FAILURE TO DETECT SENESCENCE IN PERSISTENCE OF SOME GRASSLAND RODENTS[1]

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Abstract. Several recent papers raise the question of how frequently senescence is detectable in survival estimates from natural populations of mammals. If animals do not age, the probability of disappearance is constant through time. This null hypothesis leads to the prediction that lengths of residence on a trapping grid, censused monthly, will follow a geometric distribution. After testing for survival differences between sexes and among seasons, I compared lengths of residence (persistence) from capture–recapture data for five species of small rodents in an old-field habitat near Lawrence, Kansas, USA to geometric distributions. Gender did not influence persistence on the grid for any species, but persistence of *Microtus ochrogaster* and *Reithrodontomys megalotis* varied significantly with season. All species showed a tendency for high rates of disappearance in the 1st mo after individuals were marked. When the analysis was limited to individuals residing on the area for at least 1 mo, neither *Peromyscus maniculatus, P. leucopus,* nor *Sigmodon hispidus* departed significantly from the geometric model. Seasonal analysis of *Reithrodontomys megalotis* was precluded by small samples, but data for all seasons combined seemed to indicate age- (or persistence-) specific rates of disappearance, as did *M. ochrogaster*, except those first captured in spring. To identify which patterns were consistent with senescence, I regressed rates of disappearance against persistence, testing for positive slopes. Only those *M. ochrogaster* first captured in winter and autumn exhibited senescence by these criteria, despite disappearance rates of *R. megalotis* that increased sharply beyond persistence of 5 mo. The regression test for *P. maniculatus* indicated senescence even though the geometric test failed to indicate persistence specificity. The regression method alone is not a reliable test of senescence, because it does not incorporate variances of estimated probabilities of survival. Any approach derived from horizontal life tables potentially confounds seasonality with aging, making determination of senescence equivocal. In my data there is little convincing evidence that survival in the wild decreases with age in these rodents.

Key words: age-specificity; Gompertz model; Microtus ochrogaster; Peromyscus leucopus; Peromyscus maniculatus; Reithrodontomys megalotis; senescence; Sigmodon hispidus; survival; weighted regression.

INTRODUCTION

Senescence, a decrease in reproductive output or increase in probability of death due to physiological changes associated with advancing age, is an almost universal process in mammals and other higher vertebrates (Rose 1991). Nevertheless, the frequency with which senescence can be observed in natural populations of mammals is open to question, because conventional wisdom has been that the majority of individuals die prior to significant physiological deterioration (Medawar 1952, Comfort 1979, Rose 1991). In fact, the antagonistic pleiotropy theory of the evolution of senescence holds that traits conferring benefit on young individuals at the expense of these individuals in old age will be favored simply because more individuals will be exposed to selection early in life (Williams 1957), i.e., cohort size decreases with age, even in the absence of senescence. Similarly, deleterious mutations that are expressed only late in life

may accumulate with little or no loss of fitness (see Rose 1991). If these views are correct, senescence will be difficult to detect or even irrelevant in natural populations because few organisms will live long enough to suffer physiologically determined increased rates of mortality; most will die due to exogenous sources of mortality before senescence. Two recent studies of huge cohorts of flies (Carey et al. 1992, Curtsinger et al. 1992) did not find a continuous increase in mortality rate with age and raised several issues regarding detection of senescence in heterogeneous populations, even in the absence of exogenous causes of death (Vaupel and Yashin 1985, Carey et al. 1993, Kowald and Kirkwood 1993, Robine and Ritchie 1993, Vaupel and Carey 1993). Brooks et al. (1994) demonstrated a decrease in mortality rate with age in an entire population of nematodes even though each of several subpopulations showed continually increasing age-specific mortality à la Vaupel and Yashin (1985). As with many earlier studies, this paper will focus only on senescence in survival or mortality rates; data for fecundity of unconfined animals are much more difficult to obtain.

Senescence has attracted much interest because of concerns about aging in humans and the possible relevance of animal models to those studies (Olshansky et al. 1993), but it is also of interest to population ecologists because of implications for population dynamics, wildlife management, and conservation biology. For example, senescence might drive microtine cycles (Boonstra 1994) or alter management plans for the Everglades Kite, *Rostrhamus sociabilis* (Nichols et al 1980). The argument that 8-yr-old female grizzly bears (*Ursus arctos horribilis*) have greater reproductive potential than 12-yr-old females, hence are more valuable for augmenting populations (Maguire and Servheen 1992), rests on either reproduction or survival decreasing with age. Thus, the extent to which senescence must be considered in population modeling is of both practical and theoretical interest.

