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MORTALITY RATES AND SURVIVAL OF BIRDS

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Adult birds are assumed to have a constant mortality rate in most bird population studies. Here we analyze mortality and survivorship of several species of birds for which data are reasonably good, and we conclude that a constant mortality is an unreasonable assumption. Alternative models of age-dependent mortality are discussed.

In his classic study of life tables for natural populations, Deevey (1947) reviewed available data on avian mortality and concluded, "All natural populations so far investigated in detail appear . . . to be alike in suffering a constant risk to death from early adult life to the end of the life span." This hypothesis, first introduced by Nice (1937), has been almost universally accepted in subsequent studies of avian mortality and survival (Lack 1943*a*, 1943*b*; Davis 1951; Hickey 1952; Gibb 1961; Slobodkin 1966; and others). In other words, birds are generally assumed to have a constant annual rate of adult mortality and the type III survivorship described by Slobodkin (1966), in which a constant fraction of the cohort dies during each age interval. This type of survivorship, given average annual mortality rates reported for several species of birds, would result in potential natural longevity of 100 years or more in many cases. With an annual mortality of 3%, the best present estimate, there is one chance in 1,000 that a royal albatross (*Diomedea epomorphora*) breeding in New Zealand today was 25 years old when Captain Cook made his first visit to the island in 1769! If the initial cohort were 10,000 birds, a 302-year-old bird might live in the colony today.

Fish are also believed to have an approximately constant adult mortality throughout life (Ricker 1958; Beverton and Holt 1958), but this conclusion is based on better data and more reasonable biological assumptions. Ages of most bony fish can be determined directly by counts of the annular rings on their scales, and complete samples of all age classes of a fish population can often be obtained at an instant in time, or a cohort can be followed through several years of sampling. Consequently, detailed and accurate life tables are available for many species of fish. Moreover, fish are of indeterminate size and age, they do not have the high metabolic antithermal cost of birds, and the nature of the aging process in fish would seem to be more conducive to extreme old age. Nevertheless, there are few authenticated records of fish living for more than 40 or 50 years in natural environments. The record is apparently a lake sturgeon (*Acipenser transmontanus*) that lived for 152 years (Altman and Dittmer 1962).

One possible approach to the question of potential natural longevity in animals is through records of captive animals, but these are often suspect. Because of the popularity and public-relations value of old animals in zoos, officials have sometimes replaced one individual with another to perpetuate a tradition, and there is reason to doubt many, if not most, popular accounts of very old animals. Flower (1947) examined records of ages of captive animals and found that the famous elephant, "Princess Alice," which was supposed to have lived for 157 years, changed from an African to an Indian elephant in the process! Among authenticated records of animals reaching very old age in captivity, the oldest appear to be two tortoises (*Testudo elephantopus* and *T. sumeirei*) which lived for 100–150 and 152 years, respectively. Hann (1953) listed nine species of birds with authenticated records of old age in captivity, and only three species lived for more than 50 years; the oldest was an eagle owl (*Bubo bubo*) that lived for 68 years. More recently, Davis (1969) reported a Siberian crane (*Grus leucogeranus*) that lived for 61 years and 9 months in the National Park Zoo in Washington, D.C.

Obviously, factors affecting survival in natural populations differ from those of captive animals, and few species are likely to have natural longevity approaching the maximum life spans they would reach in captivity. The record for natural longevity among wild birds is a herring gull (*Larus argentatus*), banded as a chick and recovered 36 years later (Pettingill 1967). A blackbrowed albatross (*Diomedea melanophrys*), first seen in a colony of gannets (*Sula bassana*) on Myggaenaes Holm in the Faeroe Islands in 1860, was shot in 1894, after apparently having lived in the colony for 34 years. Clapp and Hackman (1969) reported a natural longevity of 34 years for a great frigatebird (*Fregata minor*), and several records of sea birds living for 20–30 years exist (Bergstrom 1952, 1956; Clapp and Sibley 1966; Serventy 1970).

For reasons discussed later, band returns probably provide serious underestimates of natural longevity in birds, but in view of the fact that only two animals, a fish and a reptile, have been known to live for more than 150 years and only four birds have lived for longer than 50 years in captivity, a constant adult mortality rate that would result in a potential natural longevity of more than 100 years is improbable for most species of birds, and an age-dependent mortality is a more likely description of avian survivorship.

