SURVIVAL AND POPULATION DYNAMICS WITH PARTICULAR REFERENCE TO BLACK-CAPPED CHICKADEES

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When a shrike or a hawk pounces on one of the chickadees frequenting your banding station, your first reaction may be to rush to its defence. I have even heard (perish the thought) of some who react by reaching for a gun to terminate the predator's career.

Have you ever considered what might happen if birds as prolific as chickadees did *not* fall pray to shrikes or hawks rather frequently? Let us consider what would be the consequences if some good (?) fairy arranged that each chickadee should live as long as we do (say our biblical three score years and ten). A pair of chickadees may produce eight fertile eggs per year. Then at the end of the first year we would have five pairs of chickadees (the original pair plus four new ones hatched from these eight eggs: we are assuming an even sex ratio). In the following year these might produce eight eggs each — a total of 40 eggs, which with no mortality would give us 25 pairs of chickadees at the end of the second year (the five pairs with which we started the second year plus 20 new pairs from the 40 eggs). By similar reasoning we would have 125 pairs (250 chickadees) at the end of the third year. This is obviously a geometric series: 5^1, 5^2, 5^3 . . . . . so at the end of 70 years we should have 5^{70} pairs of chickadees. This number does not look so formidable when written thus but a little mathematics will convince you that there would not be space enough in the whole solar system to hold all these chickadees. Even after 30 years the whole surface of the earth would be covered chest deep with chickadees. I think that long before this happened we would be asking the good fairy to make new arrangements with respect to the length of life of chickadees. This, of course, has already been done. Shrikes and hawks are numbered among these arrangements. Even if chickadees were each to live to reproduce just once it would not be long before you would find the sun blotted out by their multitudes. So much for fairy stories, for what does *not* happen. Let us now try to build up a picture of what *does* happen.

Before we can calculate the survival of a population of chickadees, or other animals, we must define carefully what we mean by survival. Survival of *what*? Survival *from* when and *to* when? It is important for the survival of chickadees, as a species, that a certain number should survive to start each breeding season. These survivors are drawn from two sources: (1) survivors alive at the beginning of the previous breeding season and (2) survivors from the eggs which these adults laid. Mortality during the intervening year acts upon the eggs and the young which hatch from the eggs at one rate, producing a certain number of survivors to start the next breeding season. Mortality may act upon the more experienced adults at quite a different rate. We shall consider these rates separately as well as the survival of the population as a whole, made up of the two components.

SURVIVAL OF THE POPULATION AS A WHOLE

We will calculate the survival of the population of the species as a whole from one breeding season to the next, assuming (1) that the population of chickadees is stable, showing no long term trend to increase or decrease; (2) that the sex ratio is equal; (3) that all birds one year old and older will mate and reproduce with undiminished fecundity and (4) that the pairs will produce just one clutch of eggs per year. Under these conditions the survival rate of the population as a whole may be calculated from the average clutch size.

For example, if each pair of chickadees were to produce a clutch of eight eggs, it is apparent that only two of these 10 units (two adults plus eight eggs) can, on the average, survive until the following breeding season. If more survived the population would increase: if fewer survived the population would diminish. In this case the survival would be two out of ten (20 percent per annum) or the mortality would be eight out of ten (80 percent per annum). We may express this more generally as:

$$S = 1 - M = \frac{2}{2 + N} \quad \text{(1)}$$

where
- S = annual survival rate of population as a whole
- M = " mortality " " " " " "
- N = average number of eggs laid per pair of adults per year

In Table 1 are tabulated the implied mortality rates for the population as a whole corresponding to various fecundity rates.

