# AGE STRUCTURE OF SIX POPULATIONS OF
# OLD-FIELD MICE, *PEROMYSCUS POLIONOTUS*

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Despite a wealth of data on *Peromyscus*, little is known concerning mortality and age structures of natural populations of this genus (Terman, 1968). Unfortunately, much of this information cannot be obtained with present insensitive techniques. Furthermore, the time and effort required for long-range population studies are often impractical at least, and sometimes are prohibitive. As Terman (1968) has pointed out, new methods are urgently needed.

Most demographic data are analyzed in one of two basic ways. In a "horizontal" study, where a cohort is followed from birth, survivorship and mortality rate are determined. Age composition of the entire population at one time usually is not known if more than one cohort is present. In a "vertical" study, the population is sampled at one time and the ages of individuals are determined. This approach reveals an instantaneous picture of population age structure, but mortality rate and survivorship usually cannot be determined except for species with a single, restricted breeding season each year. Both types of studies are valuable, but neither has been employed extensively with most small mammals, probably because of practical limitations. For "horizontal" studies, known-age individuals must be recaptured over a lengthy period of time. Losses of marked animals due to emigration and mortality are inseparable. For "vertical" samples, an accurate method for determining age is required, but until now has been unavailable for small mammals. Finally, if either of these obstacles is overcome, mathematical procedures are needed to make valid quantitative comparisons between populations.

The present study is based on the "vertical" approach. A refined age-estimating technique, with known accuracy, and a new mathematical procedure permit a detailed, comparative examination of age in natural populations of small mammals.

## MATERIALS

Six populations of old-field mice, *Peromyscus polionotus*, were sampled between July 8 and July 25, 1969, at the following localities in southeastern United States: south-central South Carolina; central Georgia; along the Florida-Georgia border, 90-100 miles inland from the Atlantic coast; central Florida (Ocala); south-central Florida (Archbold); and southern Florida on the eastern coast (Vero Beach). The condition of each habitat and densities of the populations were estimated subjectively. Consequently, three distinct habitats were recognized: optimal inland (South Carolina,

Georgia, Ocala and Archbold), marginal inland (Florida-Georgia), and optimal beach (Vero Beach).

Mice from the five inland populations were dug from their burrows, and provided samples unbiased in regard to age (SMITH, 1968). Loose sand at Vero Beach prevented digging, and mice were live-trapped in two nights. Trapped mice showed no evidence of reproductive activity, and this sample is assumed to be representative of the population.

A total of 228 mice were used for this study: 49 from South Carorina 34 from Georgia, 39 from Florida-Georgia, 30 from Ocala, 50 from Archbold, and 26 from Vero Beach. Sexes were approximately equally represented.

## METHODS OF DETERMINING AGE

Age estimations of subadult and juvenile mice were based on pelage characteristics (GOLLEY *et al.*, 1966). Adult ages were determined by the biochemical lens method described by DAPSON *et al.* (1968) and DAPSON and IRLAND (in press). Details will not be given here. Briefly, the amount of insoluble protein in wild mouse lenses was determined and compared with known-age standards. Confidence limits about numerous ages estimated by this technique were given by DAPSON and IRLAND (in press) for this species. Age estimation is more accurate with this technique than with any other for which suitable confidence limits have been determined.

## METHODS FOR COMPARING AGE STRUCTURES

Age structure data were analyzed with ecological longevity curves, described in detail elsewhere (DAPSON, 1971). Several mathematical refinements have been made in the method, however, necessitating a review at the present time.

In a sample, each individual occurs with a frequency of 1 and a relative frequency of $1/N$. Individuals are ranked chronologically, and their relative frequencies of occurrence are accumulated from oldest to youngest. These relative cumulative frequencies (RCF) are plotted against age, the data is transformed to produce a rectilinear relationship, and the best fitting line through these values is calculated.