Although it seems entirely reasonable that adult avian mortality should be in some way age dependent, this possibility has been almost universally ignored in the literature. Perhaps this has occurred because few, if any, data seem to suggest an age-dependent rate and because, as Austin (1942) has written, it seems "of little importance biologically speaking how long members of a species live providing their life span is long enough for a generation to reach and maintain sexual maturity in order to duplicate the achievement of its predecessors." We contend that the assumption of age-independent mortality (1) leads to unreasonable predictions contradic-

tory to observation, (2) is a poor conceptual hypothesis, and (3) has non-trivial consequences in regard to bird species threatened with extinction or subject to hunting.

METHODS

We compiled a list of species (table 1) for which published records provide a range of adult mortality rates from 0.72 for the blue tit (*Parus caeruleus*) to 0.03 for the royal albatross (*Diomedea epomorpha*). We used these rates to calculate (1) the average expectation of life after a specified initial age, (2) the predicted maximum age reached by one individual in 1,000, usually known as the potential natural longevity or maximum life span, and (3) the predicted maximum age for one individual in 100,000. We use these data to develop models of age-dependent mortality which are consistent with different assumptions about the potential natural longevities of each species.

Estimates of Mortality

Life tables for birds are usually constructed from estimates of mortality and survival obtained from one or more of the following methods: (1) an annual census of banded individuals returning to breed each year in a local area or colony; (2) the age at death of birds banded as nestlings, or as young of known age, and subsequently recovered; (3) retraps of banded individuals of known age; or (4) in a stationary population, the number of new individuals breeding each year is assumed to be equal to the death rate. Various sources of error in these methods are described in detail by Davis (1951), Hickey (1952), Kadlec and Drury (1968), and others. In general, errors in these methods almost invariably result in overestimates of mortality, and we can probably assume that most published mortality rates for birds are higher than true rates (Kadlec and Drury 1968, Lack 1966).

Band Returns

Most life tables and almost all records of longevity for natural populations of birds are obtained from band returns. Table 2 shows bandings and recoveries for some of the species in table 1. These records are for birds banded in Britain from 1909 through 1969 (Spencer 1971).

Recovery rates of banded birds are usually less than 4%, and the cumulative average for 6,898,046 birds banded in Britain over the period of 60 years is 2.7%. The probability of recovery of a banded bird is influenced by factors such as its size and conspicuousness, the source and place of mortality, and whether recoveries are due to chance or deliberate search and retrieval. For example, investigators studying a particular species may systematically search for dead birds, and many returns shown in table 2

TABLE 1
ADULT SURVIVORSHIP CHARACTERISTICS FOR SEVERAL AVIAN SPECIES

SPECIES	AVERAGE ANNUAL ADULT MORTALITY	MAXIMUM RECORDED LONGEVITY (YEARS)	LIFE EXPECTANCY (YEARS)	POTENTIAL NATURAL LONGEVITY		
				(1/1,000)	(1/10,000)	(1/100,000)
Blue tit (<i>Parus caeruleus</i>)	0.72 ^a	9 ^b	0.9	6	7	10
European robin (<i>Erithacus rubecula</i>)	0.62 ^c	12 ^c	1.1	8	10	12
Redstart (<i>Phoenicurus phoenicurus</i>)	0.56 ^a	...	1.3	9	11	15
Starling (<i>Sturnus vulgaris</i>)	0.52 ^d	20 ^b	1.4	10	13	16
	0.63 ^d
Blackbird (<i>Turdus merula</i>)	0.42 ^e	7 ^b	1.9	13	17	21
Lapwing (<i>Vanelius vanellus</i>)	0.34 ^a	16 ^b	2.4	17	22	28
Grey heron (<i>Ardea cinerea</i>)	0.31 ^f	24 ^b	2.7	19	25	31
Alpine swift (<i>Apus melba</i>)	0.18 ^a	16 ^b	5.1	35	46	58
Common swift (<i>Apus apus</i>)	0.18 ^a	21 ^b	5.1	35	46	58
Yellow-eyed penguin (<i>Megadyptes antipodes</i>)	0.10 ^a	...	9.5	66	87	109
Sooty shearwater (<i>Puffinus griseus</i>)	0.07 ^g	27 ^a	13.8	96	127	159
Fulmar (<i>Fulmaris glacialis</i>)	0.06 ^h	10 ⁱ	16.2	102	149	186
Gannet (<i>Sula bassana</i>)	0.06 ^j	17 ^b	16.2	102	149	186
Herring gull (<i>Larus argentatus</i>)	0.09 ^k	36 ⁱ
	0.04 ^k	...	24.5	170	226	282
Royal albatross (<i>Diomedea epomophora</i>)	0.09 ^m	10 ^b
	0.03 ^a	...	32.8	228	302	378

NOTE.—Potential natural longevity is expressed as the expected number of years for a cohort of size n ($n = 1,000, 10,000, \text{ and } 100,000$) to be reduced to one and only one individual, assuming an age-independent mortality rate.

