of *teguina* or *xerampelinus* do not completely conform to a history of either r- or K-selection. For example, the rapid development of the young and early sexual maturity recorded for *teguina* are phenomena expected in a r-selected species; however, smaller litter size, more complex nest construction, and better protection of young are typical of K-selected species. The obverse holds for *xerampelinus* with regard to those same features of reproduction. Hence, explanation of the interspecific differences in terms of r- and K- selection is not entirely satisfactory. Moreover, as emphasized by Wilbur et al. (1974), even if one can fit aspects of a species' reproductive strategy into such a framework, it does not necessarily follow that those reproductive characteristics were primarily molded by the selective forces embodied in the concepts of r- and K- selection. Other selective pressures may be operative and be equally if not more pertinent in explaining the evolution of the life history phenomena in question. We think this particularly true for the species treated here and draw attention to another possible causative factor, namely predation pressure. A significantly higher predation mortality on populations of *teguina*, especially during the nestling period when mother and young are highly vulnerable, would tie together many of the differences in reproduction and behavior observed between it and *xerampelinus*. In pursuing this hypothesis, one might interpret the reproductive characteristics seen in *teguina* in the following manner.

Since the period that defenseless, nursing young spend in the nest is extremely risky, selection has favored those females which rear and wean their offspring in the shortest possible time. Our study indicates that duration of nest confinement of young *teguina* is about four days less than that of young *xerampelinus* although both reach

the same size (approximately 50 percent of adult weight) at weaning. Conceivably, smaller litters, increased developmental rates, and elaborate nest construction are adaptations that contribute towards this goal.

Females of *teguina* may partly achieve accelerated growth rates for their young by producing fewer individuals and investing more in their rates of development. The total biomass of a litter of *teguina* averages 6.0 gms (40 percent of adult weight) compared to approximately 7.0 gms (45 percent adult weight) in *xerampelinus*. Although this interspecific difference at birth is slight and seemingly represents only a small energy saving to a female, it must be remembered that the greatest nutritional demands on her occur during later stages of lactation (Kaczmarski, 1966; Nelson and Evans, 1961). The final savings in energy at the end of lactation realized by a female having fewer young is, therefore, considerably more substantial. In *Neotoma lepida*, for example, Cameron (1973) has demonstrated signficantly higher growth rates and correspondingly shorter weaning times in young from smaller litters and commented on the reduced risk of predation enjoyed by those young. Factors other than a reduction in litter size could account for the developmental schedule of young *teguina*. The nutritive content of insects and other food items consumed or the amount of time spent harvesting food may play important roles. A comparative analysis of the nutritional composition of the milks of *teguina* and *xerampelinus* would be illuminating in this regard. In seals, for instance, interspecific variation in nutritional value of the milk is striking and apparently correlates with neonatal growth rates (for review see Harrison, 1969).

The fineness and size of nests built by *teguina* females may also promote more rapid neonatal growth. Actually, the distinction in nest building is the opposite of what one might predict based on the climatic distribution of the two species. In several forms of *Peromyscus*, King et al. (1964) found that the amount of nesting material used was correlated with geographic distribution: northern forms utilized more material than southern ones. In *Scotinomys*, population of *xerampelinus* occupy cooler habitats in higher elevations (Hill and Hooper, 1971) but construct smaller and presumably less well-insulated nests. The effect of the nest on growth rate could be two-fold. First, a well-constructed nest in a cool climate should increase the amount of time that young remain homeothermic during absence of the mother. This has been documented for *Peromyscus leucopus* by Hill (1970) who later (1972:785) remarked that "The time during which growing young are at homeothermic temperatures is significant because body temperature likely influences growth rate and may affect other aspects of development." Secondly, a female occupying a well-insulated nest could reduce her own metabolic expenditure necessary to maintain homeothermy (see, for example, Pearson, 1960) and divert that energy to maximizing growth of her

young. If size and structure of the nest does affect growth rates, then participation of *teguina* males in building nests assumes an obvious significance. In a selective regime where high nest predation favors rapid development of one's young, males that aid in nest construction might gain some reproductive advantage.