TABLE 1. RELATIONSHIP BETWEEN FECUNDITY AND IMPLIED AVERAGE ANNUAL MORTALITY

Number of eggs per pair per year	Implied annual mortality of population as a whole
10	83%
9	82
8	80
7	78
6	75
5	71
4	67
3	60
2	50
1	33

Note that the annual mortality includes *egg* mortality as well as that of adults and young of the year. *Ed. note:* for the sake of simplicity, this percentage is stated from the laying of the egg. Thus it does not reflect mortality of adults or loss of nests under construction; for the chickadee, these points are not of great importance, but for a species like the Mourning Dove they would mean more. The dove sustains heavy loss of nests, eggs and fledglings (together with some adult mortality over a long breeding season), but usually produces an adequate number of young birds by persistence, sometimes starting 5 or 6 nests in a season).

SURVIVAL OF ADULTS

By adults we mean chickadees of reproductive age, which we have assumed to be one year old and older. The survival of such adults is probably most easily determined by banding and systematic re-trapping or by color-banding with systematic recording of subsequent observations of the color-banded individuals. I have used color-banding in my study of our local chickadees and will assume that all the birds marked continued to come to the feeding station as long as they lived. Every one marked was subsequently seen for at least two months after marking so the marking did not discourage them from coming. It may be that some left to breed elsewhere and did not find their way back in subsequent winters. Adult survival rates found by banding are therefore minimal. If we are considering the entire population of a species in a given area, the mortality rate is overstated to the extend that emigration has taken place. If, however, we are considering a specific group of birds, all banded, representing the entire population on a given area, then it does not matter whether a bird is lost by death or emigration.

When a group of chickadees is banded in the fall or early winter, as in this study, the group is likely to contain some adults and some birds of the year. These two groups may have different mortality rates. The inexperienced young may be more susceptible to trouble than the experienced adults. For this reason we should not determine their survival, as adults, from the date of banding but from the reproductive period in the following spring. The group of birds still alive at this reproductive period will, of course, be likely to consist of birds of different ages, some just one year old, some two, perhaps some three or older. The survival rate of this group, then, will be an average rate for adults of various ages. We shall assume that the rate is uniform for adults of all ages. For short-lived birds this is probably a fair approximation of the truth. For longer-lived species, senility may cause greater mortality rates in the older age classes but the evidence for this may be confused by band losses from older birds.

AGE COMPOSITION OF THE BREEDING POPULATION

The age composition of the breeding population may be calculated from the adult mortality rate. For example, let us suppose that the annual adult mortality rate is 40 percent, i.e. the survival rate is 60 per cent. Let us start at a reproductive period with a population of 100 adults of age 1. Then, one year later we should have 60 survivors two years old. Two years later we should have 60 percent of 60, or 36 survivors three years old. Three years later we should have 60 percent of 36, or 22 survivors four years old . . . and so on, so that the age composition of a stable population with 40 percent annual mortality (60 percent survival) would be:

Age:	1	2	3	4	5	6	7	8	9	10
Number	100	60	36	22	13	8	5	3	2	1 . . .

Total population: 250 adults.

We may express this more generally, as:

$$P_a = \frac{P_1}{1 - S_a} = \frac{P_1}{M_a} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (2)$$

where $\begin{cases} P_a & = \text{total adult population} \\ P_1 & = \text{population of birds of age 1.} \\ S_a & = \text{annual survival rate of adults} \\ M_a & = \text{annual mortality rate of adults} \end{cases}$

TABLE 2. CALCULATED NUMBERS OF ADULT BIRDS CORRESPONDING TO VARIOUS MORTALITY RATES

Mortality Rate	Total Adult Population	Calculated Numbers of Age 1	2	3	4	5	6	7	8	9	10
40%	250	100	60	36	22	13	8	5	3	2	1
50	200	100	50	25	13	6	3	2	1		
60	167	100	40	16	6	3	1				

Note: In this table the populations have been based on 100 birds of age 1 in each case. In Table 3 only the relative numbers of yearlings and of older adults are listed, corresponding to various mortality rates.

TABLE 3.

