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AGE STRUCTURE AND SEX RATIO IN POPULATIONS OF *REITHRODONTOMYS*

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ABSTRACT.—Age structure of populations of *Reithrodontomys megalotis longicaudus*, *Reithrodontomys raviventris raviventris*, and *Reithrodontomys raviventris halicoetes* was investigated through analysis of skulls aged by tooth wear. Age structure is similar among the three taxa. Age classes are not clearly delimited. There is no mass die-off of older adults during a specific period of the year. A long breeding period provides for recruitment into the population over an extended period of time. Sex ratios greatly favor males except in the youngest and oldest of the six age classes recognized. Selection for more males may be advantageous in small mammal populations with organizational types such as are found in these *Reithrodontomys*.

Sex ratios, age structure, and population turnover of small mammals are continuing areas of interest among ecologists and mammalogists alike. Recent studies such as those of Breakey (1963), Sheppe (1963), Terman and Sassaman (1967), and Dapson (1968) have presented considerable data, some based on tooth wear as an aging criterion; other than Brant (1962), however, little has been published in regard to these problems in the genus *Reithrodontomys*. In a study of ecology, behavior, and speciation of the *Reithrodontomys* of the San Francisco Bay region (Fisler, 1965), large samples of *Reithrodontomys megalotis longicaudus*, *Reithrodontomys raviventris raviventris*, and *Reithrodontomys raviventris halicoetes* were classified into six age categories by using tooth wear criteria. The information gained concerning age structure and sex ratio of these populations never has been reported and seems worthy of discussion.

MATERIALS AND METHODS

Estimation of age was accomplished by dividing specimens into six categories based on wear on molar teeth (see Fisler, 1965, for details). Most of the specimens used were collected in kill-trap lines set in a salt marsh (San Pablo) near Richmond, a brackish marsh 2 mi. E Martinez, Contra Costa Co., California, and in a grassland area of Strawberry Canyon, Berkeley, Alameda Co., California. Trapping was conducted from September 1958 through August 1960. There was no evident cyclical fluctuation of population size (other than seasonal) in these areas. Collections made by the author were supple-

TABLE 1.—*Relative age class and actual age for* Reithrodontomys raviventris halicoetes.

Class	Actual age in trappable population
1	2–3 months
2	3–4½ months
3	4½–6 months
4	6–8 months
5	7½–12 months
6	12–31* months

* Oldest known age (attained in laboratory).

mented through use of specimens taken in earlier years by other collectors. Specimens analyzed include 541 *R. m. longicaudus,* 351 *R. r. raviventris,* and 450 *R. r. halicoetes,* a total of 1342 specimens. About 75 per cent were collected by the author. Preliminary analysis did not reveal any notable differences in age distribution between samples from different years. Also, no differences were detectable between samples from marsh (184 specimens) and upland (357 specimens) populations of *R. megalotis.* Therefore, all data were combined and treated on a monthly basis as if from a single year. Also, for simplicity these taxa will be designated as *megalotis, raviventris,* and *halicoetes* hereafter.

Equation of the relative age classes with actual age is possible. I have measured growth rates in both *megalotis* and *halicoetes* (unpublished) which, combined with field trapping data, reveal that these mice reach the trappable population at the age of about 2 months. Data from Brant (1962) also show the same. Skulls analyzed in my earlier study (Fisler, 1965) were all from wild-trapped individuals, and the relative age classification was originally based only on wild-taken specimens. Therefore, age classes begin with the youngest trappable individuals, that is, those aged 2 months. Also, I have taken known-age animals from the field, as well as having preserved skulls of animals born in the laboratory, so that some idea of actual age within each class based on tooth wear can be obtained. The basic 40 specimens all were *halicoetes,* but they have been augmented and substantiated with specimens of *megalotis* (field and laboratory) and *raviventris* (field), so that I am confident that, although actual age is based primarily on specimens of *halicoetes* it also applies to the other two taxa. Teeth of animals kept in captivity on a diet essentially of rat chow did not wear as rapidly as did those of field-caught, individuals of known age, nor did they wear as evenly. However, having raised laboratory animals on "natural" diets as controls, and having many field-collected skulls of known age, I feel that actual age is correct in the main. From Table 1, it can be seen that age classes 2 and 3 are 1½ months long, 4 is 2 months long, and 5 is 4½ months in duration. However, some older specimens remained in the latter class as differences in tooth wear became less distinct as the ridges and cusps disappeared.