The adaptive significance of nipple-clinging behavior, which is common among species of Muridae, is thought to involve reduction of litter losses to nest predators (Rainey, 1956; Fitch, 1957; Horner and Taylor, 1968; Layne, 1968; Cameron, 1973). The tenacity with which young *teguina* grip the mother's teats is not as pronounced as that seen in some other species of murid rodents, e.g., *Neotoma* (Egoscue, 1957; Hamilton, 1953), *Nyctomys* (Birkenholz and Wirtz, 1965) and *Peromyscus* (Brand and Ryckman, 1968; McCabe and Blanchard, 1950). In these species, the young remain almost continually attached to their mother's teats from shortly after birth until weaning. Nevertheless, young *teguina* clearly surpass young *xerampelinus* in this ability. Selective value of this trait would seem dependent upon the habits of the predatory species. Clinging young obviously hamper the speed and coordination of the female, so that loss of the female and her entire litter is more likely if the predator pursues fleeing occupants of a nest. On the other hand, clinging confers advantage to both young and mother if the predator relies more on surprising and capturing its prey in the nest. Our few cross-fostering tests suggest that interspecific differences in the young more than in the female primarily account for this trait. King (1963) reached a similar conclusion in his cross-fostering attempts involving two subspecies of *Peromyscus maniculatus* which contrasted in clinging behavior. Layne observed (1968:212) that nursing young probably anticipate flight of the female and then tighten their hold by perceiving sudden changes in her alertness or movement, "...so that the female drags them involuntarily from the nest when she hastily departs." Startled shifts of position and quick changes in a female's state of attention could signal nearness of a predator.

The contrast in temperament between *teguina* and *xerampelinus* may also reflect exposure to differing levels of predation. The jumpiness, aggressiveness, and alertness display in *teguina* seem adaptive behaviorisms for mice living in environments where there is high risk of predation. Sharp distinctions in disposition have been previously reported between other closely related species and even subspecies of rodents. The subspecies *bairdi* and *gracilis* of *Peromyscus maniculatus* differ in many of the same ways that *teguina* and *xerampelinus* do. Compared with *P. m. gracilis, P. bairdi* exhibits more rapid growth rates, earlier age at eye-opening, stronger teat-clinging, greater protection of nests by females, and a more restless temperament (King 1958, 1963). King (1958:188) speculates that relative tractability of the two forms is somehow a function of their rate of development, suggesting that "...slow maturation is at least

correlated with, if not the cause of, 'tameness' or a heightened threshold of irritability." No causality need be implied since the correlation may simply reside in the fact that fast rates of development and excitable disposition are coadaptive features in populations of mice which are subjected to higher predation pressures.

Early reproduction in *teguina* may depress future longevity and reproduction or impose more severe physiological stresses on younger, less experienced females. Female *teguina* reach sexual maturity at a weight of 10.5 gms (70% of adult weight) while *xerampelinus* females are approximately 11.8 gms (80% of adult weight). The smaller size of *teguina* at the age of potential conception is consistent with their significantly smaller first litters and subsequent increase in litter size with later births. Delayed maturity in *xerampelinus* allows attainment of larger size at first reproduction (and perhaps also more learning opportunities) and consequently larger first litters. On the basis of these reproductive attributes, one might expect greater average longevity in populations of *xerampelinus* than in *teguina*. The costs associated with early maturity, however, could be more than balanced by its reproductive benefits against a selective background of higher adult predation mortality.

The suspicion that populations of *teguina* experience higher intensities of predation is founded upon the distributions of the two species. The high elevations occupied by *xerampelinus* are wetter and decidedly cooler throughout the year, and it is presumed that there are fewer predators at those altitudes. To rigorously test this hypothesis, one should know the population sizes of the different rodent predators of the region and the extent to which each preys on *Scotinomys*. While such hard data are not available, circumstantial evidence supports the hypothesis. A tabulation of the numbers of potentially predatory vertebrate species living within the geographic range of each species on the Cordillera de Talamanca, Costa Rica, indicates a much higher count of species in the range of *teguina* (Table 11). This list includes most species which possibly consume any small rodent and, as a result, is unrealistically inclusive. Of the 15 species of birds listed, for instance, most prey rarely, if at all, on small, principally diurnal, ground-dwelling rodents as *Scotinomys*: the soaring hawks focus on more open habitats and larger game; falcons feed mainly on birds; and the owls are nocturnal. Similarly, some of the reptiles are principally arboreal, and it is not known that all prey on small rodents. Even when doubtful candidates are excluded, however, the predatory species in the range of *teguina* far outnumber those in the range of *xerampelinus*.

