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VARIATION AND ECOLOGY IN A LOCAL POPULATION OF THE VESPER MOUSE (NYCTOMYS SUMICHRASTI)

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Vesper mice of the genus *Nyctomys* are relatively rare, arboreal rodents restricted to Middle America (eastern Panama to southern Mexico). Little is known concerning the biology of these secretive animals. Studies of variation of the one species, *Nyctomys sumichrasti*, have been limited to descriptions of new taxa (for example, see Goldman, 1916, 1937, and Laurie, 1953) and ecological observations have been confined to faunal accounts of political units (Goodwin, 1934; Hall and Dalquest, 1963) or were made coincidental to studies of other species (Lawlor, 1969; Fleming, 1970). Birkenholz and Wirtz (1965) recorded observations on the behavior, reproduction, and early development of young in a laboratory colony of vesper mice; the male reproductive organs and accessory structures have been described by Burt (1960), Arata (1964), and Hooper and Musser (1964).

In the summer of 1964, a local population of *Nyctomys sumichrasti florencei* was discovered at San Antonio, Departamento de Chinandega, in northwestern Nicaragua. This area was visited again in the summers of 1966 and 1967, and in the spring of 1968, and the present paper details variation in this population and records such ecological information as was obtained. The first three visits to San Antonio were in the wet season, whereas the last was in the dry season. Of the 100 specimens of vesper mice collected there, the majority (55) was taken in 1966. A few mice were obtained in traps placed on the ground at the bases of trees but most were shot with pistols (dust shot) as they perched on, or scampered along, low branches and vines in dense vegetation. It is noteworthy that only 10 *N. sumichrasti* were obtained elsewhere in Nicaragua in the four years of our field work.

All specimens discussed below are deposited in the collections of the Museum of Natural History at The University of Kansas. All measurements are in millimeters and weights are recorded in grams.

VARIATION

In the following section, four sources of nongeographic variation—age, secondary sexual, individual, and seasonal—are analyzed; these are of interest because they reveal to some extent the genetic variability within the species. An understanding of them is basic to the study of geographic variation.

Variation with Age

All specimens from San Antonio were assigned to one of five age categories. These were studied to ascertain whether significant differences relating to growth occurred between them and to determine which individuals had terminated growth, or nearly so, and could be termed "adults." Age categories were defined as outlined below—see Fig. 1 for illustration of first left upper molars typical of each category and Fig. 2 for illustration of crania of typical individuals of each except IV (crania of which are indistinguishable from those of V).

I.—Exoccipital-basioccipital sutures evident; basioccipital-basisphenoid suture open; braincase domed; temporal ridges absent or at most slightly developed; M3 not fully erupted or, if so, unworn.

II.—Exoccipital-basioccipital sutures no longer evident; molars exhibit only slight wear (the lingual cusps are first to wear and show the most wear in this group, labial cusps reveal wear only on the tips).

III.—Molars exhibit considerable wear, but cuspidate nature of teeth still evident; labial cusps worn to a much greater degree than simply on tips.

IV.—Molars worn so that cuspidate nature of the teeth is no longer readily evident; occlusal surfaces of teeth consist of a series of dentine lakes interspersed with enamel re-entrant angles and islands.

V.—All enamel re-entrant angles and islands essentially worn away, leaving a central lake of dentine surrounded by an enamel rim (especially on M2), although a small enamel re-entrant angle or island occasionally may be present.

Means for each measurement were tested for significant differences (significance level .05) among the five age categories using single classification analysis of variance; if significant differences were found, a Sums of Squares Simultaneous Test Procedure (SS-STP) was used to determine the

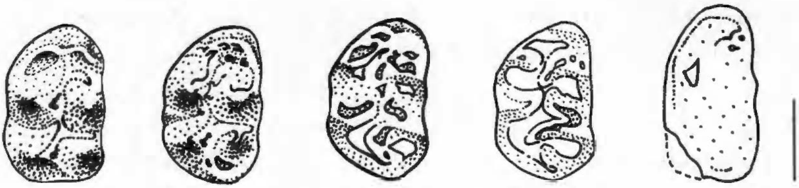

Fig. 1.—First upper left molars of *Nyctomys sumichrasti* illustrating tooth wear with age. From left to right the teeth typify the following age categories: I, KU 106655; II, KU 98059; III, KU 110503; IV, KU 106676; V, KU 106671. The scale at the right is one millimeter long.

maximally nonsignificant subsets (see Genoways and Jones, 1971, and Genoways, 1971, for discussion of these procedures). Of the six external and 10 cranial measurements tested for both sexes, only two (length of ear for females and length of maxillary toothrow for males) revealed no significant differences between the means of the five age categories (Table 1). Three nonoverlapping subsets (V-IV, III-II, I) were found for females in total length, length of head and body, and occipitonasal length, and nonoverlapping subsets of V-IV and III-II-I resulted in females for rostral breadth.