The first step in any regression analysis is the determination of the dependent variable. Customarily, age is regarded as the independent variable. On biological grounds, this choice is usually sound. In the current problem, however, certain theoretical conditions inherent in regression analysis must be considered. These conditions stipulate: (a) values of the independent variable can be fixed in advance (nonrandom) or sampled randomly, but (b) the dependent variable must be randomly sampled; (c) at each value of the independent variable, deviations in the dependent variable must be independent of one another and (d) be normally distributed; (e) these deviations must have equal variance with deviations about other values of the independent variable (STEEL and TORRIE, 1969; McCARTHY, 1957).

Populations were sampled randomly in regard to age. RCF, on the other hand,

is not random, because successive values of RCF are dependent upon previous values. Age, then, should be the dependent variable.

When several animals of the same age are sampled, corresponding RCF values are not independent of one another and are not normally distributed. Thus, age again should be considered the dependent variable. On the other hand, at any value of RCF there is only one value of age, and conditions (c), (d), and (e) cannot be applied directly. However, if all deviations from the line are transformed and graphed, they appear normally distributed. Also with these transformations, variances of the deviations in RCF along different segments of the line show no significant differences with the F test ($p$=0.05). Thus, theoretical stipulations dictate the use of age as a dependent variable. This is not without biological meaning. As shown by Dapson (1971), age (longevity) is dependent on RCF when the latter represents probability of survival.

Although age is considered the dependent variable, it will be graphed on the $X$-axis for ease in graphic interpretation. Consequently, the equation of $X$ on $Y$ is determined (see Dapson, 1971, for formulae used). In all cases studied thus far, the relationship between age and RCF is curvilinear. Several transformations, involving either or both variables, will result in nearly rectilinear association. However, only transformations of age alone will produce deviations in RCF that have normal distributions and equal variances.

The correlation coefficient ($r$) is usually used as a measure of "goodness of fit" in evaluating the effects of various transformations. However, $r$ is not applicable here because the relationship of $Y$ on $X$ cannot be estimated without bias (Simpson et al., 1960). Fortunately, it is not needed. We wish to determine the "best" transformation; that is, the one that produces a minimum of variation about the line. The variance of the estimate of $X$ on $Y$ ($S^2_{xy}$) measures the amount of variability in $X$ that is not due to the regression on $Y$ (see Eisenhart, 1939). Thus the variance of the estimate divided by total variance in $X$ ($S^2_{xy}/S^2_x$) is the percent variability in $X$ not due to regression. This term should be minimal, and is the basis for selecting the best transformation. In practice, a computer program selects the best transformation of age out of 10 possible transformations, and produces a complete analysis of that data.

## Interpretation of Ecological Longevity Curves

When a population is sampled over an extended period of time and different birth cohorts are followed independently, probability of occurrence (RCF) represents probability of survival. If RCF=0.5, the corresponding age is the median ecological longevity (MEL). Half the population dies before MEL, half survive beyond MEL. Similarly, that age at which the probability of survival or occurrence is nil is the maximum ecological longevity (MAX). MAX is the greatest age attainable under prevailing ecological conditions. Confidence limits for MEL and MAX can be determined (see Dapson, 1971, for formulae).

In the present study, only one sample was taken from each population, and many

cohorts are represented. The initial sizes of these cohorts are undeterminable, and their fates from birth to sampling are unknown. Consequently, ecological longevity curves do not provide estimates of survivorship and mortality rates, but they are useful in determining age composition of a population at a given time. Under these conditions RCF is the probability that a given age will be represented in the population at the time of sampling (July). This probability is a function of the probabilities of being born and of surviving. The two factors cannot be separated in this analysis. Thus, the probability of occurrence for a given age is determined by the amount of reproduction and mortality during the time represented by the entire curve.

The $X$-axis (age) also represents time prior to the moment of sampling (day 0). Unlike the $X$-axis of a survivorship curve, which begins at day 0 and progresses into the future, this axis starts at the present (day 0) and works into the past.

The term $1 - RCF$ is the percentage of the surviving population born between the moment of sampling and some specified time in the past. In this study, $1 - RCF$ is considered the relative production rate for a given time period. Production is defined as the number of animals born during the period that survive to day 0, and is in relation to all animals surviving at the time of sampling. Relative production rate is valuable in comparisons of relative mortality and natality in different populations.