Promislow (1991) conducted an extensive survey of age-specific survival in a variety of mammals, both to document the frequency of senescence and to test hypotheses about life historical correlates of rates of senescence. He tested for increasing mortality rates with advancing age (specifically for the Gompertz model in which the force of mortality increases linearly with age) by regressing the logarithm of mortality rate against age (Promislow 1991). A positive regression coefficient supported senescence in 46 (82%) of 56 data sets from free-living populations of mammals that he analyzed; 26 (46%) data sets yielded statistically significant positive coefficients. Gaillard et al. (1994) criticized several facets of Promislow's approach, but their reanalysis of the data found only one fewer significant indication of senescence. In contrast to this comprehensive survey, persistence records after the first recapture for *Clethrionomys glareolus* and *Apodemus agrarius* (Andrzejewski and Wierzbowska 1961) and *Mus musculus* (Wierzbowska and Petrusewicz 1963) conformed to exponential distributions, indicating constant age-specific probabilities of disappearance. In addition, persistence curves from 12 species of desert rodents (Brown and Zeng 1989) and data from at least two populations of grassland rodents (Sauer and Slade 1987) did not indicate that senescence was common in small rodents. The discrepancy between Promislow's (1991) result and these data sets might suggest that small rodents differ from most mammals, but Promislow's analysis revealed statistically significant senescence in three of five populations of murid rodents. This led me to carefully examine several data sets that my students and I have accumulated for evidence of increased mortality rate with increased age. Gaillard et al. (1994) criticized Promislow's (1991) reliance on vertical life tables; my data are from longitudinal studies, which are of the type Gaillard et al. (1994) recommend analyzing.

MATERIALS AND METHODS

From October 1973 through December 1992, populations of small mammals at the University of Kansas'

John H. Nelson Environmental Study Area, in Jefferson County, ≈14 km north-northeast of Lawrence, were monitored using standard mark–recapture techniques. Live traps were placed in a roughly square grid of two traps at each of 99 stations with 15 m between trap stations. Traps were set and monitored in the mornings and intervening evenings for 3 d each month. From the inception of the project, all hispid cotton rats (*Sigmodon hispidus*), and from July 1975 all prairie voles (*Microtus ochrogaster*), were individually marked. After April 1989, individual white-footed mice (*Peromyscus leucopus*), deer mice (*Peromyscus maniculatus*), and plains harvest mice (*Reithrodontomys megalotis*) also were marked. For each individual, the date of initial capture, sex, and length of residence on the area were recorded. Animals captured on the grid in January 1993 or thereafter were excluded from the analysis, as were any animals that died during capture or handling (<1% of total).

The time between first and last capture is referred to as persistence hereafter, following Brown and Zeng (1989), because date of birth is rarely known and disappearance from the study area may not be synonymous with death. However, this is frequently the only measure of length of life available in population studies. Persistence was analyzed for evidence of senescence, i.e., increase in probability of disappearance as persistence time increased, using the methods of both Andrzejewski and Wierzbowska (1961) and Promislow (1991). Persistence times were not continuously distributed but were clustered at discrete intervals because censuses occurred monthly. Thus, I first compared the frequency of persistence times to a geometric distribution (Hastings and Peacock 1974), the expected distribution of discrete-valued persistence in months, under the null hypothesis of constant probability of disappearance (Holgate 1964). Probability of disappearance, the sole parameter of the geometric distribution, was estimated as the inverse of mean persistence (Hastings and Peacock 1974); goodness of fit to a geometric distribution, truncated when number of survivors fell below five, was assessed with Pearson's chi-square statistic (Andrzejewski and Wierzbowska 1961). Gender and seasonal (dates of first capture in March–May = Spring, June–August = Summer, September–November = Autumn, December–February = Winter) differences in frequency distributions of persistence were tested using homogeneity chi-square tests. When significant differences among seasons were found, separate tests of goodness of fit to a geometric distribution were conducted on each seasonal group. Departures from a geometric distribution indicated persistence specificity, i.e., variation in probability of disappearance with length of persistence, but senescence in survival was supported only by higher disappearance rates in animals with longer persistence, i.e., persistence specificity is a general alternative to the null hypothesis of constant probability of disappearance,

whereas senescence is a more specific alternative. The presence of senescence was estimated by examining plots of the proportion of animals caught on the grid in 1 mo and permanently disappearing from the study area before the next census vs. time after first capture. Almost universally, distributions departed from geometric because of high frequencies of animals caught in 1 mo, but not thereafter, i.e., transients. I repeated all analyses ignoring captures in the initial month, i.e., using only residents captured in at least 2 mo. Because most of these rodents mature within 1 mo of independence (N. A. Slade, *personal observation*) during the breeding season, estimating persistence beyond the 1st mo also restricted the analysis to reproductively mature animals. Ages could be estimated from body mass for two-thirds (1391 of 2049 total or 622 of 898 residents) of the cotton rats (Campbell and Slade 1993) so probability of disappearance was analyzed by estimated age as well as by length of persistence. Because cotton rats could be assigned to age classes from 1 to 3 mo of age, the frequency distribution of disappearance times was not a simple geometric distribution even under the null hypothesis. For example, the number of 2-mo-old cotton rats included the surviving, previously marked, 1-mo-old individuals plus newly marked 2-mo-olds, and conceivably could exceed the number of 1-mo-olds. Therefore, I used Kruskal-Wallis tests for equality of median persistence among rats grouped by age at first capture.