All remaining measurements exhibited some overlapping of maximal nonsignificant subsets. Thirteen of these measurements had means that fell into only two subsets. One age category is shared between the two subsets

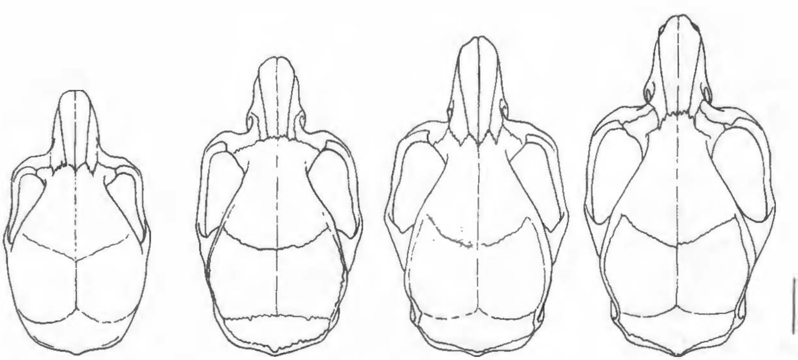

Fig. 2.—Dorsal view of the crania of four specimens of *Nyctomys sumichrasti* from San Antonio, Nicaragua, illustrating variation with age. The age categories are, from left to right: I (KU 106655), II (KU 106691), III (KU 110501), and V (KU 106696). Specimens in age category IV, which is not illustrated, have crania that are essentially the same as those in category V. The scale at the right is five millimeters long.

for length of tail for males (V-III-II-IV, IV-I) and females (IV-V-III-II, II-I), and depth of cranium in males (IV-V-III-II, II-I). In three measurements for males (length of ear, breadth of braincase, and length of palatal bridge) and five for females (interorbital constriction, breadth of braincase, depth of cranium, length of maxillary toothrow, and length of palatal bridge), two age categories were shared between two subsets. Three age categories were shared between subsets for length of hind foot for both males and females.

Nine measurements exhibited three overlapping subsets. Total length for males and length of rostrum for females were divided V-IV-III, IV-III-II, and I; length of head and body for males exhibited the same pattern of variation but the positions of categories V and IV were reversed. Subsets of V-IV-III, III-II, and I were found for rostral breadth and length of the incisive foramen of males. Means of zygomatic breadth for females were arranged in subsets of V-IV, IV-II, and II-III-I, and length of the incisive foramen in them revealed the same pattern of variation except the positions of categories II and III were reversed. Maximal nonsignificant subsets for weight of females consisted of V-IV, II-III, and III-I. The three subsets for interorbital constriction of males were broadly overlapping.

Four measurements of males were divided into four nonsignificant subsets. Three of these (weight, occipitonasal length, and zygomatic breadth) exhibited the following pattern of subsets: V-IV, IV-III, III-II, and I. The fourth measurement (length of rostrum) revealed essentially the same pattern except that the order of V and IV was reversed.

Based upon this analysis, the most parsimonious grouping of categories is: I (smallest individuals), II-III (medium-sized mice), and IV-V (largest individuals). Members of age categories IV or V were found to have the largest mean for all measurements excepting length of hind foot and length of maxillary toothrow in males and breadth of braincase in females. For all measurements except length of maxillary toothrow in females, age category I had the smallest mean. We have termed the three groups mentioned above as juvenile, subadult, and adult, respectively, and use this terminology throughout the remainder of this paper.

Secondary Sexual Variation

Adult males were tested against adult females using single classification analysis of variance to determine if means for the 16 measurements were significantly different (significance level .05) between them. In only one measurement, weight, was there a significant difference between the sexes (Table 2), males averaging nearly four grams heavier. In the remaining 15 measurements, males had the larger mean for seven (total length, length of

TABLE 1.—*Variation with age in six external and 10 cranial measurements of* Nyctomys sumichrasti *from San Antonio, Chinandega, Nicaragua. Age categories are listed in decreasing order of means. Groups of means that were found to be significantly different at the .05 level using single classification analysis of variance were tested with sums of squares-simultaneous testing procedure to find the maximally nonsignificant subsets. Groups of means that were found to be not significantly different at the .05 level are marked ns. Age categories are defined in text.*

Sex and age category	N	Mean (Range) ± 2 SE	CV	Results SS-STP
		Total length		
Male				
V	5	240.2 (231.0-246.0) ± 5.41	2.5	
IV	3	228.0 (225.0-231.0) ± 3.46	1.3	
III	9	224.0 (215.0-237.0) ± 4.32	2.9	
II	9	218.0 (208.0-233.0) ± 6.73	4.6	
I	9	195.0 (167.0-207.0) ± 7.98	6.1	
Female				
V	5	232.6 (230.0-236.0) ± 2.05	1.0	
IV	11	229.7 (219.0-242.0) ± 4.50	3.2	
III	7	215.7 (206.0-230.0) ± 6.91	4.2	
II	6	215.6 (207.0-229.0) ± 6.53	3.7	
I	8	196.4 (178.0-207.0) ± 6.36	4.6	
		Length of head and body		
Male				
IV	9	118.6 (107.0-129.0) ± 5.12	6.5	
V	6	118.0 (99.0-125.0) ± 7.85	8.1	
III	10	111.0 (104.0-116.0) ± 2.51	3.6	
II	10	108.3 (94.0-117.0) ± 4.64	6.8	
I	9	96.3 (84.0-102.0) ± 3.69	5.8	
Female				
V	8	120.3 (114.0-128.0) ± 3.27	3.8	
IV	16	116.6 (106.0-124.0) ± 2.35	4.0	
II	7	106.9 (100.0-113.0) ± 3.39	4.2	
III	8	106.1 (98.0-115.0) ± 4.51	6.0	
I	8	96.3 (83.0-103.0) ± 5.30	7.8	

