BIAS REDUCTION IN BIRD LIFE EXPECTANCY ESTIMATES

By Edwin C. Franks

The length of time between a bird's hatching and its death is its life span, and its life expectancy when just hatched is the mean of the life spans of all individuals in the population. The *further* life expectancy, or mean after lifetime, of a bird at any given age is the average length of additional life achieved by individuals of that age in the population. As a bird grows older and progressively avoids an early death, its total life expectancy steadily increases, but its further life expectancy may fluctuate and will decrease in old age. Thus, although the life expectancy of a newborn human in the United States is 71 years, a 70-year-old person has a life expectancy of 82 years; the further life expectancy decreased from 71 years at age 0 to only 12 years at age 70 (United Nations, 1973).

To calculate the further life expectancy, mortality statistics are arranged into life tables (Eberhardt, 1971). Table 1 reveals how the further life expectancy at any age can be derived arithmetically if the ages of many recaptured birds are known.

Table 1
Life table, Blue Jays recaptured alive.

Age class[1]	Final recaptures in age class	Number alive at start	Percent still surviving at start	Mean percent surviving, age i and i+1	Further life expectancy at start of age, in years
0	117	1298[a]	100.0[c]	95.5[f]	2.17[r]
1	711	1181[b]	91.0[d]	63.6[g]	1.34[s]
2	240	470	36.2[e]	27.0[h]	1.61
3	95	230	17.7	14.1[i]	1.77
4	52	135	10.4	8.4[j]	1.66
5	39	83	6.4	4.9[k]	1.38
6	23	44	3.4	2.5[l]	1.16
7	15	21	1.6	1.0[m]	0.88
8	4	6	0.5	0.3[n]	0.83
9	2	2	0.2	0.1[q]	0.50
10	0	0	0.0	0.0	0.00

[1]Age class 0 includes birds from hatching through the next 31 December, age class 1 includes birds between their first and second January 1, etc.

[a]sum of final recaptures ages 0-9

[b]sum of final recaptures ages 1-9

$$d = \frac{b}{a} \qquad e = \frac{470}{a} \qquad f = \frac{c+d}{2} \qquad g = \frac{d+e}{2}$$

$$r = \frac{\text{sum of f through q}}{c} \qquad s = \frac{\text{sum of g through q}}{d}$$

Samples of wild birds that are banded and then subsequently recaptured have been used in life expectancy calculations since the 1940's. Variations in analytic methods and the necessary assumptions about the data were reviewed by Hickey (1952) and Henny (1972).

POSSIBLE BIASES

Lack (1946) and Farner (1949) demonstrated that many species have a high mortality rate in their first several months of life and therefore recommended that life expectancy calculations be based only on birds that survive until their first 1 January. But since the number of birds still alive in an age class decreases with increasing age, life expectancy calculations for older ages are based on progressively fewer birds. To avoid excessive juvenile mortality data, and yet to have the largest possible sample size, the further life expectancy comparisons in this paper are calculated from those birds which survived until their first 1 January of life.

The calculated life expectancy may vary depending on whether the life span data are from bands found on dead birds or from bands on living recaptured birds (Hickey, 1952). Because living birds still have more life ahead of them at the time they are recaptured, it is reasonable that data based on living bird recaptures should underestimate life expectancy. On the other hand, a large sample of living birds can show that the wild population contains a large number of young birds, a smaller number of middle-aged birds, and only a few old ones; a life table from these data might be an accurate measure of the life expectancy (Farner, 1945).

The calculated life expectancy may also vary depending on whether the data are from birds recaptured near the banding location or from birds recaptured farther away. This should make no biological difference on how long the bird lives, but it may affect the life span statistics. The most probable recapture site for a small bird is at its original banding location, because most birds tend to return to the original site and because very few humans in a bird's normal travel route (except the original bander) are equipped to catch the bird. This may bias the life expectancy calculations in the following way. Suppose a bird is caught by its original bander the next year after banding, the recapture is reported to the banding office, and then the bander either moves away or stops banding. If the same bird returns to that location in subsequent years, the fact that it is still alive will not be entered in the banding files. Even if the bander continues working in the same place, he may report only the first recapture of a bird that continues to return month after month. Thus we should expect that the banding *returns* will be biased, showing a shorter life expectancy than bands recovered elsewhere (Farner, 1955; Fankhauser, 1971; Henny, 1972). Since the late 1950's, return data may show bias in the opposite direction due to the bird banding office discouraging the filing of band return records unless they demonstrate a very old age or unusual season of the year (Baysinger, 1971).