Testing for any departure from constant probabilities of disappearance should be more sensitive than testing for senescence alone, but the power of chi-square tests involving heterogeneity in probabilities of disappearance within categories, i.e., variation among years within gender, season, or persistence classes, is difficult to determine (Kendall and Stuart 1958; D. Hayne, *personal communication*). The failure of Andrzejewski and Wierzbowska (1961) and Wierzbowska and Petrusewicz (1963) to find age-specificity in probabilities of disappearance, in contrast to Promislow's (1991) results could indicate that the latter's test was more powerful. Therefore, I also applied Promislow's (1991) test to each species, stratified by season for prairie voles. I calculated q_x values, proportions of animals with a persistence of x months that were not captured subsequently, for monthly intervals combining all individuals from a species, stratifying by season of first capture for prairie voles, and treating day of first capture as day of entry into the population. Logarithms of the arcsine of the square root of q_x were regressed against months since capture, weighting by sample size rather than square root of sample size (Gaillard et al. 1994). The last q_x value for each cohort (1.0 by definition) and any q_x values from sample sizes <5 were excluded, but estimates from intervals beginning with ≥5 individuals and ending with <5 were included. Because the hypothesis of senescence predicts that q_x in-

creases with age or persistence, one-tailed P values are given for Promislow's tests.

Results

None of the five species exhibited gender-specific patterns of mortality (chi-square tests of homogeneity among persistence frequencies, $P > 0.15$), nor did survival curves differ among seasons of first appearance for either species of *Peromyscus* ($P > 0.30$). Tenure-specific rates of disappearance of cotton rats, prairie voles, and harvest mice all varied seasonally ($P < 0.0001$ for cotton rats and voles, $P < 0.03$ for harvest mice). Sample sizes for the latter were too small to allow season-specific analysis. When the analyses were restricted to animals persisting on the grid for at least 1 mo, i.e., residents, the significance of seasonality was reduced for cotton rats ($P > 0.15$). Hence, the principal seasonal variation in cotton rats was in frequency of transients (or probability of capture, Holgate 1964) rather than disappearance of resident animals. The only species analyzed seasonally was the prairie vole.

These five rodent species showed every combination of significance and nonsignificance when I tested residents for constant probabilities of disappearance, i.e., conformity to a geometric distribution of times of disappearance, and senescence in the sense of Promislow (1991), i.e., linear increase in proportion disappearing with increasing length of persistence (Figs. 1–6). (Even though the figures include disappearances prior to 1 mo, these were not used in any statistical analysis.) The patterns suggesting senescence are increases in the proportion disappearing in months ≥2 in the figures. White-footed mice showed neither significant persistence specificity in survival nor senescence (Fig. 1). I did not reject the hypothesis of constant probability of disappearance for deer mice using the test of Andrzejewski and Wierzbowska (1961), but Promislow's test indicated an increase in disappearance rate with persistence (Fig. 2). The disappearance rate of plains harvest mice decreased, then increased with persistence time, so the geometric test was almost significant at the 0.05 level (Fig. 3), but these data did not match a pattern of continuous increase in probability of disappearance (i.e., Gompertz's equation; Promislow 1991). Probabilities of prairie voles disappearing from the area were persistence-dependent in three of four seasons, but a significant pattern consistent with Gompertz's model of senescence was present only in autumn and winter (Fig. 4). Like white-footed mice, cotton rats showed neither persistence specificity nor senescence, whether persistence was computed from time since first capture (Fig. 5) or from age (Fig. 6).

Discussion

Tests of conformity to the geometric distribution of persistence indicated persistence specificity in survivorship of residents for two of five species. The P value for harvest mice was almost significant at the 0.05 lev-

Peromyscus leucopus
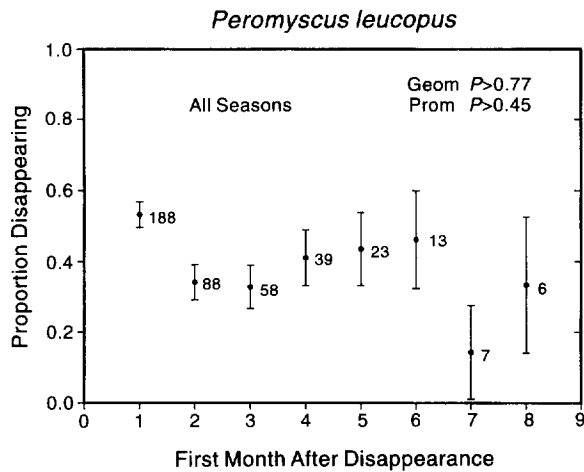

FIG. 1. Proportion of white-footed mice lost between April 1989 and December 1992 from the study area in northeastern Kansas prior to the indicated month. Animals disappearing in the 1st mo after capture are indicated as lost in month 1. Month 1 animals are defined in the text as transients, and probabilities of disappearing in the 1st mo are excluded from all statistical analyses. Error bars indicate $\pm$ 1 SE and sample sizes are given to the right of the data point. P values are for chi-square tests of conformity to a geometric distribution (Geom) and for a test of increase in probability of disappearance with persistence (Prom).