RESULTS AND DISCUSSION

Sex Ratio

Table 2 presents data on the sex ratio by age class for each taxon and the composite sex ratio for all specimens used in this study. In all, more males than females were trapped ($P < 0.01$) except in age classes 1 and 6. The sex ratio was essentially 1:1 for known complete litters for 95 *halicoetes* born in the laboratory (chi-square from 1:1 with 1 *df* is 0.29); *megalotis* (61 specimens) and *raviventris* (23 specimens) had similar ratios. Layne (1959) found

TABLE 2.—*Sex ratio by age class for three forms of* Reithrodontomys. *Number of specimens in parentheses.*

Age class	Sex ratio (males:females)		
	megalotis	*raviventris*	*halicoetes*
1	1.26:1 (79)	0.56:1 (25)	1.00:1 (36)
2	1.88:1 (170)	1.61:1 (60)	1.72:1 (182)
3	1.54:1 (173)	1.98:1 (119)	1.16:1 (93)
4	2.82:1 (42)	1.38:1 (62)	1.03:1 (63)
5	2.00:1 (75)	1.34:1 (75)	2.33:1 (70)
6	1.00:1 (2)	0.25:1 (10)	0.50:1 (6)
Composite	1.72:1 (541)	1.42:1 (351)	1.45:1 (450)
χ^2 from 1:1	37.80	10.60	14.94
Per cent males	63.2	58.7	59.1

an even sex ratio in 20 young of *R. humulis*, whereas Kaye (1961) recorded a sex ratio favoring males 2:1 for 27 young of *humulis*. The sex ratios in age classes 2 through 5 in my study greatly favored males (classes 1 through 5 for *megalotis*). Perhaps these data indicate a higher death rate for females in age class 1 for *raviventris* and *halicoetes*, or may reflect the results of wandering in both sexes prior to establishment of a home area by these prebreeding individuals. Also, sex ratios from older age classes could illustrate the slightly greater range of males (*megalotis*—Brant, 1962) or possible greater activity of males, both factors increasing their susceptibility to trapping. Recent laboratory experiments on total activity time per day showed that males and females exhibited about the same amount of activity, although total distances traveled were not investigated (Fisler, unpublished). I am inclined to believe that the actual sex ratio for all age classes combined does favor males and is not merely an artifact of trapping, partly because the data of Brant (1962) indicated only slightly larger range size in males and partly because my records for nest box occupation by *megalotis* and *raviventris* indicated a greater number of males in both breeding and nonbreeding seasons.

As further evidence, I compiled sex ratios for each of the three taxa for the 4 months of highest incidence of pregnancy and the 4 months of lowest pregnancy rate (Table 3). Males greatly outnumber females in both sets of data, but there is also a great increase in the relative number of males in the months of highest pregnancy. This would at first seem to indicate an increase in males solely as a trapping artifact, the usual reason given. Possible causes of this difference can be summarized as follows: 1) males are more active (not true as far as total active time is concerned); 2) males travel more widely during breeding season and therefore are more active as far as distance covered is concerned (not likely—see Brant's data on movement patterns for

TABLE 3.—*Sex ratios in the 4 months with highest and 4 months with lowest pregnancy rate (males:females).*

Taxon	Highest 4 months	Lowest 4 months
megalotis	2.27:1	1.33:1
raviventris	1.80:1	1.29:1
halicoetes	1.76:1	1.38:1

all times of the year and I found no difference in activity of males at any reproductive stage); 3) female activity is greater at estrus, but much depressed by ensuing pregnancy and females therefore move less and for shorter distances. Of these choices, the third would seem to be the most likely explanation for the apparent increase in number of males, but no evidence exists showing lessened activity of pregnant females. This point needs further investigation, as data on activity of pregnant and lactating females are lacking. Indeed, these females still must feed, probably more so than nonpregnant or nonlactating individuals. As there is no evidence of food storage by species of *Reithrodontomys*, pregnant females still must travel and maintain activity. Furthermore, they do not defend large areas that could be considered food territories; actually defense seems to be limited to the nest itself (nidic territory—Fisler, 1969) or there is no defense at all. Even assuming depressed female activity during pregnancy and lactation, a greater number of males was trapped at a time when female activity should have been at its greatest (lowest 4 months of pregnancy, see Table 3). It is difficult to explain this preponderance of males in any other way than through an actual numerical superiority. The composite sex ratio (Table 2) appears to be a true ratio, not an artifact of trapping, and is therefore a population characteristic. It should be pointed out that the composite sex ratios for *raviventris* and *halicoetes* are essentially equal, whereas that for *megalotis* shows relatively more males (Table 2) than do the ratios for the other two.