MEL is the median age of the population at the moment of sampling. From the standpoint of relative production rates, MEL represents the time required to produce half the population surviving to the moment of sampling. Because MAX is that age at which $1 - RCF = 1$, it is the time required for complete replacement of the population. MAX is also the predicted age of the oldest individual in the population at the time of sampling.

## RESULTS

Ecological longevity curves for the six populations are shown in Fig. 1. Dotted lines indicate median ecological longevity (MEL). The X-intercept is the maximum ecological longevity (MAX). Equations on the graph describe the best fitting lines determined by the computer program. The percent variance not due to regression ranged from 1.5 % to 3.0 %, indicating an exceptionally close fit of the line to the data in all cases. These curves are all similar in shape, although various transformations of age were used. Florida-Georgia, Georgia and Ocala received square root transformations. Archbold and South Carolina received cube root transformations, and Vero Beach required a fourth root transformation.

Table 1 summarizes various demographic features of the populations. With respect to MEL, three groups are discernible. Florida-Georgia, at 49 days, is the youngest population and is significantly different ($p=0.05$) from the others. Georgia, Archbold, South Carolina and Ocala are in the middle-aged group of populations. MEL values range from 75 to 84 days, with broadly overlapping dence intervals. One population, Vero Beach, comprises the oldest group. With a MEL of 180
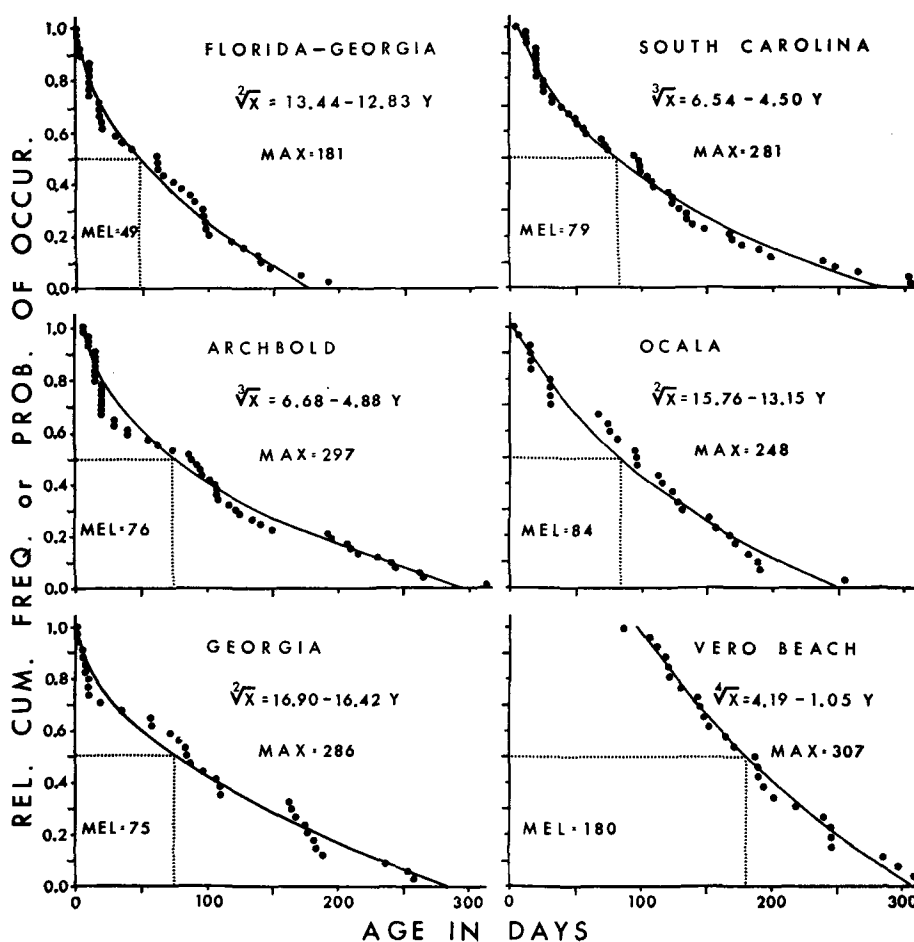
**FLORIDA–GEORGIA** $\sqrt[2]{X} = 13.44 - 12.83\,Y$ MAX=181 MEL=49