el, and three of four seasonal analyses for prairie voles were significant. Regressions, following Promislow (1991), indicated a significant increase in probability of disappearance with persistence on the area for deer mice, and two of the four seasons for voles. Two of five species or three of eight data sets is not nearly as high as 46 of 56 populations reported by Promislow (1991), but that figure was for any positive sample slope indicating increase in mortality rate with age, regardless of statistical significance (i.e., any P value < 0.50 in Figs. 1–5; I calculated positive slopes for four of eight data sets). My frequencies of statistically significant regressions are not much lower than 26 (0.05 level, two-tailed; Promislow 1991) or 25 (Gaillard et al. 1994) of 56 increases in mortality rate, but I used one-tailed tests; with two-tailed tests, only the prairie vole in winter (one data set in eight) is significant at the 0.05 level. Given the inconsistencies between the geometric fit and regression analyses, neither seems completely satisfactory. This raises the question of how one should test for senescence.

Testing for persistence specificity should be less restrictive, hence more likely to reject the null hypothesis, than testing the Gompertz model of senescence, because any deviation from a constant rate of disappearance influences the chi-square test statistic. The power of chi-square tests varies with sample size; the most definitive rejections of geometric distributions were for prairie voles, due not to exceptional variation among estimated rates of disappearance but rather to large sample sizes. Standard deviations of unweighted
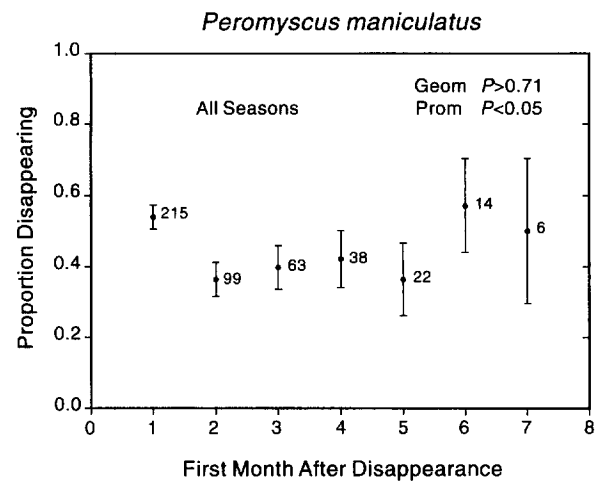
Peromyscus maniculatus

FIG. 2. Proportion of deer mice lost between April 1989 and December 1992 from the study area prior to the indicated month. Error bars, sample sizes, and P values as in Fig. 1.

estimated probabilities of disappearance for resident voles ranged from 0.0466 in autumn to 0.1265 in summer; this was less variation than for cotton rats (SD = 0.1493) and harvest mice (SD = 0.2158) and comparable to those of deer mice (SD = 0.0833) and white-footed mice (SD = 0.1057). However, $N \geq 774$ prairie voles for each season greatly reduced variances of estimated probabilities of disappearance, thus increasing the power of the chi-square (or related likelihood ratio) tests. The disadvantage of this approach is the non-specific nature of the alternate hypothesis to conformity to a geometric distribution; the chi-square test presents only a preliminary screening that must be followed by an additional test for senescence. The directional test of Promislow (1991) may not be the best test for this
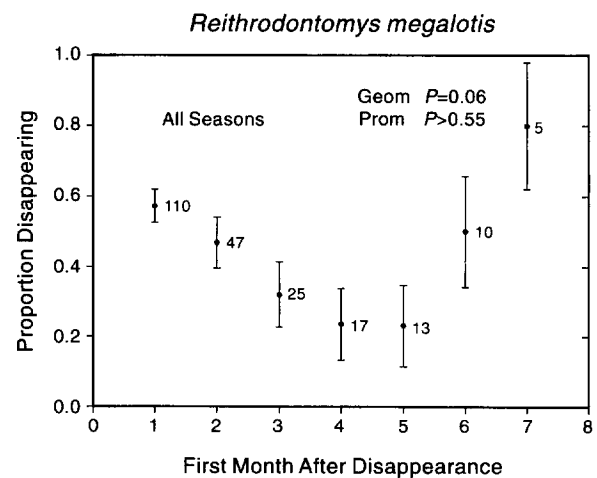
Reithrodontomys megalotis

FIG. 3. Proportion of plains harvest mice lost between April 1989 and December 1992 from the study area prior to the indicated month. Error bars, sample sizes, and P values as in Fig. 1.