Table 1.—*Continued.*

		Length of tail		
Male				
V	5	118.4 (112.0-126.0) ± 5.24	4.9	
III	8	112.8 (109.0-122.0) ± 3.06	3.8	
II	9	110.7 (99.0-121.0) ± 5.02	6.8	
IV	3	109.0 (108.0-110.0) ± 0.58	0.9	
I	9	99.2 (83.0-109.0) ± 4.95	7.5	
Female				
IV	11	113.5 (108.0-124.0) ± 2.96	4.3	
V	5	112.2 (102.0-117.0) ± 5.34	5.3	
III	7	110.0 (103.0-114.0) ± 2.99	3.6	
II	6	107.6 (101.0-117.0) ± 4.31	4.9	
I	8	100.1 (95.0-105.0) ± 2.84	4.0	
		Length of hind foot		
Male				
III	11	22.9 (22.0-25.0) ± 0.57	4.1	
II	10	22.4 (21.0-25.0) ± 0.68	4.8	
IV	9	22.2 (21.0-23.0) ± 0.65	4.4	
V	6	22.2 (21.0-23.0) ± 0.80	4.4	
I	9	21.4 (20.0-23.0) ± 0.68	4.7	
Female				
V	8	22.6 (22.0-23.0) ± 0.37	2.2	
III	8	22.4 (21.0-24.0) ± 0.65	4.1	
II	7	22.3 (21.0-24.0) ± 0.72	4.3	
IV	16	22.0 (20.0-23.0) ± 0.41	4.1	
I	8	21.3 (20.0-22.0) ± 0.63	4.2	
		Length of ear		
Male				
V	6	17.0 (16.0-18.0) ± 0.52	3.7	
II	10	16.8 (15.0-19.0) ± 0.83	7.8	
IV	9	16.7 (15.0-18.0) ± 0.67	6.0	
III	11	16.6 (14.0-18.0) ± 0.68	6.7	
I	9	15.3 (14.0-17.0) ± 0.67	6.5	
Female				
IV	16	17.0 (15.0-18.0) ± 0.41	4.1	ns
V	8	16.9 (16.0-18.0) ± 0.40	3.3	
III	8	16.8 (15.5-19.0) ± 0.75	6.3	
II	7	16.1 (15.0-17.0) ± 0.63	5.2	
I	8	16.0 (13.0-18.0) ± 1.13	10.0	

Table 1.—*Continued.*

		Weight			
Male					
V	6	50.0	(41.7-61.3)	± 5.19	12.7
IV	9	47.5	(39.3-58.5)	± 3.98	12.6
III	11	40.1	(33.3-47.2)	± 2.94	12.2
II	10	36.1	(28.5-45.5)	± 3.43	15.0
I	9	26.0	(18.1-30.6)	± 2.37	13.7
Female					
V	8	46.2	(39.0-51.5)	± 2.55	7.8
IV	16	44.3	(38.2-53.9)	± 2.14	9.6
II	7	36.8	(27.0-43.6)	± 4.24	15.3
III	8	34.6	(31.6-43.7)	± 2.78	11.3
I	8	27.7	(16.6-32.4)	± 3.54	18.1
		Occipitonasal length			
Male					
V	6	30.3	(29.7-30.6)	± 0.31	1.2
IV	8	29.4	(28.5-31.2)	± 0.62	3.0
III	11	28.4	(27.3-29.4)	± 0.42	2.5
II	9	27.8	(27.1-29.2)	± 0.48	2.6
I	7	25.9	(24.0-26.8)	± 0.69	3.5
Female					
V	8	30.0	(28.8-31.3)	± 0.61	2.8
IV	10	29.4	(28.5-30.3)	± 0.39	2.1
III	7	28.1	(27.3-28.9)	± 0.37	1.8
II	5	28.0	(27.2-28.6)	± 0.56	2.2
I	6	26.4	(25.6-27.1)	± 0.48	2.2
		Zygomatic breadth			
Male					
IV	7	17.1	(16.4-18.0)	± 0.50	3.9
V	5	17.0	(16.6-17.6)	± 0.33	2.2
III	8	16.0	(15.2-16.6)	± 0.34	3.0
II	6	15.6	(15.1-16.3)	± 0.42	3.3
I	5	14.2	(13.1-15.1)	± 0.65	5.1
Female					
V	7	17.0	(16.2-17.7)	± 0.42	3.3
IV	11	16.7	(15.8-17.8)	± 0.34	3.4
II	4	15.7	(15.3-16.1)	± 0.35	2.2
III	7	15.5	(15.0-16.2)	± 0.33	2.8
I	6	14.7	(13.4-15.5)	± 0.60	5.0

Table 1.—*Continued.*

			Interorbital constriction		
Male					
IV	9	5.6	(5.4-6.2)	± 0.18	4.9
V	5	5.6	(5.5-5.9)	± 0.15	3.1
III	10	5.5	(5.2-5.8)	± 0.11	3.2
II	10	5.3	(5.0-5.7)	± 0.13	3.9
I	9	5.2	(5.1-5.3)	± 0.05	1.4
Female					
V	8	5.6	(5.3-6.0)	± 0.19	4.9
IV	15	5.5	(5.3-5.9)	± 0.10	3.5
III	8	5.4	(5.0-5.9)	± 0.18	4.8
II	7	5.3	(5.1-5.4)	± 0.11	2.8
I	6	5.2	(5.1-5.3)	± 0.08	2.0
			Breadth of braincase		
Male					
IV	8	13.2	(12.8-13.6)	± 0.22	2.3
V	6	13.1	(12.8-13.4)	± 0.17	1.6
II	9	13.0	(12.3-13.7)	± 0.31	3.6
III	11	12.9	(12.5-13.3)	± 0.16	2.0
I	7	12.6	(12.3-12.9)	± 0.15	1.6
Female					
II	6	13.3	(13.0-13.3)	± 0.12	1.1
V	8	13.2	(12.8-13.6)	± 0.20	2.2
IV	14	13.2	(12.4-13.6)	± 0.20	2.9
III	7	13.1	(12.8-13.5)	± 0.18	1.9
I	5	12.7	(12.3-13.0)	± 0.29	2.5
			Rostral breadth		
Male					
V	6	5.7	(5.3-5.9)	± 0.19	4.1
IV	9	5.7	(5.3-6.0)	± 0.16	4.1
III	10	5.4	(5.1-5.6)	± 0.12	3.5
II	10	5.3	(5.1-5.9)	± 0.15	4.5
I	9	4.8	(4.4-5.1)	± 0.17	5.2
Female					
V	8	5.8	(5.2-6.4)	± 0.27	6.7
IV	14	5.7	(5.3-6.4)	± 0.16	5.2
III	7	5.2	(5.0-5.7)	± 0.19	4.8
II	7	5.2	(4.9-5.4)	± 0.13	3.3
I	7	5.0	(4.7-5.2)	± 0.14	3.6

