Actuarial Senescence and Demographic Heterogeneity in the Florida Scrub Jay

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ACTUARIAL SENESCENCE AND DEMOGRAPHIC HETEROGENEITY IN THE FLORIDA SCRUB JAY[1]

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Abstract. Analysis of mortality from a 25-yr sample of 380 Florida Scrub Jays, *Aphelocoma c. coerulescens,* shows that actuarial senescence (increase in mortality with age) occurs. This refutes the notion that adult mortality is independent of age in birds, and has important implications for evolutionary dynamics. We point to two major factors that may act to mask underlying patterns of actuarial senescence: (1) Selection through time (demographic heterogeneity): because selection inevitably weeds out lower quality individuals first, overall mortality may appear to be constant or even decreasing, despite an increasing force of mortality acting on birds of higher quality. (2) Conflicting processes: one source of mortality may act to decrease mortality over time (e.g., group size effects), while another acts to increase it (e.g., degenerative senescence). Age-specific data, measures of intrinsic quality that are independent of mortality, and exposure of sources of heterogeneity and of conflicting processes allow us to demonstrate a clear pattern of actuarial senescence in an unmanipulated, natural population of long-lived birds. The slow rate of increase in mortality is consistent with the hypothesis that mortality increases more slowly with age in birds than in mammals.

Key words: actuarial senescence; age-dependent mortality; demography; Florida Scrub Jay; heterogeneity; life history; mortality; senescence; vertebrate; Weibull model.

INTRODUCTION

Patterns of mortality are fundamental to population and evolutionary dynamics. The timing of mortality can affect intrinsic rates of increase as well as basic aspects of life history (Schaffer 1974, Charlesworth 1980). Mortality in birds was long assumed to be relatively constant in "adults" (Deevey 1947, Lack 1954). This assumption was challenged on theoretical grounds by Botkin and Miller (1974), and by preliminary analyses of long-term studies of marked birds (Newton 1989). Because birds are notably long-lived for their body size (Williams 1957, Finch et al. 1990, Pomeroy 1990, Austad and Fischer 1991, Partridge and Barton 1993), analyzing patterns of avian mortality may require long-term studies. Although numerous long-term studies of birds have been conducted (e.g., Newton 1989), few have analyzed age-specific patterns of mortality using statistical techniques that cope with problems of censoring and lack of independence between mortality and age. In the present study, we use maximum likelihood estimation (MLE) to analyze patterns of mortality in the cooperatively breeding Florida Scrub Jay, *Aphelocoma c. coerulescens.*

Cooperative-breeding birds are of interest to students

of life history and social evolution, in part because delayed reproduction is one characteristic of the social system (Brown 1987). Delayed reproduction, regardless of the social system, is characteristic of many long-lived birds. Florida Scrub Jays are singular breeders (one nest per territory). Young birds often delay dispersal for one to several years, and during that period usually serve as helpers at the nest (Woolfenden and Fitzpatrick 1984). Breeding dispersal (sensu Greenwood and Harvey 1982) is essentially non-existent; that is, breeders never move more than a few territory diameters from their initial breeding location. Once they begin breeding, virtually all do so annually throughout their remaining life-span. Two measures of passing time are therefore available: chronological age and breeding span, defined as time intervals from first breeding to death. Because breeding is annual, breeding span is equivalent to parity, if measured in years. Because of differing ages of first reproduction, however, individuals of the same age can differ in parity; conversely, individuals with the same parity can differ in age.

We make two major points in this paper. First, an increase in mortality with age does occur in the Florida Scrub Jay. Such an increase, which we term *actuarial senescence,* is consistent with evolutionary theories for accelerated *degenerative senescence* (Finch 1990, Abrams 1991, Rose 1991), but also could be caused by other age-dependent forces of mortality. The evolutionary mechanisms for degenerative senescence in-

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clude: (1) adaptive processes, usually based on trade-offs between fitness components early in life and the same or different components late in life (Williams 1957); and (2) a non-adaptive consequence of mutation accumulation under stronger selection early in life (Medawar 1952, Partridge and Barton 1993). The rate of increase that we demonstrate is slow and supports the hypothesis (Williams 1957, Nesse 1988, Williams 1992) that birds may differ from mammals in having generally lower rates of increase in mortality.

Second, heterogeneity among individuals and conflicting processes can obscure patterns of age-specific mortality (Keyfitz 1985:385–393, Vaupel and Yashin 1985). We point to two major factors that may hamper the detection of patterns:

1) Selection through time. As an inevitable consequence of selection and the passage of time, the ratios of subgroups with inherently different mortality distributions will change. For example, in a hypothetical population comprising two subpopulations governed by high and low mortality, respectively, the proportional representation of the subpopulation with low mortality will necessarily increase such that overall mortality may appear to decrease, despite constant mortality within each subpopulation (Keyfitz 1985).