**SOUTH CAROLINA** $\sqrt[3]{X} = 6.54 - 4.50\,Y$ MAX=281 MEL=79

**ARCHBOLD** $\sqrt[3]{X} = 6.68 - 4.88\,Y$ MAX=297 MEL=76

**OCALA** $\sqrt[2]{X} = 15.76 - 13.15\,Y$ MAX=248 MEL=84

**GEORGIA** $\sqrt[2]{X} = 16.90 - 16.42\,Y$ MAX=286 MEL=75

**VERO BEACH** $\sqrt[4]{X} = 4.19 - 1.05\,Y$ MAX=307 MEL=180

REL. CUM. FREQ. or PROB. OF OCCUR. — AGE IN DAYS

Fig. 1. Ecological longevity curves for six populations of *P. polionotus*, showing median (MEL) and maximum (MAX) ecological longevity values and equations for the lines.

Table 1. Comparison of demographic characteristics of six populations of *Peromyscus polionotus*. Numbers in parentheses are 95% confidence limits.

| Population | MEL | MAX | $1-RCF_{100}$ |
|---|---|---|---|
| Fla. -Ga. | 49 (47–52) | 181 (172–190) | 0.732 |
| Georgia | 75 (71–80) | 286 (267–305) | 0.580 |
| Archbold | 76 (73–79) | 297 (281–315) | 0.583 |
| S. C. | 79 (77–82) | 281 (268–294) | 0.577 |
| Ocala | 84 (80–89) | 248 (232–265) | 0.563 |
| Vero Beach | 180 (177–183) | 307 (299–317) | 0.022 |

MEL=Median ecological longevity (in days).
MAX=Maximum ecological longevity (in days).
$1-RCF_{100}$=Relative production rate for the 100 days prior to sampling.

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days, it is far older than any other population. Its youngest mouse is older than the MEL values for other populations, and its MEL approximates the Florida-Georgia MAX.

With regard to MAX, at least two groups are evident. Florida-Georgia has the smallest MAX (181 days), with no overlap of its confidence limits with those of other populations. Four other populations show no significant differences in MAX values, which vary from 281 days to 307 days. Ocala, at 248 days, is significantly different from other populations ($p=0.05$); however, its confidence limits are so close to overlapping that biological significance is questionable.

Relative production rates for 100 days prior to sampling show trends similar to those for MEL. Florida-Georgia has the highest rate: 73 % of the sample had been born less than 100 days previously. Georgia, Archbold, South Carolina and Ocala have essentially identical rates (56–58%). The rate for Vero Beach (2 %) is considerably lower than any of the others, and indicates that only 2 % of the sample had been born in the preceding 100 days.

<div align="center">DISCUSSION</div>

Several trends are evident in the data in Table 1. The population with the lowest MEL (Florida-Georgia) has the lowest MAX. Populations with comparable MEL values have comparable MAX values, with insignificant variations in ranking. However, the population with the highest MEL (Vero Beach) does not have a MAX significantly higher than most of the others. Thus the cessation of breeding in this population apparently has not altered the probability of finding "old" (*ca.* 250-300 days) animals.

The great similarity in relative production rates, MEL and MAX suggest that Georgia, Archbold, South Carolina, and Ocala populations are basically identical demographically. However, preliminary examination of data from another study on these populations (M. H. SMITH, unpublished) indicates considerable differences in natality and population density. Reproductive effort per female per unit time, and population density both vary linearly with latitude. Archbold, the southern-most population, has a reproductive effort 3-4 times that of South Carolina, the northern-most population. Archbold's density is 2-3 times greater than that of South Carolina. Although absolute values differ greatly in these populations, relative measures remain essentially identical. Thus mortality rate and its relationship with age are probably similar in these four populations. Differences in natality were manifested only in different population densities.