The purpose of computing sex ratios for each taxon by age class was to determine if there was a change in ratio with age because of differential mortality between the sexes. With the exceptions of age classes 3 and 4 for *halicoetes*, the change in sex ratio by age class is similar for all three. This indicates a nearly even ratio in age class 1 (the class recruiting into the trappable population), an excess of males in age classes 2 through 5, and fewer males than females in age class 6 (uncertain for *megalotis* because of few data). This might indicate an initially high female death rate (as discussed earlier), then a fairly constant rate until age class 6. The male death rate, on the other hand, would be comparatively low initially. This conclusion for males is correct even if males and females have different trap susceptibilities. There is currently no evidence for a different trap susceptibility with age. Recent work by Terman and Sassaman (1967) has shown a greater number of male *Peromyscus* at birth. Although my data indicate a

TABLE 4.—*Theoretical number entering each age class (per thousand) per year (sexes combined).*

Age class	*megalotis*	*raviventris*	*halicoetes*
1	1000	1000	1000
2	854	929	920
3	540	758	516
4	220	419	309
5	142	242	169
6	4	28	13

large number of males, this seems more a differential death rate after birth than a large secondary sex ratio aberration (from 1:1) as suggested by Terman and Sassaman for *Peromyscus maniculatus.* Perhaps a statistical difference from 1:1 could be shown for *Reithrodontomys* as well with a larger sample size (comparable to the magnitude of the Terman and Sassaman sample), but even so the magnitude of the difference in sex balance in adult harvest mice is such that any slightly higher male birth rate is changed still more drastically by differential death rates between sexes and among age classes.

Table 4, a survivorship curve (l_x) based on the population age structure and calculated by multiplying the number in each age class by $\dfrac{1000}{l_{0-1}}$ (see Deevey, 1947), shows that there is a greater number of aged mice in the *raviventris* population. Also, in light of earlier comments on death rates of females in age class 1, it should be noted that mortality rates for males as opposed to females of age class 1 are as follows: *megalotis* 13 to 18 per cent, *raviventris* 4.4 to 11 per cent and *halicoetes* 7 to 10 per cent. Otherwise, both sexes of *megalotis* follow the composite essentially as in Table 4, whereas relatively more *raviventris* females reach age classes 4, 5, and 6, and relatively more females reach age class 6 for *halicoetes.* Females of the species *raviventris* are long-lived animals. It is uncertain as to why more *raviventris* reach older ages. The protection afforded *raviventris* in its salt marsh habitat may be greater than the protection afforded *halicoetes* in brackish marshes and it is certainly greater than the protection *megalotis* derives from its grassland habitat (Fisler, 1965). Furthermore, the effect upon aging of the occurrence of daily torpidity in some *raviventris* but not in the other two kinds (Fisler, 1965) is not known, nor has the occurrence of torpidity in different age groups been investigated. Possibly this torpidity allows more *raviventris* to attain greater age.

If the sex ratios as described here are true ratios, and adult males do outnumber adult females by an impressive margin, why do more males survive initially than do females? It is usual to assume that fewer males than females are necessary because a few males can inseminate many females, and therefore it is bio-energetically more efficient for males to be expendable,