FIG. 4. Proportion of prairie voles lost between July 1975 and December 1992 from the study area prior to the indicated month, stratified by season of first capture. Sample sizes for the first and last months are 811 and 9 for winter, 774 and 6 for spring, 835 and 5 for summer, and 1035 and 8 for autumn. Error bars and P values (Ge=Geom; Pr=Prom) as in Fig. 1.
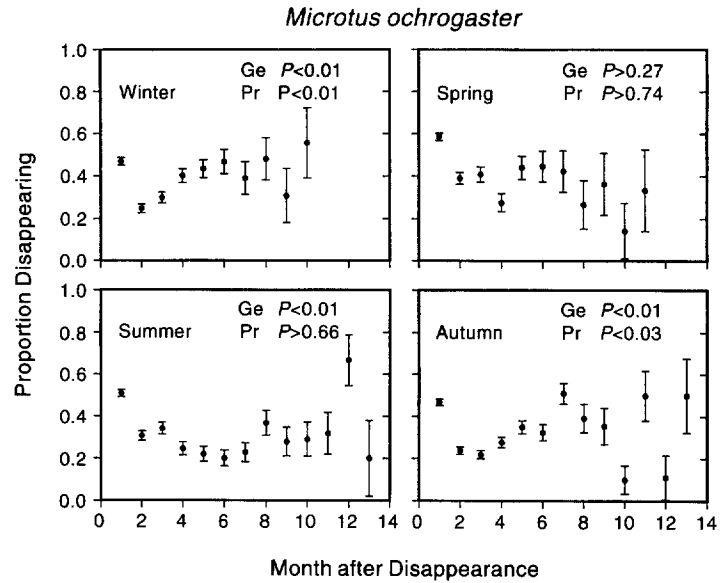
purpose. For example, simple visual inspection of plots for prairie voles captured in autumn and winter (Fig. 4) does not seem to indicate pronounced increases in disappearance rate in later life, whereas voles marked in summer show somewhat elevated rates of disappearance for months 8 through 12 as compared to months 5 through 7. Yet, the regression test indicates senescence for the former data sets but not the latter.

The directional nature of the alternative hypothesis for the regression test increases its power; in my data, three of eight one-tailed rather than one of eight two-tailed tests are significant at the 0.05 level. Even so, the stipulation of the Gompertz model that mortality rate must increase throughout life, or that it increase regularly beyond some fixed age (Olshansky et al.

1993) seems quite restrictive (Abrams 1991). Senescence could occur as a single increase in mortality rate at some age or life stage, producing a step function (i.e., voles in summer?) or steep increase at intermediate age. Further, if populations are composed of genotypes or morphotypes with varying rates of mortality and senescence, overall mortality rates can increase due to senescence within subpopulations, but then decrease with age as the forms with higher mortality rates are differentially removed from the population (Vaupel and Yashin 1985, Brooks et al. 1994). These considerations argue that the test of Promislow is conservative because it tests for a specific form of senescence and senescence is a specific type of age specificity. Nevertheless, regression indicates senescence in deer mice in the ab-
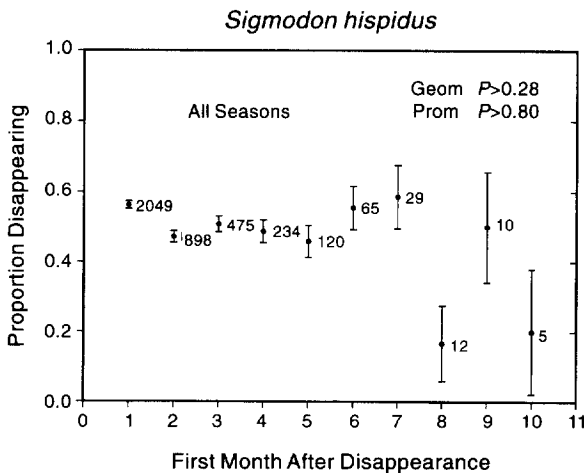

FIG. 5. Proportion of cotton rats lost between October 1973 and December 1992 from the study area prior to the indicated month. Error bars, sample sizes, and P values as in Fig. 1.
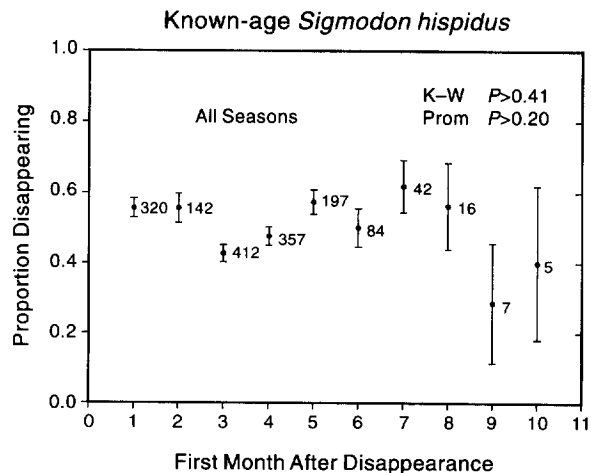
FIG. 6. Proportion of cotton rats in each monthly age class lost from the study area. Error bars and sample sizes as in Fig. 1. P values are for the regression test (Prom) and the Kruskal-Wallis test of equality of median persistence (K-W).

sence of significant departures from the geometric model as judged by the chi-square test.