2) Conflicting processes (Abrams 1991). Two sources of mortality, acting simultaneously in opposite directions, may cancel each other out, as when two sound waves of complementary shape produce apparent silence. In the present study, we are able to assess quality independent of mortality, and therefore assess the impact of selection through time on low-quality individuals with high rates of early mortality, and high-quality individuals with low initial mortality that increases with age (constituting actuarial senescence).

Materials and Methods

The data come from an ongoing 25-yr study of co-operative-breeding Florida Scrub Jays at Archbold Biological Station, Florida (27°11′ N, 81°21′ W) (Woolfenden and Fitzpatrick 1984, 1990, Fitzpatrick and Woolfenden 1986, 1989) . The sample comprised 193 females and 187 males, all of which became breeders. Jays included in the analyses were banded between 1969 and 1992, and were followed until their disappearance or the termination of the sample period in July 1994. Within the study area, G. Woolfenden has conducted complete censuses every month since April 1971. A recent exhaustive census of 890 pairs of scrub jays in the entire county surrounding the study area revealed no dispersed breeders (D. B. McDonald and B. Stith, *personal observations*). Breeding dispersal during the 25 yr of this study and during an 8-yr study of 40 adjacent territories (R. L. Mumme, *personal communication*) was restricted to moves of one or a few territory diameters, and occurred only following a mate's disappearance or territory degradation. Thus, because of the complete monthly censuses and the sed-

entary nature of breeders, disappearance of a breeder means death. We define a breeder as a female that has laid at least one egg in her lifetime, or a male paired with a laying female. Birds still alive at the end of the study period (15 July 1994) were labeled as "censored" for mortality analysis ($N = 82$, 22%). Two major samples existed within the data set: (1) birds of known age, (2) birds whose age was not known with certainty, but whose date of first breeding was strongly suspected because of social status when banded.

Known-age sample

Of the total sample of 380 birds, 250 were banded before the first definitive prebasic molt (Bancroft and Woolfenden 1982), and were thus of known age. Half (126) of the known-age individuals first bred at age 2 yr, whereas most of the rest (85) first bred at age 3 yr. We use the term "fast" breeder to describe the subsample of birds that first bred at age 2 yr, and "slow" breeder to describe those that first bred at age 3 yr. A few ($N = 11$) individuals first bred at age 1 yr, whereas 28 individuals first bred at age 4 yr or older. Most of the known-age individuals hatched locally (within the study area).

Unknown-age sample

Of the total sample, 130 were birds of unknown age that were banded as apparent prebreeders, so that their subsequent date of first breeding was known. For these unknown-age birds, we analyzed mortality as a function of breeding span. Breeding span was defined as the number of time intervals (months or years) between first breeding and time of death or censoring. It was indexed from 1, such that an individual that died at any point in its 1st yr of breeding would be considered to have a breeding span of 1 (year). Because age at first breeding varies, birds of a given breeding span in this sample constituted a heterogeneous pool in terms of chronological age. A majority of these unknown-age birds were immigrants to the study area. Almost certainly, few or none had previously bred.

Mortality analysis

We measured mortality from the complete monthly censuses. For each individual, the data consisted of time (in months) beginning with date of first breeding and ending with death or censoring.

In many mark–recapture studies, disappearance cannot be assumed to mean death. Extensive literature exists for estimating mortality in the face of uncertainty concerning disappearance (e.g., Pollock et al. 1990, Clobert and Lebreton 1991). For many species, such techniques are a necessary precursor to the analyses presented in this study. In our study of Florida Scrub Jays, disappearance of a breeder means death. Rather than estimating mortality, therefore, our analyses assess the overall pattern of mortality.

Estimates of survival and mortality parameters de-

TABLE 1. Parameters of mortality distributions for four subsamples of a sample of 380 Florida Scrub Jay breeders, using maximum likelihood estimation (MLE) of accelerated failure models with BMDP 2L (Dixon 1990). Confidence intervals refer to calculation prior to sequential Bonferroni adjustment. All Weibull parameters were estimated from monthly mortality data.