TABLE 5.—*Monthly percentage within each age class and monthly average age.*

Age class	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
megalotis												
1	32.0	10.6				15.2	28.8	5.6	12.2	19.1	26.0	5.7
2	26.0	24.7	17.3	27.0	20.0	18.2	23.3	50.0	56.8	38.3	44.4	37.1
3	36.0	47.1	48.1	37.8	20.0	30.3	11.0	27.8	17.6	36.2	18.5	45.7
4	4.0	8.2	15.4	21.6	60.0	6.1	8.2	5.6	2.7	2.1	11.1	
5	2.0	9.4	17.3	13.5		30.3	27.4	11.1	10.8	4.3		11.4
6			1.9				1.4					
Mean age	2.18	2.81	3.39	3.22	4.40	3.18	2.86	2.72	2.43	2.39	2.15	2.74
Number	50	85	52	37	10	33	73	18	74	47	27	35
raviventris												
1	20.0		8.4		5.0	10.6	3.7	6.2		2.5		29.6
2	32.0	30.6	8.3	10.9	5.0	15.8	3.7			25.0		25.9
3	44.0	42.8	50.0	37.5	40.0	21.1	40.7	31.2		30.0		11.1
4		6.1	20.9	21.9	35.0	24.6	18.5	12.4		17.5	50.0	14.8
5	4.0	20.4	12.5	26.6	15.0	26.3	33.3	37.5		15.0	50.0	18.5
6				3.1		1.8		12.4		10.0		
Mean age	2.36	3.16	3.21	3.73	3.50	3.46	3.74	4.13	0	3.48	5.00	2.67
Number	25	49	24	64	20	57	27	16	0	40	2	27
halicoetes												
1	8.4	9.2	3.1	7.7			11.5	2.0		11.8	13.0	15.9
2	70.9	67.4	18.7	23.1	15.4	15.4	3.8	13.7	33.3	51.0	52.1	34.0
3	20.9	19.1	31.3	23.1	53.9	38.4	15.4	13.7		25.5	34.8	22.7
4		1.4	18.7	38.5	26.9	38.5	3.8	45.1	66.7	5.8		9.0
5		2.8	25.0	30.8	3.8	7.7	57.7	23.6		5.9		18.2
6			3.1				7.7	2.0				
Mean age	2.13	2.21	3.53	3.92	4.19	4.38	4.15	3.80	4.00	2.43	2.22	2.80
Number	24	141	32	13	26	13	26	51	6	51	23	44

whereas females are at a premium because they bear the young. However, for a small, secretive mammal, there may be a selective advantage in having many reproductively active males moving about to assure insemination of any females that come into estrus, rather than assuming that one male may contact several females. More male *Reithrodontomys* are sexually active for longer periods of the year than are females; thus the few females that reach estrus at less favorable times of the year may be inseminated. The organizational system of these mice has been presented previously (Fisler, 1965, 1969), and the types involved, hierarchical spatial territory for breeding males of *megalotis*, shifting nidic for females in breeding condition, and individual undefended home ranges for breeding and nonbreeding *raviventris*, would indicate that excess males are advantageous in assuring insemination through more frequent contact of male and female.

Age Composition

Table 5 presents the age class composition by per cent for each taxon during each month of the year. There is a general trend for average age of the trappable population to increase from December and January to an older age in May, June, and July. This latter time period corresponds to the time of least recruitment. After midsummer, average age declines as more young are recruited into the trappable population. It would appear that *R. megalotis* and *R. raviventris* live to a maximum age of about 10 months in the wild (after reaching trappable age). The oldest animals in the wild for which I have minimum total age records are 18 months for *megalotis* and 13 months for *raviventris* (no records for *halicoetes*). Few individuals attain these ages; most probably survive less than 6 months after reaching trappable age.

The clearest trends of age change are found for *megalotis* and *halicoetes*. In these, the oldest average ages and the least recruitment periods occur in the same months. For *raviventris*, the older age classes are predominant in the same months as *megalotis* and *halicoetes*, but recruitment occurs more evenly (Table 5). Also, the oldest average age occurs 2 months later in the year for *raviventris*.

The number of individuals entering each age class is given in Table 4. Many individuals die in age classes 2 through 5. There is more or less steady loss of animals after age class 1 (even allowing for aging of living individuals) until age class 6 is reached. No well-defined chronological age classes occur because of the long reproductive period and relatively few mice reach the oldest age class at any one time of year. Therefore, no mass die-off of old adults in a postreproductive or nonreproductive part of the yearly cycle (roughly January to March or April) occurs, but rather deaths occur at about the same rate throughout the year and a mass die-off of older adults at one time seems to occur only because there are relatively more adults in the population in months of least recruitment. Deaths in all age classes occur through the year so that actual population turnover occurs as a gradual

TABLE 6.—*Reproductive and recruitment rates.*

	Per cent of yearly pregnancies within bimonthly periods					
	N–D	J–F	M–A	M–J	J–A	S–O
megalotis	12	3	16	15	37	17
raviventris	3	0	48	31	12	6
halicoetes	36	10	0	10	27	17
	Per cent of yearly recruitment within each bimonthly period					
	J–F	M–A	M–J	J–A	S–O	N–D
megalotis	31	0	6	28	24	11
raviventris	20	8	28	8	4*	32
halicoetes	42	3	0	11	17*	27

* No September data.

process, primarily because the breeding period is long and recruitment into the population occurs in most months of the year. Mass postbreeding die-offs have been refuted for shrews (*Blarina brevicauda*) by Pearson (1945) and Dapson (1968). Probably mass postbreeding die-offs occur only in areas where the weather varies quite drastically over the year so that reproduction is restricted to a short, favorable period and age classes become sharply defined. In less severe situations of weather where reproduction may extend over much of the year, age classes become obscure, indeed, may not exist as identifiable entities, and population turnover is gradual rather than abrupt.