Contradictions between the results of chi-square tests and regressions suggest that one should use a two-step process for assessing senescence from survival data. First, one should reject the hypothesis of age-invariant mortality rate vs. a general alternative hypothesis using a test that incorporates variances of estimates of mortality. Second, one could look for specific patterns, such as an increase in mortality with increasing age, given that age specificity had been demonstrated. In practice, these tests could be performed simultaneously, either by fitting a specific model of age specificity and assessing its lack of fit via log-linear models (Bishop et al. 1975, Lebreton et al. 1992) or by using multiple cohorts that permit estimates of the variance of survivorships within age classes (Loery et al. 1987). Loery et al. (1987) tested for differences among survival probabilities of specific age groups with t tests, then used regression to test for senescence. However they did not weight estimated probabilities of survival by the sample size used in generating the estimate; thus, they treated every estimate as equally reliable. Promislow (1991) used weighted regression, thus recognizing the importance of sample size in determining the significance of age-specific variation; that is, the difference between 80% survival and 70% survival is statistically significant (at the 0.05 level) if estimated from 200 individuals in each group, but not if estimated from $N = 20$. The variance of an estimated probability of survival is proportional to the inverse of N, and chi-square or likelihood ratio tests of multinomial models reflect sample size. However, weighted regression uses sample sizes only to weight observations relative to others in the same data set; an estimate from a sample of 20 is given twice the weight of an estimate from 10 individuals, but one would obtain identical estimates of regression coefficients, standard errors, t, and F values from another data set with samples of 200 and 100 or 500 and 250. Thus, the significance of regression and the estimated slope (as in Promislow 1991 and Gaillard et al. 1994) depends on the pattern of estimated q_x values and their relative weights, but not on absolute sample sizes. If one relies on regression alone, slight changes in probability of disappearance with a generally increasing trend will be judged significant even if sample sizes are so small that estimated probabilities are not sufficient evidence of real age differences, e.g., deer mice in Fig. 2. Therefore, I recommend that, before one examines the pattern of variation among mortality or disappearance rates, significant variation with age or persistence should be demonstrated with a test sensitive to variance of estimated rates (e.g., Pearson's chi-square, a likelihood ratio test, or logistic regression).

Promislow recognized that weighted regression analysis also introduces another vagary into the analysis, by giving greater weight to large samples early in life

or persistence, whereas senescence is most likely to be manifested late in life, when cohort size has decreased (Gaillard et al. 1994). The highly significant regressions for voles first captured in autumn and winter reflect the increase in mortality rates from months 2 through 7 (Fig. 4); high mortality rates may persist thereafter in the winter data, but the pattern is even less evident among animals caught in autumn. In contrast, visual inspection of persistence-specific rates of disappearance seems to indicate that prairie voles first captured in summer and harvest mice both show increases in disappearance rates beyond the midpoint of the distribution of persistence (Figs. 3 and 4). Neither of these data sets generates a significant regression; in fact, both regression coefficients are opposite the expectation of Gompertz's rule, because the trend from months 2 through 5 is for rates of disappearance to decrease. Both species are reproductively mature at 2, and certainly 3 mo, of age so decrease and subsequent increase in rates of disappearance occur among adult animals, but the regression technique of Promislow (1991) does not detect this pattern. Loery et al. (1987) used unweighted regression to test for decreased probabilities of survival with persistence, and relied on observed variation among replicates to indicate lack of fit. A combination of replication and weighting would be preferable to either approach. If only a single cohort is available or cohorts must be pooled to offer sufficient sample sizes, log-linear analyses (Bishop et al. 1975) should be employed.

How frequent is senescence in the rodents I studied? My conclusion, which is consistent with those of Andrzejewski and Wierzbowska (1961), Wierzbowska and Petrusewicz (1963), and Brown and Zeng (1989), is that none of these rodents shows convincing patterns of senescence. Prairie voles clearly show heterogeneous disappearance rates, but these rates and their persistence-specific patterns vary seasonally. If senescence results from age-related physiological changes, it should be observable in all seasons, particularly in voles that can reproduce throughout the year in northeastern Kansas (Rose and Gaines 1978). Absence of senescence among a substantial portion of the population is reinforced by considering records of longevity in captive rodents. Several individuals from small stocks of two different subspecies of *Peromyscus maniculatus* lived more than 3 yr in captivity and showed declining reproduction only after 2.5 yr (Sumner 1922, Dice 1933), but 95% of resident deer mice disappeared from my area within 7 mo of capture. Captive *Reithrodontomys megalotis* are still reproductive after 1.5 yr (Bancroft 1967); again, almost all have disappeared from the field after 7 mo. Significant fractions of captive cotton rats (Birney et al. 1975) and prairie voles (Gier and Cooksey 1967) live beyond 500 d, but in the field large cohorts were extinguished in <400 d.

Only the pattern of disappearance of harvest mice is consistent with senescence. Low sample size late in

life reduces the statistical significance of the pattern, but it suggests increasing mortality with length of persistence. However, seasonality also is important in these data. Probabilities of capture for harvest mice decrease in spring and summer as a result of behavioral changes (Johnson and Gaines 1988, Foster and Gaines 1991). Apparent survivorships reflect these changes; median persistence times are 4, 2, 1.5, and 1 mo for resident harvest mice first captured in autumn, winter, spring, and summer, respectively. Thus, there is a tendency for resident animals to disappear from capture records in late spring and summer, regardless of length of persistence. In my data, 40 of 47 resident harvest mice were marked in late autumn, winter, and early spring so increased rate of disappearance in months 4 through 7 coincides with the arrival of summer.