Sample	Time variable (months)	N	Shape, p	95% CI (shape)	Location, λ $(e^{-\alpha})$	Best fitting distribution	Mortality pattern
"Fast" breeders[†]	Age[‡]	126	1.25	1.07 to 1.46[§]	0.0189	Weibull	Increasing
Known-age (1–7 yr)[¶]	Breeding span	250	1.14	1.02 to 1.27[‖]	0.0209	Weibull	Increasing
"Slow" breeders[†]	Age[‡]	85	1.14	0.94 to 1.39	0.0204	Weibull	Cannot reject constant
Unknown-age	Breeding span	130	1.00	0.86 to 1.17	0.0254	Exponential	Constant

[†] "Fast" breeders first bred at age 2 yr, "slow" at age 3 yr.
[‡] Analyzed from age of first reproduction.
[§] Confidence interval does not overlap 1.0, even with sequential Bonferroni adjustment.
[‖] Confidence interval overlaps 1.0 following sequential Bonferroni adjustment.
[¶] Age at which birds in subsample first bred; this subsample comprises all the known-age birds, including the "fast" and "slow" breeders.

rived from maximum likelihood estimation (MLE) have advantages over those derived from least squares regression methods in terms of bias reduction, assumptions of independence, and accommodation of censored data. We therefore estimated mortality parameters by MLE, using the accelerated failure model of BMDP 2L without covariates (Dixon 1990). We compared the fit of potential distributions using the natural logarithms of the maximized partial likelihood functions (Kalbfleisch and Prentice 1980:65). The Weibull distribution produced the best fitting accelerated failure model for all subsamples (Table 1) except the unknown-age birds, for which the exponential and Weibull distributions had equivalent log-likelihood scores (both −188.454). Adequacy of the Weibull model was demonstrated by the approximate linearity of all subsamples when the natural logarithm of time to death was plotted against the natural logarithm of the percentile of the cumulative hazard function (Nelson 1982: 132–134). We therefore use the term "Weibull model" when referring to results from the BMDP 2L accelerated failure model with Weibull distribution.

The two-parameter Weibull distribution (Kalbfleisch and Prentice 1980:23–24) has the hazard function

$$\lambda(t) = \lambda p(\lambda t)^{p-1}$$

and is governed by a location parameter, λ (where $\lambda = e^{-\alpha}$, and α is the "constant" parameter in BMDP 2L output), and a shape parameter, p (the inverse of the "scale" parameter in BMDP 2L output). If $p > 1.0$, then mortality increases with age. If $p = 1.0$, then mortality is constant (and a Weibull model is equivalent to an exponential model). We compared parameters among subsamples by the method of simultaneous confidence limits (Nelson 1982:533).

We compared the entire mortality curves for different subsamples (e.g., known-age vs. unknown-age) using Kaplan–Meier (product limit) estimates (BMDP 1L: Dixon, 1990) and a nonparametric linear rank test (Breslow logrank test, which weighs early observations more heavily). Because of the ongoing nature of the study, we included censored observations. The MLE accelerated failure models and Kaplan–Meier techniques are designed to accommodate such censoring.

Months were the time units for most of the analyses (e.g., accelerated failure model hazard functions). For month-based measures the age indexing subscript x was superscripted by m; e.g., l_x^m. For some calculations, however, the time units were years (subscript x superscripted by y), and we then assessed mortality over the 1-yr interval from the beginning of one breeding season (15 March) to the beginning of the next. Using annual units for some calculations avoided smoothing functions required by months with zero mortality, and allowed calculation of traditional measures used in vertebrate demography, such as age-specific annual mortality, q_x^y. For example, q_2^y would refer to individuals dying at any point in the year-long interval between passing their second "birthday" (15 March, 2 yr after hatch) and reaching their third (see Caswell 1989 for a discussion of indexing in continuous and discrete formulations). Calculations that involved breeding span were subscripted b (rather than x), with superscripts m or y, as described. To compare observed mortality with that estimated from the Weibull model, we used the scale and shape parameters from the month-based Weibull model to calculate the monthly survivor function, $l_x^m = \exp[-(\lambda \times x)^p]$, and thence annual survival, l_x^y. Annual mortality then follows as $q_x^y = 1 - (l_{x+1}^y / l_x^y)$.

The force of mortality, μ, is a measure of the instantaneous force of mortality. It is calculated as

$$\mu \approx -\ln(1 - q_x^y), \quad \text{with} \quad \text{SE} \approx \sqrt{\frac{q_x^y}{n_x^y(1 - q_x^y)}},$$

where $q_x^y = d_x^y / n_x^y$, d_x^y is the number of individuals dying in the interval x to $x + 1$, and n_x^y is the number of individuals entering the interval (Elandt-Johnson and Johnson 1980, Tatar et al. 1993). Unlike q_x, μ is not dependent on the sample interval. The natural logarithm of μ can be used, with suitable caveats, to assess the degree to which the observed mortality distribution fits a Gompertz model (Tatar et al. 1993). Under a Gompertz model, the slope, b, of a plot of $\ln \mu$ against
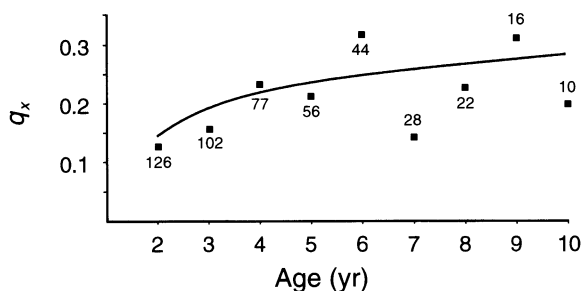
FIG. 1. Age-specific, annual mortality, q_x^y, of "fast" breeders. Curve: mortality calculated from the parameters of an accelerated failure model with Weibull distribution. Scatter plot: observed mortality among 126 "fast" breeders at ages for which sample size was ≥10 birds. Sample size, shown above or below scatter plot markers, decreased as individuals died or were censored.