The greatest contrast is in number of reptiles, all of which are snakes. Differential predation by snakes may be most significant, for a snake's hunting habits bring to bear on terrestrial rodents predation strategies which are unlike those employed by birds or mammals. Snake species are concentrated in the lower part of the

TABLE 11

Potential predators of *Scotinomys* on the Cordillera de Talamanca, Costa Rica.

Predator	*teguina*	*xerampelinus*
Mammalia		
Didelphis marsupialis	+[1]	-[1]
Philander opossum	+	-
Caluromys derbianus	+	-
Mustela frenata	-	+
Eira barbara	+	-
Procyon lotor	+	-
Conepatus semistriatus	+	+
Nasua nasua	+	+
Jentinkia sumichrasti	+	-
Urocyon cinereoargenteus	+	-
Felis tigrina	+	+
F. pardalis	+	-
F. wiedii	+	+
Total	12	5
Aves		
Harpagus bidentatus	+	-
Buteo platypterus	+	+
Buteo jamaicensis	-	+
Leucopternis albicollis	+	-
L. semiplumbea	+	-
Buteogallus urubitinga	+	-
Micrastur ruficollis	+	-
Otus guatemalae	+	-
O. clarkii	-	+
Lophostrix cristata	+	-
Pulsatrix perspicillata	+	-
Ciccaba virgata	+	-
C. nigrolineata	+	-
Tyto alba	+	-
Aegolius ridgwayi	-	+
Total	12	4
Reptilia		
Chironius fuscus	+	-
Chironius sp.	+	-
Clelia clelia	+	-
Dendrophidion clarki	+	-
D. percarinatum	+	-
D. vinitor	+	-
Drymobius melanotropis	+	-
D. rhombifer	+	-
Erythrolamprus mimus	+	-
Lampropeltis triangulum	+	-

Predator	*teguina*	*xerampelinus*
Table 11 Continued		
Leptophis ahaetulla	+	-
Mastigodryas melanolomus	+	-
Pseustes poecilonotus	+	-
Spilotes pullatus	+	-
Bothrops asper	+	-
B. godmani	+	+
B. lateralis	+	-
B. nasutus	+	-
B. nigroviridis	+	+
B. nummifer	+	-
B. schlegelii	+	-
Total	21	2
Grand Total	44	11

[1]Presence (+) or absence (-) of these possible predators is indicated for localities within the altitudinal belts inhabited by *teguina* (represented by Tapanti, 1200 m, and Las Cruces, 1250 m) and by *xerampelinus* (represented by localities above 2900 m in vicinity of Cerro de la Muerte and Volcán Chirripó Grande).

range of *teguina*, and these ectothermic vertebrates, especially sensitive to cool-wet environments, decline precipitously in numbers with increasing elevation. Ten of the 21 species of snakes almost surely range no higher than 1400 m, and another eight or nine species probably drop out before the 2500 m level. This leaves only two species of *Bothrops* and possibly one of *Lampropeltis* which may extend into the range of *S. xerampelinus*.

Altitudinal variation is also seen in various characters of *Scotinomys* both within and between the two species, for example in litter size and temperament. Thus, we suggest that predation pressure varies clinally, and that observed anatomical and behavioral patterns agree with those expected on the basis of fewer or more predators.

Contiguous Allopatry and Interspecific Competition

The two species of *Scotinomys* are derivable from a common ancestor. Possibly segments of a widespread polytypic species were isolated by some geographic barrier in Middle America, such as a water gap or inhospitable lowlands as exist today in southern Nicaragua (Buchanan and Howell, 1967). The southern segment became *xerampelinus* while the northern one differentiated as *teguina* and subsequently, in geologically Recent time, spread southward to make contact with *xerampelinus*. Whatever the validity of this scenario, the two species are now altitudinally zoned such that their ranges are contiguous with local narrow belts of overlap. How is the geographic relationship maintained? The patterns of contiguous

allopatry and altitudinal stratification suggest interaction of competitive interference and environmental gradients.

Competitive exclusion is frequently cited in situations of contiguous allopatry of closely related species (for discussions see Grant, 1972; Jaeger, 1974; Terborgh, 1971). The rationale for invoking competitive exclusion is that closely related species, descended from a common ancestor, share many morphological, behavioral and trophic similarities. Hence, they compete for largely the same resources where secondary contact occurs.