Table 1.—*Continued.*

			Length of rostrum			
Male						
V	6	10.4	(9.7-11.0)	± 0.34	4.0	
IV	8	10.1	(9.8-10.7)	± 0.19	2.7	
III	11	9.7	(9.2-10.2)	± 0.17	3.0	
II	10	9.3	(8.5-10.1)	± 0.29	4.9	
I	8	8.5	(7.7-8.9)	± 0.27	4.5	
Female						
V	8	10.3	(9.6-10.7)	± 0.28	3.8	
IV	12	10.1	(9.4-10.7)	± 0.28	4.8	
III	7	9.6	(9.1-10.3)	± 0.33	4.6	
II	6	9.5	(9.0-9.9)	± 0.25	3.2	
I	7	8.6	(7.7-9.0)	± 0.32	5.0	
			Depth of cranium			
Male						
IV	6	11.2	(10.8-11.6)	± 0.26	2.8	
V	6	11.0	(10.5-11.6)	± 0.34	3.8	
III	11	10.9	(10.2-11.4)	± 0.21	3.2	
II	7	10.7	(10.2-11.2)	± 0.24	2.9	
I	7	10.2	(9.6-10.8)	± 0.31	4.1	
Female						
V	8	11.1	(10.2-11.5)	± 0.30	3.9	
IV	13	11.0	(10.5-11.5)	± 0.17	2.8	
II	6	10.9	(10.6-11.2)	± 0.25	2.8	
III	6	10.9	(10.7-11.0)	± 0.09	1.0	
I	5	10.4	(10.2-10.6)	± 0.15	1.6	
			Length of maxillary toothrow			
Male						
II	5	4.5	(4.4-4.6)	± 0.07	1.9	ns
V	3	4.4	(4.4)			
IV	9	4.4	(4.3-4.6)	± 0.06	2.1	
III	11	4.4	(4.1-4.7)	± 0.11	3.9	
I	6	4.4	(4.3-4.6)	± 0.09	2.5	
Female						
V	5	4.5	(4.3-4.7)	± 0.13	3.3	
IV	14	4.5	(4.2-4.7)	± 0.08	3.2	
III	6	4.4	(4.4-4.5)	± 0.04	1.2	
I	8	4.3	(4.1-4.5)	± 0.11	3.6	
II	4	4.2	(4.1-4.3)	± 0.10	2.3	

Table 1.—*Continued.*

		Length of incisive foramen			
Male					
V	6	5.2	(4.9-5.6)	± 0.20	4.7
IV	8	5.1	(4.8-5.4)	± 0.15	4.1
III	10	4.9	(4.7-5.1)	± 0.08	2.5
II	10	4.7	(4.4-5.0)	± 0.11	3.6
I	7	4.3	(3.9-4.6)	± 0.17	5.4
Female					
V	8	5.2	(4.6-6.3)	± 0.34	9.3
IV	16	5.0	(4.3-5.5)	± 0.15	6.1
III	8	4.6	(4.4-4.9)	± 0.11	3.2
II	7	4.6	(4.2-5.0)	± 0.22	6.3
I	8	4.4	(4.1-4.7)	± 0.15	4.9
		Length of palatal bridge			
Male					
V	6	4.4	(4.1-4.7)	± 0.18	4.9
II	10	4.4	(4.0-4.6)	± 0.11	3.9
IV	9	4.3	(4.0-4.6)	± 0.11	3.7
III	10	4.3	(3.7-4.7)	± 0.19	6.9
I	9	4.1	(3.8-4.2)	± 0.09	3.2
Female					
V	8	4.5	(4.1-4.7)	± 0.13	4.1
III	8	4.4	(4.3-4.7)	± 0.09	2.9
II	6	4.4	(4.2-4.6)	± 0.12	3.4
IV	16	4.4	(3.9-4.7)	± 0.11	5.3
I	8	4.1	(4.0-4.4)	± 0.09	3.1

head and body, length of tail, occipitonasal length, zygomatic breadth, interorbital breadth, and depth of cranium) and females the larger for two (length of ear and length of maxillary toothrow). In the other six measurements (length of hind foot, breadth of braincase, rostral breadth, length of rostrum, length of incisive foramen, and length of palatal bridge), the sexes had the same mean value. In all nonsignificant measurements in which one sex averaged larger than the other, the difference was small.

It is evident from the above analysis that there is little or no secondary sexual dimorphism between males and females in the San Antonio population of *Nyctomys sumichrasti.* Based on this finding, it would seem justifiable to combine values for the sexes in any analysis of geographic variation.