Seasonal changes in behavior may occur in other species in this study, but they are not as extreme as with harvest mice. Nevertheless, this illustrates a difficulty with using horizontal life tables for studies of aging; any temporal variation in vital rates will be confounded with age of a single cohort. If temporal patterns are repeated, even using replicate cohorts may not rectify the problem. If detailed knowledge of individual species and field situations are required for correct interpretation of data, the comparative method becomes very difficult; one cannot expect persons doing an extensive review of published studies to be intimately familiar with the vagaries of every data set relevant to their study. Perhaps spurious patterns are rare and are minor components of large surveys, but when comparative data are partitioned by taxon, body size, or other criteria, single data sets may be quite influential. Clearly, temporal variation on seasonal, annual, and multi-annual scales is likely to be important in the demography of short-lived animals such as grassland rodents. This makes considerations of senescence in wild populations complex, both biologically and statistically.

Even without seasonal variation, capture–recapture methods introduce bias into estimates of survival. First and last captures occur at some time after birth and before death, hence persistence is less than longevity. The extent of this bias depends on probability of capture. If probability of capture is uniformly high, bias will be minimal, but any age-invariant probability of capture less than one, can introduce the appearance transients (an abundance of animals captured only once) in survival data (Holgate 1964, 1966). Heterogeneity among probabilities of capture among individuals can cause apparent age-related decreases in Jolly-Seber estimates of probabilities of survival in the absence of senescence (Buckland 1982). With sufficient sample size, it is possible to estimate age-specific survival rates, adjusting for yearly probabilities of capture (Loery et al. 1987), or for "transients" (Pradel et al. 1995) and to test for senescence (Loery et al. 1987).

In this paper, I, like Andrzejewski and Wierzbowska

(1961), Wierzbowska and Petrusewicz (1963), and several of the authors cited by Promislow (1991), ignored problems with probability of capture, assuming that probability of capture was high and constant over the period for which persistence was determined. I have referred to persistence on and disappearance from my study area rather than age and death, because only rarely could I document birth or death of animals. With cotton rats, I did analyze the data by age and by persistence and the conclusions were identical; there was no evidence of age or persistence-specific departures from constant disappearance rates. More than three-fourths of cotton rats that were assigned ages (1092 of 1391) were captured before they were 2 mo old. This is early enough in life that first capture can be considered as recruitment into the population at an age of ≈ 1 mo.

As noted, the probability of disappearing following the initial capture or initial month of capture is high, perhaps due to dispersal from the area. Once an animal has settled on the area, it is much more likely to remain. Despite several other small mammal studies in the immediate vicinity, animals that had been resident on my area were rarely trapped elsewhere. Thus, among residents, disappearance seems likely to be synonymous with death. Regardless, movement off the study area will be confounded with death in most studies of unconfined populations, so the data presented here should be comparable to previous studies. The most serious bias in equating disappearance with death is seasonal or other changes in behavior as occur in harvest mice on my area. Thorough analyses with statistical procedures such as in program CAPTURE (Pollock et al. 1990) or RELEASE and SURGE (Lebreton et al. 1992) should reveal such biases when they exist. These modern techniques should be applied to large sets of capture records for species suspected of behavioral variability.

CONCLUSION

I do not claim that my data represent anything other than a few species from a single place, hence these are not sufficient to draw general conclusions about the prevalence of senescence in survival of free-living small mammals worldwide, but these long-term data are consistent with the previously espoused view that senescence is difficult to demonstrate in wild mammals. This is contrary to Promislow's (1991) report of statistically significant evidence for senescence in three of five members of family Muridae. I hope that presenting this detailed analysis, including what I see as potential pitfalls in the data and statistical analyses, will stimulate other ecologists to examine their data. Perhaps comparative studies can be generated from synthetic analyses of studies directed to particular questions of general interest, rather than having to glean data from prior studies that may address the issues only tangentially.

LITERATURE CITED

Abrams, P. A. 1991. The fitness costs of senescence: the evolutionary importance of events in early adult life. Evolutionary Ecology 5:343–360.

Andrzejewski, R., and T. Wierzbowska. 1961. An attempt at assessing the duration of residence of small rodents in a defined forest area and the rate of interchange between individuals. Acta Theriologica 5:153–172.

Bancroft, W. L. 1967. Record fecundity for *Reithrodontomys megalotis.* Journal of Mammalogy 48:306–308.

Birney, E. C., R. Jenness, and D. D. Baird. 1975. Eye lens proteins as criteria of age in cotton rats. Journal of Wildlife Management 39:718–728.

Bishop, Y. M. M., S. E. Fienberg, and P. W. Holland. 1975. Discrete multivariate analysis. Massachusetts Institute of Technology Press, Cambridge, Massachusetts, USA.

Boonstra, R. 1994. Population cycles in microtines: the senescence hypothesis. Evolutionary Ecology 8:196–219.

Brooks, A., G. J. Lithgow, and T. E. Johnson. 1994. Mortality rates in a genetically heterogeneous population of *Caenorhabditis elegans.* Science 263:668–671.