This paper investigates the effects of these possible biases to determine which types of band-recapture data provide the most accurate life expectancy estimates.

METHODS

Life tables for eight species were constructed from band encounter data compiled through August 1970 by the Bird Banding Laboratory of the U. S. Fish and Wildlife Service. All data used were from birds banded at a known age (local, hatching year, second year). Ages were determined on a calendar year basis only, so that each bird graduated to the next higher age class on 1 January each year. The birds used in the statistical treatment were those that were banded in 1963 or earlier, to allow at least seven years for individuals to be recaptured. For bands with more than one recapture reported, only the final recapture was used. Out of 25 passerine species summarized by the BBL for this study, 8 had enough recaptured birds that had been banded at a known age before 1963 to be useful: Blue Jay (*Cyanocitta cristata*), Tufted Titmouse (*Parus bicolor*), Brown Thrasher (*Toxostoma rufum*), Wood Thrush (*Hylocichla mustelina*), Northern (Baltimore) Oriole (*Icterus galbula*), Brewer's Blackbird (*Euphagus cyanocephalus*), Golden-crowned Sparrow (*Zonotrichia atricapilla*), and White-throated Sparrow (*Zonotrichia albicollis*). Five life tables were constructed for each species: (1) from those individuals that were released alive at the time of final recapture, (2) from those individuals that were either found dead, or were killed, at the time of final encounter, (3) from those individuals that were recaptured or found dead in the same 10-minute quadrangle of latitude and longitude in which they were banded (the *returns*), (4) from those individuals that were recaptured or found dead at least 20 minutes of latitude or longitude from the banding site (the *recoveries*), and (5) from all records for the species regardless of condition or location of recapture. Recaptures lacking definite information on whether a bird was alive or dead were excluded from categories 1 and 2. Recaptures in a 10-minute quadrangle adjacent to the banding quadrangle were excluded from categories 3 and 4 because of possible ambiguities in the banding or recapture location.

Life tables developed for this study were of the composite type (Hickey, 1952), in that the birds in any one age class were banded over a broad span of years and recaptured over a broad span of years. The further life expectancy values given in the following tables apply to birds that have just reached their first 1 January (the start of age class 1) and the sample size (n) is the number of birds alive at the start of age class 0. The species included in each table are those with at least 15 birds in the sample.

RESULTS AND DISCUSSION

The difference in calculated further life expectancy (mean after lifetime) that can be caused by the sample consisting only of living recaptures as opposed to birds found dead, or consisting only of banding area returns as opposed to more distant recoveries, are listed for the Blue Jay in Table 2. Values in the top line of this table are taken from Table 1; all other lines were derived similarly.

TABLE 2
Blue Jay, further life expectancy at first 1 January.

Type of sample	Further life expectancy, yrs.	Sample size (n)
Living birds only	1.34	(1,298)
Dead birds only	2.01	(839)
Returns only	1.56	(1,673)
Recoveries only	1.69	(194)
All records	1.60	(2,183)

To determine whether the differences in calculated further life expectancy evident in Table 2 represent distinct biases or are simply due to vagaries of the sample, data from several species were compared and tested for significant differences by using a *t*-test with paired samples (Freund, Livermore, and Miller, 1960). Table 3 compares the further life expectancy based on birds found dead with the further life expectancy based on birds of the same species that were recaptured alive. For each species, the value based on live recaptures is shorter than the value based on birds killed or found dead. The difference is statistically significant, $P < .01$. Live recaptures apparently must provide an unduly short further life expectancy estimate.

TABLE 3
Further life expectancies, dead recaptures vs. live recaptures.

Species	Dead birds	(n)	Live birds	(n)
Blue Jay	2.01	(839)	1.34	(1,298)
Tufted Titmouse	1.17	(40)	1.08	(206)
Brown Thrasher	1.80	(151)	1.36	(185)
Wood Thrush	1.47	(50)	1.01	(79)
Brewer's Blackbird	1.44	(90)	1.19	(44)
Golden-crowned Sparrow	1.63	(104)	1.19	(804)
White-throated Sparrow	1.17	(137)	1.06	(532)
Mean	1.53		1.18	

Table 4 combines the living and dead recaptures, but divides them in categories of returns vs. recoveries. In each species, the

TABLE 4
Further life expectancies, returns vs. recoveries.