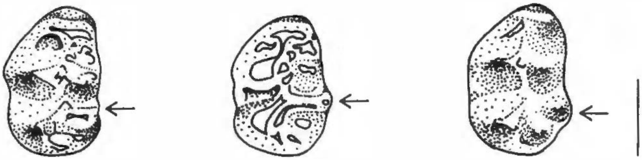

Fig. 3.—First upper left molars of three specimens of *Nyctomys sumichrasti* illustrating variation in development of the mesoloph and mesostyle in the population from San Antonio, Nicaragua. Arrows indicate the position of the mesoloph and mesostyle on each tooth. The specimens illustrated are, from poorly-developed mesoloph and mesostyle (left) to well-developed (right), KU 98056, KU 106662, and KU 106689. The scale at the right is one millimeter long.

Individual Variation

Coefficients of variation for dimensions of adult males and adult females are given in Table 2. Weight for both sexes has the highest coefficient of variation of the 16 measurements tested. Only three other measurements for males (length of head and body, length of tail, and length of ear) and three for females (rostral breadth, length of incisive foramen, and length of palatal bridge) have coefficients of variation of 5.0 or more. Coefficients generally agree with those given by Long (1968, 1969) for rodents of a similar size. Males had the higher coefficient of variation in nine measurements and females had the higher value in seven.

Most individuals of *Nyctomys sumichrasti* from San Antonio have a poorly developed mesoloph and, if present, a poorly developed mesostyle on Ml (see Hooper, 1957:9, for dental nomenclature). However, in a few individuals (KU 106687 and 106689, for example) the mesostyle is a large cusp at the outer edge of the tooth (Fig. 3). Other individuals (KU 98056 and 106662, for example) have a distinct mesostyle that is intermediate in size between the two extremes.

A subadult male (KU 98061) taken on 9 July 1964 had the rostrum deflected sharply to the right. This may have resulted from a congenital defect or an injury early in life, but there was no evidence that the bones in this area ever had been broken. Two individuals (KU 106667 and 115489) exhibited dental deterioration, possibly resulting from caries.

Seasonal Variation

We were unable to detect variation in color or other seasonal differences, except for active molt, among individuals collected in the dry season and those taken in the wet season. Fifteen specimens, all taken in the first 10 days of July, appear to have been molting from one adult pelage to another. Seven subadults that were molting were taken at the same

TABLE 2.—*Secondary sexual variation in six external and 10 cranial measurements of adult* Nyctomys sumichrasti *from San Antonio, Chinandega, Nicaragua. Means for males and females that are significantly different at the .05 level are indicated by an asterisk; those that are not significantly different are marked ns.*

Sex	N	Mean (range) ± 2 SE	CV	
		Total length		
Male	8	235.6 (225.0-246.0) ± 5.63	3.4	ns
Female	16	230.1 (219.0-242.0) ± 3.12	2.8	
		Length of head and body		
Male	15	118.3 (99.0-129.0) ± 4.22	6.9	ns
Female	24	117.8 (106.0-128.0) ± 2.00	4.2	
		Length of tail		
Male	8	114.9 (108.0-126.0) ± 4.67	5.7	ns
Female	16	113.1 (102.0-124.0) ± 2.54	4.5	
		Length of hind foot		
Male	15	22.2 (21.0-23.0) ± 0.49	4.2	ns
Female	24	22.2 (20.0-23.0) ± 0.32	3.5	
		Length of ear		
Male	15	16.8 (15.0-18.0) ± 0.45	5.1	ns
Female	24	17.0 (15.0-18.0) ± 0.30	4.3	
		Weight		
Male	15	48.5 (39.3-61.3) ± 3.11	12.4	*
Female	24	44.9 (38.2-53.9) ± 1.67	9.1	
		Occipitonasal length		
Male	14	29.8 (28.5-31.2) ± 0.44	2.8	ns
Female	18	29.7 (28.5-31.1) ± 0.37	2.6	
		Zygomatic breadth		
Male	12	17.1 (16.4-18.0) ± 0.31	3.1	ns
Female	18	16.8 (15.8-17.8) ± 0.27	3.4	

Table 2.—*Continued.*

			Interorbital constriction			
Male	14	5.6	(5.4-6.2)	± 0.13	4.2	ns
Female	23	5.5	(5.3-6.0)	± 0.09	4.0	
			Breadth of braincase			
Male	14	13.2	(12.8-13.6)	± 0.15	2.1	ns
Female	22	13.2	(12.4-13.6)	± 0.14	2.6	
			Rostral breadth			
Male	15	5.7	(5.3-6.0)	± 0.12	4.0	ns
Female	22	5.7	(5.2-6.4)	± 0.13	5.7	
			Length of rostrum			
Male	14	10.2	(9.7-11.0)	± 0.19	3.4	ns
Female	20	10.2	(9.4-10.7)	± 0.20	4.5	
			Depth of cranium			
Male	12	11.1	(10.5-11.6)	± 0.22	3.4	ns
Female	21	11.0	(10.2-11.5)	± 0.15	3.2	
			Length of maxillary toothrow			
Male	12	4.4	(4.3-4.6)	± 0.06	1.8	ns
Female	19	4.5	(4.2-4.7)	± 0.06	3.1	
			Length of incisive foramen			
Male	14	5.1	(4.8-5.6)	± 0.12	4.3	ns
Female	24	5.1	(4.3-6.3)	± 0.15	7.5	
			Length of palatal bridge			
Male	15	4.4	(4.0-4.7)	± 0.09	4.1	ns
Female	24	4.4	(3.9-4.7)	± 0.09	5.0	

time, and one subadult was in the process of molt on 10 March 1968 and another on 19 August 1967. Of nine individuals actively molting from juvenile pelage, eight were taken between 5 and 10 July and the other on 9 March.