Brown, J. H., and Z. Zeng. 1989. Comparative population ecology of eleven species of rodents in the Chihuahuan Desert. Ecology 70:1507–1525.

Buckland, S. T. 1982. A mark-recapture survival analysis. Journal of Animal Ecology 51:833–847.

Campbell, M. T., and N. A. Slade. 1993. Effect of mass on seasonal survivorship in northern cotton rats. Journal of Mammalogy 74:971–981.

Carey, J. R., J. W. Curtsinger, and J. W. Vaupel. 1993. Response to Kowald and Kirkwood and to Robine and Ritchie. Science 260:1665–1666.

Carey, J. R., P. Liedo, D. Orozco, and J. W. Vaupel. 1992. Slowing of mortality rates at older ages in large medfly cohorts. Science 258:457–461.

Comfort, A. 1979. The biology of senescence. Third edition. Churchill Livingstone, Edinburgh, UK.

Curtsinger, J. W., H. H. Fukui, D. R. Townsend, and J. W. Vaupel. 1992. Demography of genotypes: failure of the limited life-span paradigm in *Drosophila melanogaster.* Science 258:461–463.

Dice, L. R. 1933. Longevity in *Peromyscus maniculatus gracilis.* Journal of Mammalogy 14:147–148.

Foster, J., and M. S. Gaines. 1991. The effects of a successional habitat mosaic on a small mammal community. Ecology 72:1358–1373.

Gaillard, J-M., D. Allaine, D. Pontier, N. G. Yoccoz, and D. E. L. Promislow. 1994. Senescence in natural populations of mammals: a reanalysis. Evolution 48:509–516.

Gier, H. T., and B. F. Cooksey, Jr. 1967. *Microtus ochrogaster* in the laboratory. Transactions of the Kansas Academy of Science 70:256–265.

Hastings, N. A. J., and J. B. Peacock. 1974. Statistical distributions: a handbook for students and practitioners. Butterworth, London, England.

Holgate, P. 1964. A modified geometric distribution arising in trapping studies. Acta Theriologica 9:353–356.

———. 1966. Contributions to the mathematics of animal trapping. Biometrics 22:925–936.

Johnson, M. L., and M. S. Gaines. 1988. Demography of the western harvest mouse, *Reithrodontomys megalotis,* in eastern Kansas. Oecologia (Berlin) 75:405–411.

Kendall, M. G., and A. Stuart. 1958. The advanced theory of statistics. Volume I. Hafner, New York, New York, USA.

Kowald, A., and T. B. L. Kirkwood. 1993. Explaining fruit fly longevity. Science 260:1664–1665.

Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

Loery, G., K. H. Pollock, J. D. Nichols, and J. E. Hines. 1987. Age-specificity of Black-capped Chickadee survival rates: analysis of capture-recapture data. Ecology 68:1038–1044.

Maguire, L. A., and C. Servheen. 1992. Integrating biological and sociological concerns in endangered species management: augmentation of grizzly bear populations. Conservation Biology 6:426–434.

Medawar, P. B. 1952. An unsolved problem in biology. H. K. Lewis, London, England.

Nichols, J. D., G. L. Hensler, and P. W. Sykes, Jr. 1980. Demography of the Everglades Kite: implications for population management. Ecological Modelling 9:215–232.

Olshansky, S. J., B. A. Carnes, and C. K. Cassel. 1993. The aging of the human species. Scientific American 268:46–52.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 107:1–97.

Pradel, R., J. E. Hines, J.-D. Lebreton, J. D. Nichols, and A. Viallefont. 1995. Estimating survival probabilities and proportions of "transients" using capture-recapture data. Biometrics 51, *in press.*

Promislow, D. E. L. 1991. Senescence in natural populations of mammals: a comparative study. Evolution 45:1869–1887.

Robine, J. M., and K. Ritchie. 1993. Explaining fruit fly longevity. Science 260:1665.

Rose, M. R. 1991. Evolutionary biology of aging. Oxford University Press, New York, New York, USA.

Rose, R. K., and M. S. Gaines. 1978. The reproductive cycle of *Microtus ochrogaster* in Eastern Kansas. Ecological Monographs 48:21–42.

Sauer, J. R., and N. A. Slade. 1987. Size-based demography of vertebrates. Annual Review of Ecology and Systematics 18:71–90.

Sumner, F. B. 1922. Longevity in *Peromyscus.* Journal of Mammalogy 3:79–81.

Vaupel, J. W., and J. R. Carey. 1993. Compositional interpretations of medfly mortality. Science 260:1666–1667.

Vaupel, J. W., and A. I. Yashin. 1985. Heterogeneity's ruses: some surprising results of selection on population dynamics. American Statistician 39:176–185.

Wierzbowska, T., and K. Petrusewicz. 1963. Residency and rate of disappearance of two free-living populations of the house mouse (*Mus musculus* L.). Ekologia Polska A11: 557–574.

Williams, G. C. 1957. Pleiotropy, natural selection and the evolution of senescence. Evolution 11:398–411.