time gives the rate of change in mortality and can be used to calculate mortality rate doubling time (MRDT; Finch et al. 1990) using the relationship

$$\text{MRDT} = \frac{\ln(2)}{b}.$$

From the observed annual mortality, we also calculated life expectancy from age of first reproduction, e_α, as a basis for comparison among subsamples, where α is the age of first reproduction. Finally, from observed annual mortality, we calculated life table entropy, H, which measures the evenness of mortality as a function of age ($0.0 \geq H \leq 1.0$). A value for H of 0.0 means that all individuals die at the same age, and a value of 1.0 means that the probability of death is the same at every age (Carey 1993:39–40). It is calculated as

$$H = \left\{ \sum_{x=\alpha}^{\omega} e_x d_x \right\} \Big/ e_\alpha.$$

Note that H was calculated from α, the age of first reproduction, which was the starting point for all mortality analyses; w is the maximum age, at which all individuals are dead.

RESULTS

Known-age samples

For the "fast" breeders, the 95% confidence interval around the Weibull shape parameter ($p = 1.25$) did not overlap 1.0, and mortality thus increased significantly with age (Table 1). For comparison to measures of mortality more common in previous studies of avian demography, age-specific annual mortality, q_x^y, was calculated from the Weibull parameters (Fig. 1). The mortality estimated from the Weibull parameters closely matches the observed age-specific mortality for the "fast" breeders.

Fig. 2 shows ln μ, based on the observed mortality, which can then be used for Gompertz analysis and calculation of MRDT, the mortality rate doubling time

(Finch et al. 1990). In the present case, the data are quite noisy (Fig. 2) and ln μ may not be linear, as assumed by the Gompertz model (Tatar et al. 1993) . Given that caveat, the slope assessed by least squares regression weighted by sample size ($b = 0.109$; Fig. 2) yields an estimated MRDT of 6.4 yr.

The sample of 85 "slow" breeders had a Weibull shape parameter ($p = 1.14$) whose confidence interval overlapped 1.0. Therefore, although an increasing trend exists, the hypothesis that mortality was constant cannot be rejected (Table 1). To match the sample of "slow" breeders ($N = 85$), we analyzed mortality in those "fast" breeders that survived to age 3 yr or beyond ($N = 101$). The Weibull shape parameter, p, for this "fast" breeder subsample remained 1.25, with a 95% CI from 1.06 to 1.48. In contrast to "slow" breeders, therefore, mortality of "fast" breeders increased significantly with age, even when assessed from age 3 yr.

We also assessed the pattern of mortality of the full known-age sample (first breeding at ages 1–7 yr), by breeding span rather than by age (Table 1). Because the 95% CI around the Weibull shape parameter did not overlap 1.0 (without Bonferroni adjustment), mortality increased significantly with time (measured here as breeding span). For the known-age sample that bred at age 3 yr or older ("slower" breeders), however, the Weibull shape parameter was 1.06 with a 95% CI from 0.90 to 1.25. The hypothesis of constant mortality therefore could not be rejected. Basing known-age analyses on breeding span (heterogeneous for age) allowed direct comparison with analyses of the unknown-age sample (Figs. 3 and 4).

The maximum recorded life-span in the sample of 250 known-age birds was 15.2 yr. Twenty-one individuals (8.4%) attained an age of ≥10 yr. Life expectancy from age of first reproduction, e_α, for the "fast" breeders was 4.8 ± 4.3 yr (mean ± 1 SD), dropping to 4.2 yr at age 3 yr. For the "slow" breeders, e_α (from