Molt from juvenile pelage appears to follow a definite sequence. It begins ventrally and proceeds over the sides to meet middorsally. From the middorsal area, molt proceeds anteriorly and posteriorly; the head and rump molt last. No such pattern was observed in subadult or adult specimens, in which molt appeared to proceed irregularly over the dorsum.

ECOLOGICAL COMMENTS

Description of the Area

San Antonio lies in the Pacific lowlands of northwestern Nicaragua about 5 kilometers south-southwest of Chichigalpa and 15 kilometers southeast of Chinandega (Fig. 4). A series of isolated volcanos, dominated by Volcan Casita and Volcan San Cristobal, lie approximately 20 kilometers to the east and north of San Antonio, and the shore of the Pacific Ocean is about 15 kilometers to the west. Vegetation of this part of Nicaragua was termed "semi-evergreen forest" by Taylor (1963:33) and "lowland dry forest" by Stuart (1966:693). Essentially, this forest type is composed of 30 to 50 per cent deciduous trees of two stories, with the canopy being formed by the upper story. Unfortunately, most, if not all, of this original forest has been destroyed and mature secondary forest is uncommon (see Taylor, 1963:37). Most of this area now is highly agriculturalized, with sugar cane and cotton the primary crops. The soils in the vicinity of San Antonio are generally young soils of volcanic origin (Taylor, 1963:31; Stevens, 1964:308).

San Antonio can be classified as having a "tropical wet-and-dry climate" (Vivo Escoto, 1964:212), which is characterized by distinct wet and dry seasons. The dry season begins in late November and extends into May, with March and April the hottest months. Maximum rainfall usually occurs in September and October. Precipitation records from Chichigalpa, which receives more than 82 inches (2098 millimeters) of rain annually, are typical of this area. Following is the average monthly rainfall for Chichigalpa, in millimeters (after Taylor, 1963:30): January, 1; February, 1; March, 3; April, 25; May, 255; June, 343; July, 193; August, 273; September, 414; October, 499; November, 84; December, 7.

Habitat and Interspecific Relationships

The area in which vesper mice were taken at San Antonio was a riparian community along a tributary of the Rio Amalia between San Antonio and Chichigalpa. Vegetation along the stream was never more than 50 meters wide on either side and usually was much narrower. Extensive sugar cane fields were located beyond the riparian community. The lower story of

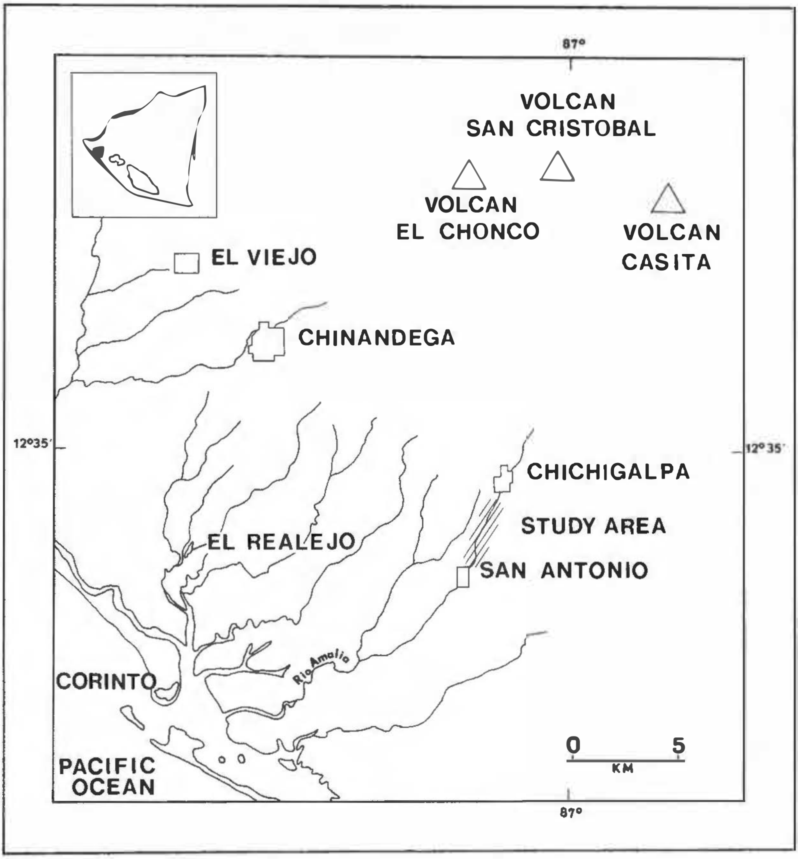

Fig. 4.—Map of northwestern Nicaragua showing the location of the study area. The insert map at the upper left indicates the position of enlarged area within Nicaragua.

vegetation was composed of dense second-growth shrubs and small trees, primarily *Cordia diversifolia* (family Boraginaceae) and two species of the family Ribiaceae, in which numerous woody vines were intwined. This lower story was nearly impenetrable except for a few paths that paralleled the stream. The upper story of vegetation was composed of figs (*Ficus*) and other tall tropical trees, many of which were more than 100 feet in height. The stream averaged eight to 10 feet wide in the rainy season, but was much narrower in the dry season.