The two species of *Scotinomys* fit those specifications. They have aspects of a recently evolved, sibling species-pair with no evidence of hybridization either in the field or laboratory. They are both small, approximately equal in size, and live on the ground. In habitats where they have been taken together, they frequent the same sorts of cover and runways. The two are diurnally active with most activity confined to morning and early afternoon. Vocal and olfactory modes of communication are well developed in both. Their dentitions and the anatomy of their digestive tracts suggest similar feeding adaptations, and both are mainly insectivorous with much dietary overlap in the major taxonomic groups of insects consumed. Thus, *teguina* and *xerampelinus* have much in common with respect to food and spatial resources, an important requisite for competitive exclusion (Jaeger, 1974).

Direct evidence of interspecific competition is scanty. Our laboratory tests provide no conclusive results regarding interspecific dominance. Aggressive encounters or competitive interference based on dominance are thought to delimit the contact zone between various species of chipmunks which are stratified altitudinally (Brown, 1971; Heller, 1971; Sheppard, 1971). Yet the pugnacious, vigilant behavior display by *teguina* may be related equally well to procuring food (capture of adult versus larval insects) or to predation pressure as discussed above. The fact that highland stocks of *teguina* occurring adjacent to populations of *xerampelinus* are less aggressive than lowland ones supports the hypothesis of predation rather than that of competitive exclusion.

Our few data suggesting a shift in food habits of the two where they are sympatric, and at least partially overlap in foraging space, are particularly relevant to the question of competition. Competitive interaction has been inferred in two species of *Neotoma* on the basis of differences in amounts of preferred foods in allopatry and sympatry (Cameron, 1971). In our samples, *teguina* consumed more insects than did *xerampelinus* in areas of sympatry; the opposite relationship prevailed in samples from areas of allopatry (Table 4). The *xerampelinus* also ate proportionately fewer adult insects in the presence of *teguina*, an observation which accords with the superior ability of *teguina* in capturing highly mobile prey in the laboratory. While these results are tantalizingly suggestive of direct competition,

they must be interpreted cautiously. Perhaps more larvae were available at that time of year or at those particular sites, for stomachs of *teguina* also contained proportionately more larvae in the areas of sympatry. Additional stomach samples from other regions of contact of the species, together with surveys of kinds of insects and life stages present, are desirable. If other replicates reveal similar shifts in diet, then one may more confidently implicate interspecific competition as an integral factor maintaining the contiguous distributions.

While contiguous allopatry may sometimes be associated with competitive exclusion it also reflects adaptations of the animals to environmental gradients (Terborgh, 1971). Environmental temperature and rainfall, for example, obviously can effect a given species' distribution. The altitudinal stratifications of *teguina* and *xerampelinus* may simply correspond to their particular temperature preferences, and the 2900 to 2950 m level on Volcán Irazú, for example, may be a critical one below and above which *xerampelinus* and *teguina*, respectively, are at a selective disadvantage (Hill and Hooper, 1971). The steep negative correlation of temperature and elevation in the neotropics and the annual uniformity of temperature patterns within a given elevational belt (Janzen, 1967; Terborgh, 1971) lend some support to this idea.

On the other hand, temperature and moisture indirectly may influence the two species through effects on the type or density of plant cover or on the distribution or habits of their insect prey. The number of species and biomass of insects diminish at high elevations in the region; especially noteworthy is the decline in Coleoptera and Hemiptera (Janzen, 1973, Tables 4 d-f). The sharp truncation in numbers of hemipterans at high altitudes, for instance, may explain their relatively infrequent occurrence in the stomach samples of *xerampelinus*. Janzen (op. cit.) speculates that on wet-cool tropical mountains the resistance of the moist ground to diurnal warming inhibits the activity of substrate-foraging insects, accounting for their paucity at high altitudes. Furthermore, larval periods of insects are longer at high elevations, and the emergence of adults tends to concentrate in the short dry season (Janzen, pers. comm.). These schedules, and the restricted activity of adult insects due to the irregular and short periods of sunshine, may have led to the specialization on larvae by the highland species *xerampelinus*, while *teguina* concentrated on adult insects which at intermediate elevations are numerous and available for most of the year. Interspecific differences in eye size and prey capture techniques accord with this view. The species' contiguous allopatry thus may reflect the distribution of prey items harvested most efficiently by each species, and at the same time illustrate the interplay of the physical environment and competitive exclusion in influencing contiguous allopatry (Jaeger, 1974).