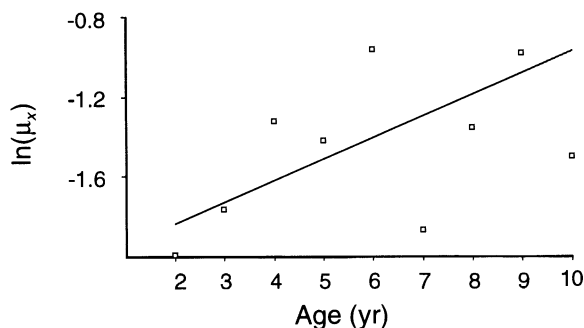
FIG. 2. Logarithm of the force of mortality, ln(μ), for the "fast" breeders plotted in Fig. 1. The slope of the ln(μ) curve, fitted by least squares regression weighted by sample size, provides a measure of the rate of increase in mortality under a Gompertz model, given the caveats outlined in the text. The mortality rate doubling time (MRDT) calculated by this method was 6.4 yr. Sample sizes at each age are shown in Fig. 1.
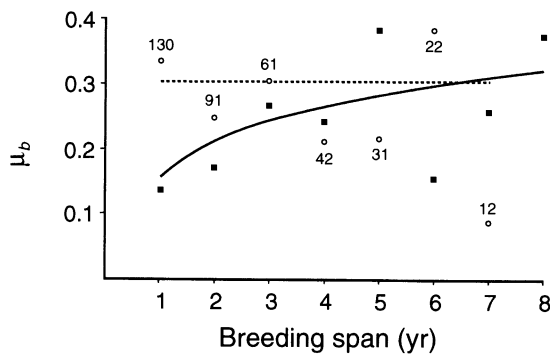
FIG. 3. Force of mortality, μ, for "fast" breeders and unknown-age Florida Scrub Jays as a function of breeding span. Solid squares: observed force of mortality for 126 "fast" breeders, most of whom hatched in the study area. Solid curve: force of mortality for "fast" breeders, calculated from the parameters of a Weibull model. Because "fast" breeders first bred at age 2 yr, breeding span values are one less than their age (e.g., at a breeding span of one, birds are 2 yr old. See *Methods* for indexing definitions). Sample sizes for "fast" breeders are given in Fig. 1. Open circles: observed force of mortality for 130 unknown-age breeders, most of whom were immigrants (as prebreeders). Sample sizes for unknown-age breeders are shown above the scatter plot markers. Dashed line: force of mortality for unknown-age breeders, calculated from the parameters of a Weibull model.

age 3 yr) was 4.0 ± 4.2 yr. Life table entropy, H, was 0.64 for "fast" breeders and 0.79 for "slow" breeders.

Unknown-age sample

For the unknown-age sample, two results indicated that mortality was constant as a function of breeding span (Table 1; Fig. 3). First, the Weibull shape parameter, p, was 1.00 (constant mortality). Second, this subsample was the only one analyzed in which the log-likelihoods of the exponential (constant mortality) and Weibull models were precisely the same. High mortality in the first 24 mo produced a constant force of mortality, μ (Fig. 3). The life expectancy from age of first reproduction, e_α, was only 3.2 yr, compared to 4.1 yr for known-age breeders. H for the unknown-age sample was 0.93.

Comparisons across samples

The mortality distribution for the homogeneous "fast" breeder sample differed from that of the heterogeneous unknown-age sample under a Breslow test based on Kaplan–Meier survival estimates (Breslow test statistic = 8.25, $P = 0.004$). We calculated the force of mortality, μ, of "fast" breeders and of unknown-age birds from observed mortality, as well as from the parameters of the Weibull model (Fig. 3). The difference between an increasing force of mortality for the "fast" breeder sample vs. a constant force of mortality for the unknown-age sample was largely due to considerably higher mortality in unknown-age birds during the 24 mo following first breeding (Fig. 3).

Annual fledging success serves as a measure of qual-

ity. The lifetime mean annual fledging success of "fast" breeders was higher (1.98 ± 1.5 fledglings/yr, mean $\pm$ 1 SD; $N = 355$ breeder years) than that of "slow" breeders (1.71 ± 1.5 fledglings/yr, $N = 270$; $P = 0.024$; two-tailed t test). This suggests that age of first breeding is inversely related to inherent quality (Fitzpatrick and Woolfenden 1989). The suggestion is further supported by a longer term measure, the mean number of breeders produced by a breeder. "Fast" breeders produced more breeders in their lifetimes (1.33 ± 1.8 breeders; $N = 92$ "fast" breeder lifetimes) than did "slow" breeders (0.85 ± 1.2 breeders; $N = 60$ "slow" breeder lifetimes; $P = 0.046$, two-tailed t test with unequal variances). Thus, "fast" breeders not only produced more fledglings, but those fledglings were more likely to survive to become breeders than were the fledglings of "slow" breeders. Survival curves of "fast" and "slow" known-age breeders did not, however, differ significantly, as assessed by the nonparametric linear rank test (Breslow test).