Reproduction

The timing of births in the population seems to depend on the cycle of the female, as reproductively active males have been found in all months of the year for all three taxa, except for November and January for *raviventris* where no data are available (Fisler, 1965). Breakey (1963) reached the same conclusion for *Mus musculus* in the San Francisco Bay region. Table 6 compares the reproductive rate in percentage of females pregnant or lactating (excluding those too young to breed—data from Fisler, 1965) with the total yearly recruitment of age class 1 into the population divided into bimonthly periods by per cent. In order to show the nature of the correlation correctly, the data for the reproductive rate have been shifted 2 months before the recruitment data for age class 1, because 2 months is the earliest actual age for age class 1. When this is done, a close correspondence between the time of birth and the time of recruitment is obtained for *halicoetes*, but the fit is less impressive although still recognizable for *megalotis* and *raviventris*. Rank correlation for the monthly data shifted 2 months shows significance for *halicoetes* ($P = 0.05$) but not for *megalotis* ($P = 0.19$) or *raviventris* ($P = 0.15$), although the latter two figures are small enough to be suggestive. Recruitment rates and pregnancy rates are similar within each form.

CONCLUSIONS

1.   The age structure of populations of *Reithrodontomys megalotis longicaudus, Reithrodontomys raviventris raviventris,* and *Reithrodontomys raviventris halicoetes* is similar throughout the year. A yearly cycle of age classes is not well-defined and is even less distinct for *R. r. raviventris* because of slightly greater ages reached by individuals of this taxon.

2. The sex ratio greatly favors males at ages other than the youngest (1:1) and oldest (females predominant). This disparity of the sex ratio (from 1:1) is at least partly real rather than merely an artifact of trapping and differential activity patterns.

3.   A selective advantage for a sex ratio greatly favoring males may occur in populations of small mammals with organizational types such as those of *Reithrodontomys.*

4.   Laboratory and field data indicate that there is an essentially complete yearly turnover of individuals in the population with a few mice reaching the age of 12 months. The turnover occurs gradually through the year and there is no mass die-off of old individuals at any time but rather a gradual attrition. Mass die-offs of older age classes should be expected only for populations in which the breeding periods are restricted to a limited time and thereby clear-cut age classes can be formed.

5.   Recruitment of 2-month-old individuals into the trappable population occurs in most months, except spring, with some variation among the three taxa.

6.   Correspondence between recruitment and reproduction (shifted 2 months prior to recruitment into the trappable population) occurs strongly for *R. r. halicoetes,* but less so (although still evident) for *R. megalotis* and *R. r. raviventris.*

LITERATURE CITED

BRANT, D. H.   1962.   Measures of the movements and population densities of small rodents. Univ. California Publ. Zool., 62:105–184.

BREAKEY, D. R.   1963.   The breeding season and age structure of feral house mouse populations near San Francisco Bay, California. J. Mamm., 44:153–168.

DAPSON, R. W.   1968.   Reproduction and age structure in a population of short-tailed shrews, *Blarina brevicauda.* J. Mamm., 49:205–214.

DEEVEY, E. S., JR.   1947.   Life tables for natural populations of animals. Quart. Rev. Biol., 22:283–314.

FISLER, G. F.   1965.   Adaptations and speciation in harvest mice of the marshes of San Francisco Bay. Univ. California Publ. Zool., 77:1–108.

————.   1969.   Mammalian organizational systems. Contrib. Sci., Los Angeles Co. Mus., 167:1–32.

KAYE, S. V.   1961.   Laboratory life history of the eastern harvest mouse. Amer. Midland Nat., 66:439–451.

LAYNE, J. N.   1959.   Growth and development of the eastern harvest mouse, *Reithrodontomys humulis.* Bull. Florida State Mus., Biol. Sci., 4:61–82.

PEARSON, O. P.   1945.   Longevity of the short-tailed shrew. Amer. Midland Nat., 34: 531–546.
SHEPPE, W.   1963.   Population structure of the deer mouse, *Peromyscus*, in the Pacific Northwest. J. Mamm., 44:180–185.
TERMAN, C. R., AND J. F. SASSAMAN.   1967.   Sex ratio in deer mouse populations. J. Mamm., 48:589–597.

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