- ^a Lack 1954.
- ^b Rydzewski 1962.
- ^c Lack 1943b.
- ^d Lack and Schifferli 1948.
- ^e Lack 1943a.
- ^f Lack 1949.
- ^g Richdale 1963.
- ^h Dunnott, Anderson, and Cormack 1963.
- ⁱ Thomson & Leach 1952.
- ^j Nelson 1964.
- ^k Kadlec and Drury 1968.
- ^l Pettingill 1967.
- ^m Westerskov 1963.

TABLE 2
RECOVERIES OF BIRDS Banded IN BRITAIN FROM 1909 THROUGH 1969 (SPENCER 1971)

Species	Total Banded	Total Recovered	Recovery Rate (%)
Manx shearwater (<i>Puffinus puffinus</i>) ...	175,745	2,356	1.3
Fulmar (<i>Fulmaris glacialis</i>)	17,993	206	1.1
Gannet (<i>Sula bassana</i>)	33,785	1,821	5.4
Heron (<i>Ardea cinerea</i>)	6,411	986	15.4
Lapwing (<i>Vanellus vanellus</i>)	89,662	1,976	2.2
Herring gull (<i>Larus argentatus</i>)	99,718	3,928	3.9
Kittiwake (<i>Rissa tridactyla</i>)	31,053	762	2.4
Common swift (<i>Apus apus</i>)	66,309	1,404	2.1
Blue tit (<i>Parus caeruleus</i>)	340,399	5,430	1.6
Blackbird (<i>Turdus merula</i>)	509,983	19,662	3.8
Redstart (<i>Phoenicurus phoenicurus</i>) ...	28,625	168	0.6
European robin (<i>Erithacus rubecula</i>) ...	167,308	3,769	2.2
Starling (<i>Sturnus vulgaris</i>)	549,802	20,880	3.8

are also of birds recaptured and released at some time after their initial bandings. These factors are undoubtedly important in the relatively high recovery rate for the gannet, as compared with the rates for other sea birds in this list. Waterfowl have relatively high recovery rates because they are hunted and retrieved; only 582 white-fronted geese (*Anser albifrons*) were banded in Britain but 190 were recovered, for a return rate of 32.6%. The recovery rate of 15.4% for the heron is undoubtedly due to the fact that it is a very large, conspicuous bird, and populations of this species have been investigated for many years (Lack 1966). Recovery rates for small, inconspicuous birds are, however, often quite low (many species have recovery rates of less than 1%). Of 161,809 willow warblers (*Phylloscopus trochilus*) banded in Britain through 1969, 417 were recovered, for a return rate of only 0.2%. Because of the number of years required for long-lived birds to express their maximum life spans and the low recovery rates and high mortality rates of short-lived birds, a very large number of individuals must be banded, in either case, to have a reasonable expectation of recovering a bird of maximum natural longevity.

This problem is further complicated by the fact that the majority of bandings of all species have been made in recent years, and records of maximum longevity of long-lived birds presently depend on relatively small initial cohorts. The history of herring gull (*Larus argentatus*) bandings in the United States shows this. There is no record of when the first herring gulls were banded—there are references to bandings in the early 1920s but this species was probably banded when the banding program was begun by the American Bird Banders' Association in 1909 (B. Sharp, personal communication). Records of the U.S. Fish and Wildlife Service Bird Banding Laboratory show that 18,567 herring gulls had been banded in the United States by 1931 and that bandings have increased almost exponentially since then, except for the decrease in banding activity during the decade of World War II (1941–1950). As a result of this trend, 46% of the total of 646,055 herring gulls banded in the United States were banded in the past decade (1961–1970), and approximately 68% of the total were

banded after 1950. The bandings up to and including 1931 constitute only 3% of the total, and this cohort of 18,567 birds banded over a period of about 15 years is the only one that might reveal a gull that had reached an age of 40 years or more. Kadlec and Drury (1968) estimate that 30%–70% of banded chicks die in their first year and that the adult mortality rate of the New England herring gull population is between 4% and 9% per year. The recovery rate of banded herring gulls in the United States is almost identical with that in Britain, about 4% (Kadlec and Drury 1968), so that the probability of recovering an individual banded before 1931 is quite low.