Other small, nonvolant mammals taken in this area along with vesper mice were *Didelphis marsupialis*, *D. virginiana*, *Caluromys derbianus*, *Marmosa mexicana*, *Sciurus variegatoides*, *Liomys salvini*, *Oryzomys palustris*,

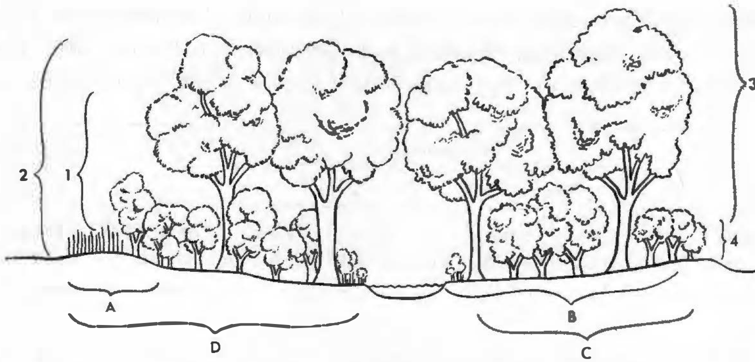

Fig. 5.—Schematic illustration of spatial distribution of 14 species of small, nonvolant mammals at San Antonio, Chinandega, Nicaragua. Approximate vertical distribution is shown to the left and right as follows: 1, *Nyctomys sumichrasti*; 2, *Didelphis marsupialis* and *D. virginiana*; 3, *Caluromys derbianus*, *Sciurus variegatoides*, and *Coendou mexicanus*; 4, *Marmosa mexicana*, *Reithrodontomys gracilis*, and *Ototylomys phyllotis*. Approximate horizontal distribution of terrestrial taxa is shown below: A, *Liomys salvini* and *Sigmodon hispidus*; B, *Oryzomys fulvescens* and *O. palustris*; C, *Reithrodontomys gracilis*, *Peromyscus mexicanus*, and *Ototylomys phyllotis*; D, *Didelphis marsupialis* and *D. virginiana*.

O. fulvescens, *Ototylomys phyllotis*, *Reithrodontomys gracilis*, *Peromyscus mexicanus*, *Sigmodon hispidus*, and *Coendou mexicanus*. Utilization of the third dimension (arboreal) of the habitat is the means by which at least 14 species of small mammals are able to coexist in this restricted area (Fig. 5). Individuals of *Nyctomys sumichrasti* usually were observed in the lower story of vegetation in the wet season, frequently at heights of 10 to 20 feet. During the dry season, however, many of these mice were observed much higher, especially in fig trees, where they appeared to be feeding. This species rarely comes to the ground as evidenced by poor trapping success in this unusual area of high population density. Few of the individuals trapped (usually at the bases of trees) or shot but a few feet above the ground were adults.

The woolly opossum (*Caluromys derbianus*), variegated squirrel (*Sciurus variegatoides*), and Mexican porcupine (*Coendou mexicanus*) are three other species that live almost exclusively in tall trees and seldom come to the ground. The two opossums (*Didelphis marsupialis* and *D. virginiana*) probably are the most ubiquitous species in the area, being found from high in the trees to along the edges of sugar cane fields. The few mouse opossums (*Marmosa mexicana*) observed or collected at San Antonio generally were found in lower vegetation (usually four to six feet above the ground) than were vesper mice, but none was seen on the ground. Climbing rats (*Ototylomys phyllotis*), which also were abundant

TABLE 3.—*Sex ratio and age structure of the population of* Nyctomys sumichrasti *at San Antonio, Chinandega, Nicaragua, in the wet seasons of 1966 and 1967. The age groups for the small sample taken in the dry season of 1968 are also shown.*

Age categories	Wet season					Dry season
	1964		1966			1968
	Male:Female	Total individuals	Male:Female	Total individuals	Grand total individuals	Total individuals
I	4:3	7	3:3	6	13	3
II	6:3	9	6:1	7	16	2
III	4:3	7	6:8	14	21	0
IV	3:3	6	2:11	13	19	3
V	0:2	2	6:6	12	14	0

in this area (see Lawlor, 1969), and slender harvest mice (*Reithrodontomys gracilis*) occurred on the lower branches and vines, generally below the stratum occupied by vesper mice. Both species have been observed on the ground. Lawlor (1969:37) noted that when climbing rats were pursued they moved laterally through the vegetation rather than upward.

The remaining five species evidently are terrestrial. The two rice rats (*Oryzomys palustris* and *O. fulvescens*) and the Mexican deer mouse (*Peromyscus mexicanus*) seemingly were restricted to riparian vegetation in this area and usually were found in mesic situations near the stream. Salvin's spiny pocket mice (*Liomys salvini*), and cotton rats (*Sigmodon hispidus*) were taken in the drier areas on the edge of the riparian vegetation; both were trapped also at the edge of sugar cane fields.

Sex Ratio and Age Structure

Because most animals in our sample were shot at night from arboreal vegetation, the bias introduced by trapping (Fisler, 1971) to analyses of sex ratio and age structure in populations should be reduced. Nevertheless, those individuals that had not yet left the nest are not represented in our sample, and those that were mostly active in relatively low vegetation might predominate in the sample; also, animals with a large home range might have a greater likelihood of being taken than those with a restricted home range.