Comparison of the full sample of known-age birds ($N = 250$) with the 130 unknown-age birds indicated a significant difference in overall mortality using a Breslow test based on Kaplan–Meier survival estimates (Breslow test statistic = 4.10, $P = 0.04$). Survival rate as a function of breeding span, $q_b{}^y$, for the known-age and unknown-age samples is shown in Fig. 4. The known-age sample largely corresponded to the set of birds hatched within the study area, whereas the unknown-age sample contained a majority of immigrants. At the age of first reproduction, life expectancy, e_α, for known-age birds (3.8 yr) was greater by 6 mo than that for unknown-age birds (3.3 yr). This difference decreased at later ages, such that mean difference in life expectancy beyond the 2nd yr of breeding was 1.5 mo. Fledging success of the unknown-age birds (1.90 ± 1.4
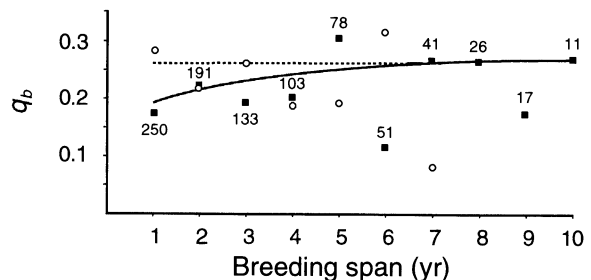

FIG. 4. Annual mortality, q_b, as a function of breeding span, for the full sample of 250 known-age and 130 unknown-age Florida Scrub Jays. Solid squares: observed mortality for 250 known-age breeders, with sample size shown above scatter plot markers. Most of the known-age breeders hatched in the study area. Solid curve: annual mortality for known-age breeders, estimated from the parameters of a Weibull model. Open circles: observed mortality for 130 unknown-age breeders. Sample sizes are shown in Fig. 3. Most of the unknown-age breeders were immigrants to the study area (as prebreeders). Dashed line: annual mortality for unknown-age breeders, estimated from the parameters of a Weibull model.

fledglings/yr, $N = 281$ breeder years), however, was equivalent to that of the full sample of known-age breeders (1.92 ± 1.4 fledglings/yr, $N = 704$).

Mortality did not differ between the sexes. Of the "fast" breeders, 62 were female and 64 were male. The linear rank test based on Kaplan–Meier survival estimation indicated no sex difference in mortality (Breslow test statistic $= 0.05$, $P = 0.83$). The Weibull shape parameter, p, of the accelerated failure model was 1.27 ± 0.08 (mean ± 1 SE) for males, and 1.22 ± 0.10 for females ($P > 0.5$). Analyzing the full sample of 380 breeders (193 females and 187 males) as a function of breeding span also failed to support a sex difference in mortality.

DISCUSSION

The major result of the present study is demonstration of actuarial senescence in an unmanipulated, natural population of birds. The age-dependent increase emerged most clearly from the most homogeneous sample: birds of high quality (as assessed by higher annual fledging rate and greater longevity) that first bred at age 2 yr. These "fast" breeders had a higher Weibull shape parameter (1.25) than did all other subsamples, especially more heterogeneous subsamples of birds that bred at later ages or were of unknown age. To our knowledge, this is the first demonstration of actuarial senescence, using the most demographically appropriate method (MLE of accelerated failure models) from direct mortality data, in a wild population of birds. Although the pattern of actuarial senescence is consistent with evolutionary theories of degenerative senescence (sensu Abrams 1991), the pattern could be the result of other causes, such as increased reproductive effort, that would not fall under the rubric of degenerative senescence. Senescence is manifested as a reduction in reproduction, in survival, or in both. Gustafsson and Part (1990) experimentally demonstrated reproductive senescence in a natural population of birds. Our study complements their result by demonstrating actuarial senescence in an unmanipulated natural population.

Our findings also illuminate the ways in which heterogeneity and conflicting processes can mask patterns of mortality.

Selection through time (demographic heterogeneity)

With variation in intrinsic quality, individuals of low quality will tend to suffer high rates of initial mortality (Vaupel and Yashin 1985). As a result, mortality may appear to be constant or even declining, simply as a result of changing ratios of high- and low-quality individuals. That is, high mortality among low-quality individuals early in the life-span may overwhelm an intrinsic pattern of increasing mortality caused by forces, such as degenerative senescence, acting on the remaining individuals. Such selection through time may be acting even in the most homogeneous sample of the present study, the "fast" breeders, for which a decelerating increase is apparent in the Weibull model estimates of mortality, q_x (Fig. 1) and the force of mortality, μ (Fig. 3). Rexstad and Anderson (1992) provide an example of the effects of such heterogeneity on estimated survival rates in mallards Anas platyrhynchos. Carey et al. (1992) analyzed mortality at advanced ages in Mediterranean fruit flies Ceratitis capitata. They suggested that the deceleration seen in the force of mortality in the oldest individuals could be caused by selection through time.