Mortality Rate	Total Adult Population	One Year Old	Older Than One Year
10	1000	100	900
20	500	100	400
30	333	100	233
40	250	100	150
50	200	100	100
60	167	100	67
70	143	100	43
80	125	100	25
90	111	100	11

SURVIVAL OF SUBADULTS

If we know the survival rate (or mortality rate) of the population as a whole and of the adult population we are in a position to calculate the survival rate of the subadults (i.e. of the eggs and birds less than one year old). Let us consider the case where the mortality rate for the population as a whole is 80 percent and for the adults is 40 percent per annum. If we consider the population of birds one year old to be 100, then from Table 2 we see that a mortality rate of 40 percent implies a total adult population of 250 birds. If the sex ratio is equal we will have an adult population of 125 pairs. From Table 1 we see that a mortality rate of 80 percent for the population as a whole implies that eight eggs per pair will be laid, i.e. a total of 1000 eggs for the 125 pairs. If the population is to remain stable we must end the year with 100 birds one year old; i.e. from 1000 eggs we must have a survival of only 100 birds one year old. This is a survival of 10 percent during the first year of life (or a mortality of 90 percent during the first year).

By similar reasoning we may calculate the implied first year mortality rates corresponding to various rates of annual egg production and various adult mortality rates. Some of these are tabulated in Table 4.

Table 4. First Year Mortality Rates Corresponding to Various Fecundity and Adult Mortality Rates

Number of Eggs Per Pair Per Year	Implied First Year Mortality When Adult Mortality Rate Is 40% / Year	50% / Year	60% / Year
10	92%	90%	88%
9	91	89	87
8	90	88	85
7	89	86	83
6	87	83	80
5	84	80	76
4	80	75	70
3	73	67	60
2	60	50	40
1	40	0	(impossible)

ACTUAL SURVIVAL OF COLORBANDED CHICKADEES

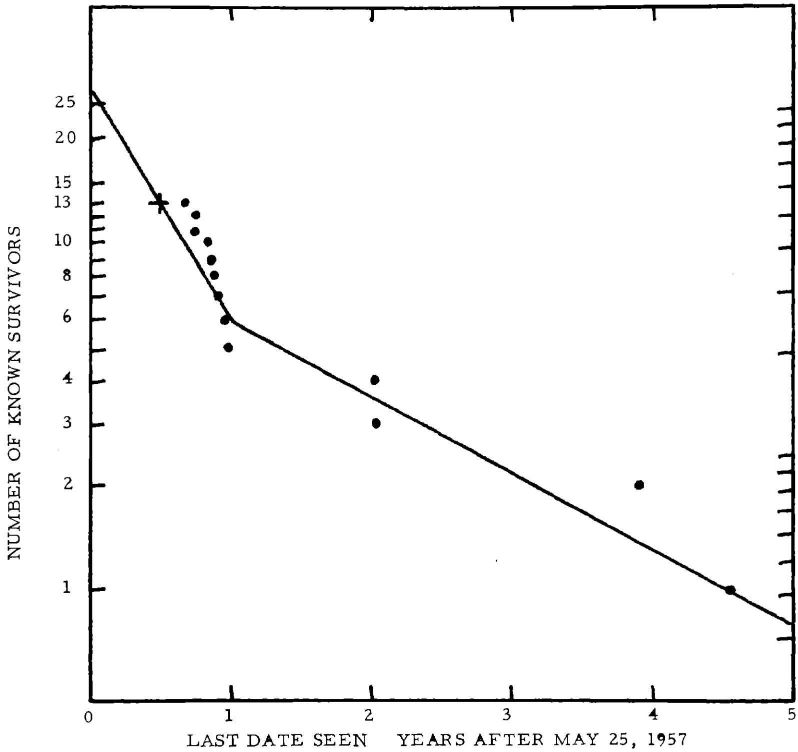
Thirteen Black-capped Chickadees were banded on Nov. 17, 1957, using numbered government aluminum bands and unnumbered aluminum bands anodized red, blue, green or gold. Different color combinations were used on each individual bird so that it could be recognized subsequently as it came to our feeding station. Records were kept of each bird as seen each day. From these records the last date when each was seen alive is tabulated in Table 5.