Even with these possible biases in mind, the data presented below are the best estimates of population structure in *N. sumichrasti* available at this time. Sex ratios for the various age categories of specimens taken in 1964 and 1966 are shown in Table 3. Because collecting was conducted at nearly the same time (wet season) in these two years (6-13 July 1964 and 5-10 July 1966), data from each were combined for statistical testing. In age categories II and IV, there was a significant deviation at the .05 level (but not the .01 level) from the expected 1:1 ratio of sexes using Chi-square. In age category II, males outnumbered females 12 to four and in category IV males were outnumbered five to 14. The latter difference might be explained as differential survival between males and females, but this difference was not reflected in the oldest age class (V) in which males were outnumbered only six to eight by females. When the sex ratio is compared without regard to age category, the ratio of 40 males to 43 females does not differ significantly from a 1:1 ratio.

As can be seen in Table 3, more individuals representing age groups III and IV were taken in 1964 and 1966 (data combined) than were mice of the other three age categories. However, when these differences were tested (Chi-square) they were found not to differ significantly from the hypothesis that all age categories are equally represented in the population. We suppose that two factors could combine to form a population in which all age categories are equally represented. First, the species reproduces throughout the year (as our data combined with those of Fleming, 1970, indicate for *Nyctomys*), and second, that the population is relatively free of predatory pressure so that once an individual leaves the nest there is a reasonable likelihood that it will live to reach the oldest age category. Vesper mice at San Antonio probably are preyed upon only by nocturnal raptors; predation, however, is mitigated by the heavy vegetation in which these mice live. Our sample from the dry season, on the other hand, although small, does favor younger animals. This may result from sampling bias, however, because during this season many vesper mice were observed high in trees from which they could not be collected.

Food Habits

The food of *Nyctomys* consists primarily of seeds, fruits, and other vegetative matter. During the wet season at San Antonio, numerous individuals were observed feeding on fruits of the borage, *Cordia diversifolia,* and madders (Rubiaceae). In the dry season, most individuals that we observed appeared to be taking wild figs (*Ficus*). One juvenile was shot as it fed near the ground on the flower of a composite, a plant abundant along the edge of the riparian community. In Guatemala, *Nyctomys* has been recorded as eating avocados and wild figs (Goodwin, 1934:51).

Reproduction

Of the 22 adult (age categories IV-V) and 11 subadult (III) females taken at San Antonio in the first two weeks of July, only one was pregnant and one was lactating. The pregnant female contained a single embryo in the left uterine horn that measured 6 in crown-rump length on 10 July. The lactating female was obtained on 6 July. One of three females taken on 19 August carried four embryos (two in each horn) that measured 2 in crown-rump length; another possessed an enlarged uterus, but no embryos were visible in gross examination. The only adult female obtained on 10 March evinced a placental scar in each uterine horn.

Nine adult males taken between 5 and 9 July had testes that averaged 12.2 (11-15) in length. Two males taken on 10 March and individuals obtained on 7 August and 18 August all had testes that measured 12; two males collected on 19 August had testes 14 and 15 long. We have juveniles that were obtained on the following dates: 9 March (two) and 10 March; 5 July (two), 6 July (four), 7 July, 8 July, 9 July, and 10 July (three).

Elsewhere in the geographic range of *Nyctomys*, several females taken in Colima in August and early September were reported (Walker *et al.*, 1968:772) as carrying two to four well-developed embryos. In Veracruz, Hall and Dalquest (1963:295-296) obtained five adult females with small young clinging to their teats in the last week of March and first weeks of April. Fleming (1970:481), in Panama, obtained pregnant females on 5 February and 2 June and lactating females on 4 and 5 March. He also reported finding two subadults with perforate vaginas and a third with two small embryos, but no dates of capture were given. Birkenholz and Wirtz (1965:183) raised vesper mice in the laboratory and found the average number of young born in seven litters was two, with a range of one (two litters) to three (two litters). One female gave birth to five litters during a seven-month period, with two litters being born 38 days apart.

These data clearly indicate that vesper mice reproduce during both the wet and dry seasons and probably are capable of reproduction the year around. Litter size evidently varies from one to four, with two probably being the mode.

Ectoparasites

The commonest ectoparasite of *Nyctomys sumichrasti* at San Antonio was the laelapid mite, *Androlaelaps fahrenholzi* (=*Haemolaelaps glasgowi*), which was found on 36 of the 85 specimens taken in 1964 and 1966. Other taxa of laelapids found were a new species of *Androlaelaps* (on 10 specimens) and *Eubrachylaelaps circularis* (on one specimen). A trombiculid, *Fonsecia* (*Parasecia*) *longicalcar*, was found on three specimens and *Speleocola secunda* was taken from a single specimen. A tick, *Ornithoderas talaje*, was recorded from three animals and an unidentified species of the genus *Ornithoderas* from another individual.

Elsewhere in Nicaragua, the mites *Eutrombicula alfreddugesi* and *Listrophorus* (new species) were found on specimens collected at Santa Rosa in Departamento de Boaco. *Microtrombicula mesoamericana* (Webb and Loomis, 1971:326) was found on specimens taken at Hacienda Bellavista, Chinandega, and near Diriamba, Carazo. The only other records of ectoparasites from *Nyctomys* are reports of the laelapid mite, *Androlaelaps fahrenholzi* (Tipton *et al.*, 1966:34) and the flea, *Pleochaestis dolens dolens* (Tipton and Mendez, 1966:311), from Panama.

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Statistical analyses were performed on the GE-635 computer at The University of Kansas. Ectoparasites were identified by Russell W. Strandtmann (Laelapidae), Richard B. Loomis (Trombiculidae), Eleanor K. Jones and Glen M. Kohls (Argasidae), and Burruss McDaniel (Listrophoridae). Mr. Thomas Swearingen prepared the drawings of teeth and crania and Miss Patricia Allgood made the finished version of Fig. 5.

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