In the case of Florida Scrub Jays, it is fortunate that a measure of quality is available that is independent of mortality: annual fledging rate. Mortality in the high-quality "fast" breeders increased with age, whereas the hypothesis of constant mortality could not be rejected among lower quality "slow" breeders (Table 1). Because potential breeders always outnumber breeding vacancies (Woolfenden and Fitzpatrick 1984), the subsample of "slow" breeders contained a mixture of individuals of relatively high quality that reached age 2 yr at a time when no vacancies occurred, as well as individuals failing to gain breeding status because of lower intrinsic quality. By concentrating on a homogeneous sample of high-quality birds less subject to the force of selection through time, our analysis demonstrates that actuarial senescence occurs, but can be masked by excessive heterogeneity among individuals.

In contrast to "fast" breeders, which were homogeneous for age, the unknown-age sample was heterogeneous for age. That its Weibull model shape parameter was close to 1.0 (Table 1), and that the force of mortality was constant (Fig. 3), are attributable to high early rates of mortality, seen especially in the 24 mo following first breeding (Fig. 3). Together with the difference in mortality (Fig. 4) and life expectancy between known-age (largely local; $e_\alpha = 4.1$ yr) and unknown-age birds (largely immigrants, $e_\alpha = 3.2$ yr), this result is consistent with the hypothesis that immigrants, which constituted the bulk of the unknown-age sample, may suffer high initial mortality compared to locally produced birds. The difference did not appear to be one of quality, as indexed by mean annual fledging success, because fledging success of unknown-age birds ($\bar{X} = 1.90$ fledglings/yr) was equivalent to that of known-age birds ($\bar{X} = 1.92$ fledglings/yr). Further, the difference in life expectancy between known-age and unknown-age birds largely disappeared beyond the 2nd yr of breeding. Until the immigrants become more familiar with their new surroundings, they may be more vulnerable to mortality from predation and competition than are long-time residents. The constant mortality indicated by the Weibull shape parameter ($p = 1.00$) is consistent with the hypothesis that high initial mortality among immigrants tapers off to a level approximately equivalent to that attained as a function of the increasing (but decelerating) mortality among the sur-

vivors, and comparable to that of locally hatched birds (Figs. 3 and 4).

When we compared "fast" and "slow" breeders, the mortality curves did not differ, but fledging success did. Conversely, for "fast" and known-age (local) birds vs. unknown-age (immigrant) birds, mortality differed but fledging success did not. In the first case, we attribute the lack of significantly increasing mortality among the "slow" breeders to demographic heterogeneity (variation in quality) in the subsample. For "slow" breeders of a given quality level, we suggest, the underlying pattern would be increasing mortality (actuarial senescence), as seen in the more homogeneous "fast" breeder subsample. In the second case, we tentatively attribute the lack of increase in mortality not to demographic heterogeneity, but to an effect of unfamiliarity and initially heightened risk of mortality among all immigrants. Each of these results points to the complex suite of factors that can affect patterns of mortality among different subsets of a population.

Conflicting processes

We have suggested that controlling for heterogeneity among individuals is likely to be a useful step in clarifying patterns of mortality. Even in a homogeneous subsample, however, conflicting processes working on the same individuals can obscure patterns. For example, group size effects may decrease mortality as older birds accumulate group members for duty as sentinels, even as degenerative senescence or other factors promote increasing mortality. Although reproductive success increases with age for several years in Florida Scrub Jays (Woolfenden and Fitzpatrick 1984, 1990, Fitzpatrick and Woolfenden 1989, Marzluff et al. 1996), we have measured no corresponding increase in reproductive effort. Indeed, evidence for a decrease in one aspect of reproductive effort with age comes from the effects of group size on reproduction and survival in this species. Earlier studies (Woolfenden and Fitzpatrick 1984) showed that breeding success increased with age, in part because of recruitment of helpers. The major cause of mortality in Florida Scrub Jays is predation. Vigilance by family members plays an important role in decreasing this risk of predation (McGowan and Woolfenden 1989). Because average group size increases with breeder age (Woolfenden and Fitzpatrick 1984) , the portion of the costs of reproduction attributable to vigilance and predation should not. The pattern of increasing group size with age should work to decrease mortality with age, and it therefore seems likely that the underlying force driving increasing mortality actually may be stronger than what we have estimated. Strong inference concerning reproductive effort and costs of reproduction would, however, require experimental study (Reznick 1985, Gustafsson and Part 1990).

A potential confounder of patterns of mortality in other species, although not in Florida Scrub Jays, would be sex differences. Other potentially important sources of variation among subsamples include genetic, temporal, and spatial variation. Our population of Florida Scrub Jays has been essentially stationary (neither growing nor declining), with the possible exception of epizootics that occur with an apparent periodicity of ≈20 yr (Woolfenden and Fitzpatrick 1991). Because such temporal variation in mortality is largely restricted to prebreeders (Woolfenden and Fitzpatrick 1991), we tentatively conclude that temporal variation was a relatively minor influence on patterns of mortality in our study.