Another important factor, especially for relatively long-lived birds that frequent salt water, is that aluminum bands become corroded and worn and may be lost before the death of the bird. Several authors (Kadlec and Drury 1968; Ashmole 1971; and others) have suggested that mortality tables based on band recoveries are unreliable and bear little relation to real patterns of mortality and survivorship. Band loss undoubtedly reduces the probability of recovering very old birds, at least in some species, but this factor may not be serious enough to eliminate the possibility of some long-lived birds reaching their maximum potential natural longevity with intact and legible bands. Harris (1964) studied wear and loss of bands on manx shearwaters (*Puffinus puffinus*) and concluded that 4 years is the useful life of bands on most of these birds. Kadlec and Drury (1968) estimated band loss in herring gulls by calculating the amount of loss required to adjust mortality tables derived from banding to data of assumed mortality rates in censused populations. They concluded that band loss does not start until the third or fourth year and reaches a constant rate after about the sixth year. According to their calculations, which assume a constant true rate of adult mortality, band loss might be as high as 20% per year after the sixth year, and almost all bands would be lost after about 20 years.

Earlier we mentioned many records of birds recovered with their bands intact and legible after 20 or 30 years, but the probability of such returns could be quite low; thus, we do not yet know whether longevity records of long-lived species will increase substantially with time and additional bandings, or whether banding data more often measure the life of the band rather than the bird. In either case, considering various sources of error in band returns and the fact that a very large proportion of the total bandings are fairly recent, the potential natural longevity of many species listed in table 1 are undoubtedly much greater than present records indicate.

Life Tables

Deevey (1947) and Hickey (1952) described different methods used to construct life tables for birds. As juvenile mortality is considerably higher than adult mortality in birds (Lack 1954), the conventional practice is to

calculate the rate of mortality for those individuals which survive after a selected initial age and to use this value to describe the survivorship characteristics of the species. The selected initial age is usually 0.5 years, but may be 1.5 years or greater, depending upon the breeding behavior of the species.

Average Annual Adult Mortality

Average annual adult mortality is often calculated as a simple arithmetic mean of all years for which mortality is observed, but most authorities use weighted annual mortality rates which usually are calculated as $M_w = (D_1 + D_2 + D_3 \dots D_n) / (D_1 + 2D_2 + 3D_3 \dots + nD_n) = \Sigma D_i / \Sigma iD_i$, where $D_1, D_2, D_3, \dots D_n$ are the number of deaths in each year and M_w is the weighted mean annual mortality rate. Here we accept the mortality rates published by several authors and do not attempt to distinguish between weighted and arithmetic means, both of which are noted simply as M .

Expectation of Life

Given that M is known and mean annual mortality rates for each age group do not differ appreciably from the overall mean for the population, expectation of life from the specified initial date can be calculated as $e_1 = (1/M) - (1 - p)$, where e_1 is expectation of life, from time t , and p is the mean period survived during the year of death. However, a uniform mortality rate throughout the year is a reasonable approximation, and expectation of life can be calculated more simply as $e_1 = (2 - M) / 2M$.

Potential Natural Longevity

Assuming annual mortality is age independent, the probability, P , that an individual will survive a given number of years, A , is $(1 - M)^A = P$ or $A = \ln P / \ln(1 - M)$, where \ln is the logarithm to the base e . Potential natural longevity is usually defined in terms of $P = 1/1,000$, but this is a convention in which the actual sample size is adjusted to 1,000 to allow comparisons between different populations. We used values for M in table 1 to calculate A for $P = 1/1,000$, $1/10,000$, and $1/100,000$ to show a range of potential natural longevity for different sized cohorts.

RESULTS

Table 1 shows average annual mortality rates and maximum recorded life spans for selected species. The authority shown for each annual mortality rate calculated and reported this rate, but is not necessarily the author of the original research. Because of potential errors in estimating mortality rates referred to above, we used the lowest reported rate for each species. Rates shown in table 1 were used to calculate the potential natural

longevities that would result from the assumption of a constant, age-independent mortality.