All information at hand considered, we have no compelling

evidence that either of these species is restricting the density or distribution of the other. Transplant or perturbation experiments such as those performed by Grant (1972) and Schroder and Rosenzweig (1975) on field populations could ascertain whether some sort of repulsion interaction is occurring between the two species. However, as cautioned by the latter authors (op. cit.), even if such short-term manipulations yield negative results, it does not necessarily follow that competition was never operative in stabilizing the current distributional pattern.

Widespread human interference is greatly changing the species' distributions, and perhaps doing so unequally. Clearing of the land for pasture, with the resultant influx of secondary shrubs, berry tangles and growth of grass over felled logs, has created favorable cover and runways for both species. Both have also been sampled in impressive numbers about fencerows bordering cornfields or vegetable plots, in barns and under houses, and even in flower gardens next to human habitations. The benefit to these mice, in view of their predominantly insectivorous diet, may be that human alteration of the environment fosters ample insect populations in addition to providing additional cover. While some clearing of the land may favor both species, complete removal of cloud forest may be more detrimental to *xerampelinus* than *teguina*. If *xerampelinus* prefers low light levels and cooler temperatures as suggested by its geographic distribution and laboratory tests, then removal of the forest would probably have a warming and drying effect, thereby creating conditions more suitable for *teguina*. Such an explanation might account for the disappearance after 1962 of *xerampelinus* from the area above San Juan Chicoa on Volcán Irazú. The distributional and habitat data of this report provide a basis for monitoring future changes in the populations of these species.

LITERATURE CITED

Birkenholz, D. E., and W. O. Wirtz. 1965. Laboratory observations on the vesper rat. J. Mammal., 46:181–189.

Brand, L. R., and R. E. Ryckman. 1968. Laboratory life histories of *Peromyscus eremicus* and *Peromyscus interparietalis*. J. Mammal., 49:495–501.

Brown, J. H. 1971. Mechanisms of competitive exclusion between two species of chipmunks. Ecology, 52:305–311.

Buchanan, O., and T. R. Howell. 1967. Zoogeography of *Scotinomys* in Middle America, with the description of a new subspecies from Nicaragua. J. Mammal., 48:414–419.

Cameron, G. N. 1971. Niche overlap and competition in woodrats. J. Mammal., 52:288–296.

————— 1973. Effect of litter size on postnatal growth and survival in the desert woodrat. J. Mammal., 54:489–493.

Carleton, M. D. 1973. A survey of gross stomach morphology in New World Cricetinae (Rodentia, Muroidea), with comments on functional interpretations. Misc. Publs Mus. Zool. Univ. Mich., 146:1–43.

Carleton, M. D., E. T. Hooper, and J. Honacki. 1975. Karyotypes and accessory reproductive glands in the rodent genus *Scotinomys*. J. Mammal., 56:916-921.

Carr, A. F. 1950. Outline for a classification of animal habitats in Honduras. Bull. Amer. Mus. Nat. Hist., 94:567-594.

Egoscue, H. J. 1957. The desert woodrat: a laboratory colony. J. Mammal., 38:472-481.

Enders, R. K., and O. P. Pearson. 1939. Three new rodent subspecies of *Scotinomys* from Chiriquí, Panamá. Notulae Naturae, Acad. Nat. Sci. Philadelphia, 34:1-4.

Fitch, H. S. 1957. Aspects of reproduction and development in the prairie vole (*Microtus ochrogaster*). Univ. Kans. Publs Mus. Nat. Hist., 10:129-161.

Grant, P. R. 1972. Interspecific competition among rodents. A. Rev. Ecology Systematics, 3:79-106.

Hamilton, W. J. 1953. Reproduction and young of the Florida woodrat, *Neotoma f. floridana*. J. Mammal., 34:180-188.

Harrison, R. J. 1969. Reproduction and reproductive organs, pp. 253-348. *In*: The Biology of Marine Mammals (H. T. Anderson, ed.). New York: Academic Press.

Heller, H. C. 1971. Altitudinal zonation of chipmunks (*Eutamias*): interspecific aggression. Ecology, 52:312-319.

Hill, J. L. 1974. *Peromyscus*: Effect of early pairing on reproduction. Science, 186:1042-1044.

Hill, R. W. 1970. The ontogeny of homeothermy in neonatal *Peromyscus leucopus noveboracensis*. PhD dissertation, The University of Michigan, pp. x + 203.