Conclusions

The long-held assumption (Nice 1937, Deevey 1947, Williams 1957) that mortality over most of the lifespan in birds is age-independent was challenged on theoretical grounds (Botkin and Miller 1974), but empirical data were lacking. Early evidence of actuarial senescence in Pied Flycatchers *Ficedula hypoleuca* (Berndt and Sternberg 1963) seemed to conflict with studies that showed mortality decreasing with age in the Red-billed Firefinch *Lagonosticta senegale* (Morel 1964), and apparent age-independent mortality in Common Terns *Sterna hirundo* (Austin and Austin 1956). Indeed, data on breeding spans of Florida Scrub Jays were used as evidence for constant mortality followed by abruptly increasing mortality in the oldest individuals (Woolfenden and Fitzpatrick 1990) .

Results of the present study suggest that the (decelerating) increase in mortality begins at the age of first reproduction. Abrams (1991) pointed out that the fitness costs of senescence may often be considerable in early maturity. Although assessment of these fitness costs requires experiment (Reznick 1985, Gustafsson and Part 1990) and is outside the scope of the present paper, the pattern of increasing mortality beginning at age of first reproduction in Florida Scrub Jays clearly represents an example in which such costs accrue early in life. With respect to models of population dynamics, the reduced survival of older individuals is unlikely to have major impact on estimates of the population growth rate, λ, but may have considerable effect on other demographic measures, such as generation time, that are important to conservation and evolutionary studies (McDonald and Caswell 1993:166–168).

Recently, several studies, in a variety of avian taxa, have produced evidence for actuarial senescence. Holmes and Austad (1995a) listed 22 species of birds for which increasing mortality was suggested. Additional evidence comes from studies of Wandering Albatross, *Diomeda exulans* (Weimerskirch et al. 1992), Common Eider, *Somateria mollissima* (Coulson 1984), and Large Cactus Finch, *Geospiza conirostris* (Grant and Grant 1989). Several of these studies suggest a threshold after which mortality increases sharply (e.g., Aebischer and Coulson 1990, Weimerskirch 1992). Because these analyses were not strictly comparable to

those of the present study, it remains to be determined whether or not these thresholds represent true change points in the force of mortality curve. Although no evidence of increasing mortality was found in a 30-yr study of Northern Fulmars *Fulmarus glacialis* (Ollason and Dunnett 1988), we speculate that even 30 yr of data may be insufficient to show the full extent of the curve in this exceptionally long-lived species. We suggest that attention to possible sources of heterogeneity and conflicting processes, and use of models like those in the present paper, will provide a basis for rigorous and widespread demonstration of actuarial senescence in natural populations of birds.

Williams (1957, 1992) and Nesse (1988) noted that avian mortality appears to increase much more slowly than that of mammals. The results presented here fit the pattern of a slow increase in mortality rather than an abrupt increase at advanced ages. Promislow (1991) and Gaillard et al. (1994) found evidence for senescence in mammals, with onset apparently delayed beyond age of first reproduction. Although the data used to estimate mortality rate doubling time in the present study were noisy (Fig. 2), the long MRDT (6.4 yr) estimated in the present study echoes that found by Finch et al. (1990) in birds, using maximum recorded life-spans. Williams (1957), Pomeroy (1990), and Austad and Fischer (1991) suggested that flight confers reduced vulnerability to predation and may be an important influence on longevity as well as the rate of increase in mortality. The relatively long life-spans of bats and gliding mammals (Austad and Fischer 1991, Holmes and Austad 1995b) provide support for the hypothesis within mammals. This advantages-of-flight hypothesis deserves further testing in birds.

Three major obstacles have hampered the demonstration of increasing mortality in natural populations of birds. First, accumulating sufficient data for long-lived animals requires long-term monitoring of marked individuals. Second, heterogeneity among individuals may obscure patterns that would be apparent within homogeneous groups. High early mortality of individuals of lower quality may produce declining mortality with time, at least until the susceptible individuals are a negligible proportion of the total. An additional complication, in some cases, is that conflicting processes may come to bear even on rather homogeneous populations. Although properly designed experiments can control for many sources of heterogeneity (e.g., Tatar et al. 1993), they are often feasible only with short-lived species whose mortality patterns and sources of heterogeneity may be very different from those of long-lived natural populations of vertebrates. Finally, mortality may generally increase more slowly with age in birds than in many mammals, increasing the difficulty of detection. By overcoming some of the obstacles raised by heterogeneity and conflicting processes, and by using techniques well-suited to detecting patterns of mortality, our study suggests that age-specific mor-

tality increases in birds as it does in other animal groups. Whether this pattern of increasing mortality is true degenerative senescence or is driven by other mechanisms, and whether avian mortality does generally increase more slowly with age than in mammals are intriguing questions that require further comparative, experimental and long-term observational studies (Finch and Ricklefs 1991).

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