For birds with reported annual mortality rates of 30% or more and life expectancies of less than 5 years, the reported maximum longevity is often greater than the predicted potential natural longevity as it is currently defined ($P = 1/1,000$). The observed life span of the starling, for example, exceeds the predicted lifetime of 1/100,000. This suggests perhaps that the observed annual mortality is too high or that survival improves with age for some age classes of this species. The observed longevity for the blue tit and European robin exceed the predicted lifetimes of 1/100,000 and also suggest that estimated annual mortalities for these species may be too high. The recorded maximum lifespans of 21 years for the common swift (*Apus apus*) and 16 years for the alpine swift (*Apus melba*) are somewhat less than their potential natural longevity of 35 years, but the latter value might be a reasonable approximation of real survivorship.

Deevey's (1947) conclusion that there is an approximately constant annual mortality in adult birds was based on a limited number of available life tables for species with life expectancies of from 1.0 years for the European robin to 2.4 years for the lapwing, and average annual adult mortality rates of 0.34 or more. For the lapwing, a constant annual mortality of 0.34 results in a 1/1,000 survival probability of 17 years, which agrees well with the recorded lifespan of 16 years for this species. The remaining species, with average annual adult mortality rates of 12% or less and theoretical life expectancies of over 50 years, show increasingly large differences between their potential natural longevity predicted from age-independent mortality rates and recorded maximum longevity, as well as with lifespans that are reasonably consistent with the records of old age in animals.

For example, the predicted probable lifetime of one sooty shearwater in 1,000 is $3\frac{1}{2}$ times the longest observed. For the fulmar, the ratio is 10:1, for the gannet 6:1, the herring gull about 5:1, and the royal albatross 23:1. Since the total populations of these species in the last few centuries could easily have been 10,000 or 100,000 or more birds, the assumption of age-independent mortality leads to possible lifetimes even more at variance with observation. Clearly, the following three statements cannot be true simultaneously, and one or all of them must be false: recorded maximum longevity accurately reflects true longevity, recorded annual mortality accurately measures true mortality, and adult mortality is age independent.

As suggested above, recorded maximum longevity are very likely too low, but it is unreasonable to expect, on the basis of observations of reptiles and mammals as well as birds, that the longevity of even the longest-lived species would exceed 150 years.

The problem would be trivial if the assumption of age-independent mortality led to the prediction that only a few individuals in a cohort would remain alive at the time of observed maximum longevity. Then one could say that adult mortality was age independent until that final year, when

the remaining few individuals would die of senility. However, using the table 1 values for M , 23% of the original cohort of herring gulls would remain alive at year 36 and 8% of the population at year 60. If we assume a pure death process (Chiang 1968), the probability that 1,000 sooty shearwaters would be reduced to 10 individuals or less in 30 years is vanishingly small.

Age-dependent Mortality

In light of the previous discussion, it seems only reasonable to assume that mortality increases with age at least in older individuals. Lacking further evidence, nothing definite can be said regarding the kind of age-dependent effects that might occur, and indeed those who hope to understand the population dynamics of birds clearly must obtain more information regarding these effects.

The simplest assumption regarding mortality and age is that the rate of mortality increases linearly with age so that m_i , the mortality rate of age class i , is $m_i = \alpha + m_{i-1}$, where α is a constant and m_{i-1} is the mortality rate of the previous age class. Adding only this assumption to previous ones, we constructed hypothetical cohorts for a number of species and determined the age-dependent rate required to reduce 1,000 birds in year 1 to one bird at the maximum reported age (table 3). Here the reported annual mortality rate is taken as the initial rate. Figure 1 shows the resulting survivorship curve for the sooty shearwater assuming a maximum longevity (1/1,000 probability) of 30 years and an initial adult mortality of 0.07. While the curve for age-independent mortality leaves approximately 12% of the birds alive at their observed maximum age, the simple assumption of a constant increase in mortality of 0.01 per year leads to a reduction in 30 years to one individual in 1,000.