The Florida-Georgia population is obviously different from the other inland populations. Its higher relative production rate for the 100 days prior to sampling could have been due to one or several of the following factors: (a) natality was greater, or (b) mortality was less during this period; (c) natality was less or (d) mortality was greater before this period. If natality or mortality differed between two populations, but either was uniformly greater or less over the time represented on the graph, there

would be no difference in relative production rate for a specific period, because the relative effects would be unchanged.

M. H. SMITH (personal communication) has found two types of populations of *P. polionotus*, those in optimal habitat with high densities, and those in marginal habitat with low densities. Impressions gained at the time of sampling support this idea, and indicate that the Florida-Georgia population was marginal. If, on one hand, reproductive effort had been comparable to other populations, only a different mortality rate could have produced such a curve. Again, a uniformly higher mortality rate would have had no effect on relative cumulative frequency. If, on the other hand, the mortality rate was comparable to other populations, the timing of reproduction must have differed. Apparently, then, either this population breeds at different times of the year, its mortality rate is more heavily biased against old individuals, or its mortality rate was greater 100 days before sampling.

In *P. polionotus*, a minimum of 72 days is needed from birth of a female to weaning of her first litter: 29 days before first estrus, 23 days gestation, and 20 days for weaning (LAYNE, 1968). In four of the populations, approximately 50% of the females were old enough to have weaned a litter. In the Florida-Georgia population, only 38% of the females would have done so. As expected, the population with the fastest complete replacement time (lowest MAX) has the lowest proportion of individuals of reproductive age.

Post-natal mortality data are scant for *Peromyscus*, and range from 63% to 99% for the first year in *P. maniculatus gracilis*, *P. m. bairdi* and *P. leucopus* (TERMAN, 1968). In July, 1969, when my samples were taken, none of the populations had year-old animals. Since reproduction was occurring in five populations at this time, it is not unrealistic to assume that individuals were born in July, 1968. Thus, longevity in *P. polionotus* apparently is considerably shorter than in certain other species of *Peromyscus*.

The demographic parameters studied show striking relationships with habitat. Populations from similar habitats have much in common. The timing of reproduction and relationship of mortality rate to age or season seem identical, despite quantitative differences in reproductive effort and density. On the other hand, populations from divergent habitats were qualitatively dissimilar, with different reproductive seasons and/or different age or season-dependent mortality rates.

## SUMMARY

An accurate age-estimating technique, based on biochemical changes in eye lens protein, was used to study age structures of six populations of the old-field mouse, *Peromyscus polionotus*. A new mathematical procedure permitted quantitative comparisons of these populations. Four inland populations had essentially the same median ages (75-84 days), maximum ages (248-297 days) and relative production rates (56-58% of the surviving population had been born in the 100 days prior to sampling).

Approximately 50% of the females were old enough to have weaned a litter. One inland population had a lower median age (49 days), a lower maximum age (181 days) and a higher relative production rate (73%). Relatively fewer females (38%) could have weaned a litter. The single beach population was also different, with higher median age (180 days), and lower relative production rate (2%). All females were old enough to have weaned a litter. Maximum age was essentially the same as for the four similar, inland populations. Factors which may have contributed to observed differences in these populations are discussed.

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# ネズミの1種 *Peromiscus polionotus* の 異なる個体群間の年令構成の比較

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*Peromiscus polionotus* の個体群の年令組成を6つの地域について調べ，個体群間の特性のちがいを分析した。年令組成の決定には別稿（本誌 p. 152〜160）にのべた眼球の生化学的分析による方法を用い，その結果の分析は新たに考案した数学的手法によった。内陸部の5つの個体群の内4つは中央年令 (median age)，最大年令，相対繁殖効率 (relative production rate) のどれについてもほぼ同様であったが，残りの1つは中央・最大年令ともやや低く，また相対繁殖効率は高かった。海岸部の個体群は内陸部のものに比べ中央年令は著しく高く，相対繁殖率はずっと低かった。これらの相違がどのような意味を持つかをそれに関与すると思われる要因との関連の上で論じた。