———————— 1972. The amount of maternal care in *Peromyscus leucopus* and its thermal significance for the young. J. Mammal., 53:774-790.

Hill, R. W., and E. T. Hooper. 1971. Temperature regulation in mice of the genus *Scotinomys*. J. Mammal., 52:806-816.

Hooper, E. T. 1972. A synopsis of the rodent genus *Scotinomys*. Occ. Pap Mus. Zool. Univ. Mich., 655:1-13.

———————— 1975. Orbital region and size of eye in species of *Scotinomys* (Rodentia). J. Mammal., 56:667-671.

Horner, E. B., and J. M. Taylor. 1968. Growth and reproductive behavior in the southern grasshopper mouse. J. Mammal., 49:644-660.

Jaeger, R. G. 1974. Competitive exclusion: comments on survival and extinction of species. Bioscience, 24:33-39.

Janzen, D. H. 1967. Why mountain passes are higher in the tropics. Am. Nat., 101:233-249.

———————— 1973. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. Ecology, 54:687-708.

Kaczmarski, F. 1966. Bioenergetics of pregnancy and lactation in the bank vole. Acta Theriol., 11:409-417.

King, J. A. 1958. Maternal behavior and behavioral development in two subspecies of *Peromyscus maniculatus*. J. Mammal., 39:177-190.

———————— 1963. Maternal behavior in *Peromyscus*, pp. 58-93. *In*: Maternal Behavior in Mammals (H. L. Rheingold, ed.). New York: John Wiley & Sons, Inc.

King, J. A., D. Mass, and R. G. Weisman. 1964. Geographic variation in nest size among species of *Peromyscus*. Evolution, Lancaster, Pa., 18:230-234.

Layne, J. N. 1968. Ontogeny, pp. 148-253. *In*: Biology of *Peromyscus* (Rodentia) (J. A. King, ed.). Spec. Publs Am. Soc. Mammal., No. 2.

MacArthur, R. H., and E. O. Wilson. 1967. The Theory of Island Biogeography. New Jersey: Princeton University Press. Pp. xviii + 203.

McCabe, T. T., and B. D. Blanchard. 1950. Three Species of *Peromyscus*. Santa Barbara: Rood Associates. Pp. v + 136.

Myers, C. W. 1969. The ecological geography of cloud forest in Panama. Am. Mus. Novit., 2396:1-52.

Nelson, M. N., and H. M. Evans. 1961. Dietary requirements for lactation in the rat and other laboratory animals, pp. 137-191. *In*: Milk: The Mammary Gland and its Secretion (S. K. Kon and A. T. Cowie, eds.). New York: Academic Press.

Pearson, O. P. 1960. The oxygen consumption and bioenergetics of harvest mice. Physiol. Zool., 33:152-160.

Rainey, D. G. 1956. Eastern woodrat, *Neotoma floridana*: life history and ecology. Univ. Kans. Publs Mus. Nat. Hist., 8:535-646.

Sawyer, J. O., and A. A. Lindsey. 1971. Vegetation of the life zones in Costa Rica. Indiana Acad. Sci., Monogr. 2, 214 pp.

Schroder, G. D., and M. L. Rosenzweig. 1975. Perturbation analysis of competition and overlap in habitat utilization between *Dipodomys ordii* and *Dipodomys merriami*. Oecologia (Berl.), 19:9-28.

Sheppard, D. A. 1971. Competition between two chipmunk species (*Eutamias*). Ecology, 52:320-329.

Stuart, L. C. 1966. The environment of the Central American cold-blooded vertebrate fauna. Copeia, 1966:684-699.

Terborgh, J. 1971. Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcamba, Peru. Ecology, 52:23-40.

Tosi, J. A. Jr. 1969. Republica de Costa Rica Mapa Ecologico según la clasificacion de zonas de vida del mundo de L. R. Holdridge. Escala 1:750,000. San Jose: Tropical Science Center.

Vorontsov, N. N. 1967. Evolution of the alimentary system of Myomorph rodents. Novosibirsk: Publ. House Nauka, 235 pp.

Wagner, P. L. 1964. Natural vegetation of Middle America, pp. 216-264. *In*: Handbook of Middle American Indians, Vol. 1 (Wauchope, R. and R. C. West, eds.). Texas: Univ. Texas Press.

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