Table 3 shows that comparatively small age-dependent rates are required to fulfill expected real lifetimes. It is therefore not surprising that age-dependent rates have not been observed. In fact, the kind of studies that have been made tend to obscure the existence of such rates. Given the stochastic properties of a real population and the difficulty of observing

TABLE 3
AVERAGE ANNUAL MORTALITY RATES, ASSUMED POTENTIAL NATURAL LONGEVITIES,
AND REQUIRED AGE-DEPENDENT MORTALITY RATE FOR SOME SPECIES

Species	Reported Average Annual Mortality	Assumed Maximum Lifetime	Required Age-dependent Rate
Blue tit	0.72	9	0.0
Lapwing	0.34	17	0.0
Common swift	0.18	25	0.006
Sooty shearwater	0.07	30	0.01
Herring gull	0.04	40	0.00636
Royal albatross	0.03	60	0.00284

NOTE.—The age-dependent rate is the constant annual increase in mortality necessary to decrease a cohort of 1,000 at the start of adulthood to one or less by the assumed maximum age.

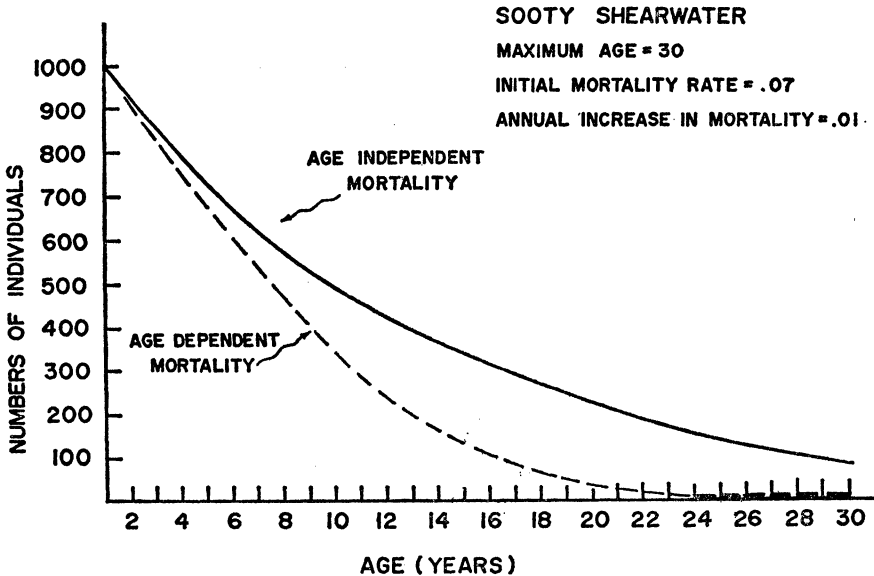


FIG. 1.—Theoretical survivorship curves for the sooty shearwater assuming age-independent and age-dependent mortality. The age-dependent factor was chosen to reduce an initial cohort of 1,000 birds in their first year of adulthood to one or less in 30 years, the reported maximum lifetime.

such a population, one would expect age-dependent rates to be revealed most clearly in long-term studies of stationary populations. As we have pointed out, even the best banding studies have not existed long enough or involved enough individuals to provide such data. Furthermore, the species most often banded, the herring gull, has been rapidly expanding during the twentieth century. The rapid expansion of this population would greatly obscure age-dependent mortality factors. Finally, the “mortality” of inert objects such as the bands themselves would tend to follow an age-independent rate. Studies heavily dependent on banding would for this reason also tend to obscure the existence of age-dependent mortality in the birds.

An age-independent mortality clearly must be rejected. What should replace it? The only justification for assuming a constant age-dependent factor is its simplicity. No doubt those familiar with the study of avian physiology or populations can suggest other kinds of age-varying mortality more consistent with their own understanding and intuition. For example, a plausible argument could be made that long-lived species would have a survivorship curve similar to that reported by Jordan, Botkin, and Wolf (1971) for moose (*Alces alces*). In this curve, annual mortality reaches a minimum in midadulthood, increasing afterward. The reduction of mortality in the early stages of adulthood in birds might occur through learning behavior, for example, in regard to avoidance of predation.

With the use of current knowledge, perhaps more conceptually satis-

factory models of avian population dynamics could be generated and used to construct hypothetical populations, which could then be compared with observed ones.

SUMMARY

Birds have been assumed to have a constant adult mortality rate in which a constant fraction of a cohort dies in each age interval. Average annual mortality rates reported for many species would result in exceedingly long potential life spans, and it seems more reasonable to assume that avian mortality is age dependent. Data on the mortality and survivorship of several species of birds are analyzed and alternative models of age-dependent mortality are discussed.

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