Species	Returns	(n)	Recoveries	(n)
Blue Jay	1.56	(1,637)	1.69	(194)
Brown Thrasher	1.52	(215)	1.57	(63)
Baltimore Oriole	1.73	(32)	1.93	(16)
Brewer's Blackbird	1.29	(99)	1.81	(17)
White-throated Sparrow	1.01	(524)	1.30	(73)
Mean	1.43		1.66	

sample based on returns showed a shorter further life expectancy than the sample based on recoveries. The difference is significant, $P < .05$, and agrees with the hypothesis that the degree of persistence of the bander, combined with the normal homing behavior of the birds themselves, causes the returning birds to appear to have a shorter life expectancy than those recovered elsewhere. The less-biased data, then, are probably from the birds recovered away from the banding area.

If the preceding statement is correct, live recaptures provide unduly short further life expectancy estimates. The four species that appear in Tables 3 and 4 are summarized in Table 5. The mean life expectancy of the recoveries (probably relatively unbiased) is 1.59 years, not significantly different from that of the same species found dead (1.61 years) but consistently and significantly

TABLE 5
Further life expectancies of the four species included in live, dead, and recovery samples.

Species	Recoveries	(n)	Dead	(n)	Alive	(n)
Blue Jay	1.69	(194)	2.01	(839)	1.34	(1,298)
Brown Thrasher	1.57	(63)	1.80	(151)	1.36	(185)
Brewer's Blackbird	1.81	(17)	1.44	(90)	1.19	(44)
White-throated Sparrow	1.30	(73)	1.17	(137)	1.06	(532)
Mean	1.59		1.61		1.24	

greater than that of the same species recaptured alive (1.24 years, $P < .05$). Although only four species had sufficient sample sizes for this comparison, it appears safe to conclude that birds recaptured alive provide biased data leading to a calculated further life expectancy that is unduly short.

Because data on birds found dead are therefore less biased than data on birds recaptured alive, and because data on birds recovered away from the banding area are less biased than data on banding area returns, one might suppose that data from individuals that were both dead *and* not near the banding area would be least biased of all. Table 6 shows that for some species, the dead *returns* showed the greater further life expectancy at age 1, but for other species, the dead *recoveries* showed the greater value. The direction of difference is clearly not consistent among species, so there can

TABLE 6
Further life expectancies of dead returns vs. dead recoveries.

Species	Dead returns	(n)	Dead recoveries	(n)
Blue Jay	2.07	(477)	1.59	(148)
Brown Thrasher	2.10	(49)	1.57	(42)
Brewer's Blackbird	1.37	(50)	1.96	(15)
White-throated Sparrow	1.02	(21)	1.38	(50)

be no generalization that samples should be limited to dead birds recovered away from the banding quadrangle. To limit the data in that way would reduce the number of birds in the sample without necessarily improving the accuracy of the life expectancy estimate.

All of the above comparisons are based on relatively few species, and in some cases, on small sample sizes. Conclusions must be viewed with these conditions in mind. Apparently the comparisons showing consistent and significant differences may be applicable to many similar species, whereas comparisons showing inconsistent or non-significant differences may be less worthy of generalization.

SUMMARY AND CONCLUSION

Using data from recaptured bird bands on several species, the life span of each bird was measured from its first 1 January of life (about 6 months old) until the band was finally recaptured. Average further life expectancies varied according to how the sample was selected. Birds recaptured near the banding location provided data showing a shorter further life expectancy than those found at least 20 minutes of latitude or longitude away, and those that were alive when recaptured provided data showing a shorter life expectancy past their first 1 January than those found dead. Biases in calculating average life expectancies from general band recapture data may be reduced by excluding individuals that were recaptured alive near the banding location.

ACKNOWLEDGMENTS

This study was prompted by a discussion with Joseph J. Hickey. Computer programming was accomplished by Jeffrey Osborne. Funds were provided by N. S. F. Institutional Grant GU-3350, and computer time was furnished by Western Illinois University.

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Department of Biological Sciences, Western Illinois University, Macomb, Illinois 61455. Received 11 January 1975, accepted 15 May 1975.