Table 5. Survival Data for 13 Black-Capped Chickadees Color-Banded on Nov. 17, 1957

Band Number	Last Date Seen Alive	Known Survival After Banding Years	Months	Days	Survival After May 25, 1957 Years	Months	Days
20-39838	Jan. 22, 1958	0	2	5	0	7	28
20-39841	Feb. 12, 1958	0	2	26	0	8	18
20-39836	Feb. 14, 1958	0	2	28	0	8	20
20-39842	Mar. 16, 1958	0	4	0	0	9	23
20-39840	Mar. 28, 1958	0	4	11	0	10	3
20-39835	Apr. 4, 1958	0	4	18	0	10	10
20-39833	Apr. 13, 1958	0	4	27	0	10	19
20-39837	May 4, 1958	0	5	17	0	11	9
20-39839	May 21, 1958	0	6	4	0	11	26
20-39834	May 27, 1959	1	6	10	2	0	2
20-39844	June 3, 1959	1	6	17	2	0	9
20-39843	Apr. 17, 1961	3	5	0	3	10	23
20-39832	Dec. 9, 1961	4	0	22	4	6	14

Data for 20 nests of Black-capped Chickadees in southern Ontario were obtained at the Royal Ontario Museum by courtesy of James L. Baillie and James Woodford. From these data the median date for full sets of unincubated eggs was calculated to be about May 25.

Figure 1. Comparison of actual survival of 13 Black-capped Chickadees color-banded at Rouge Hills, Ont., on Nov. 17, 1957 (circles) with theoretical survivals of 78 percent in the first year and 40 percent per annum thereafter (solid lines). The cross shows the banding date of the 13 chickadees. The survival scales are logarithmic.



This date is only approximate as back calculations had to be made to allow for various recorded stages of incubation and these were admittedly guesses. This median date (May 25, 1957) has been taken as the "zero date" in Table 5 and in Fig. 1.

For 21 nests with information on the number of eggs or young, nine young were found in two nests; eight eggs (not incubated) were found in two nests; five nests contained seven eggs each, all in some stage of incubation so presumably complete clutches; five nests contained six eggs each (but three of these were fresh so may have been incomplete clutches); one nest contained six young (possibly survivors from a larger set of eggs); and six nests contained from two to five eggs, or young (the eggs either fresh or with no data on incubation). We shall assume that seven eggs is the average clutch size in this part of southern Ontario. From Table 2 we see that this implies an annual mortality in this region of 78% of the population as a whole.

COMPARISON OF ACTUAL AND CALCULATED SURVIVAL RATES

In Fig. 1 the dots show the actual known survival of the 13 Black-capped Chickadees which were color-banded on Nov. 17, 1957. The calculated survival line in Fig. 1 has two portions. The steep portion for the first year corresponds to a mortality rate of 78 percent, which we have seen above is the expected mortality rate for the population as a whole when the fecundity rate is 7 eggs per year, which appears to be the best average value for southern Ontario chickadees. After this date we know that all the survivors were adults. We have taken the adult mortality rate for chickadees to be 40 percent in accordance with the data presented by Wallace (1941: 50, 63) and Odum (1942: 156) and reviewed by Farner (1955: 437).

Thirteen birds is, of course, too small a population for us to expect any significant results. However, the correspondence between the observed and calculated survivals as shown in Fig. 1 is good enough to suggest that a larger scale study along the same lines would be well worth while.

SUMMARY

Equation (1) and Table 1 show the relationship between the average number of eggs produced per pair of birds per year and the annual mortality of the population as a whole (including eggs, young and adults). It is apparent that most passerines will have overall mortality rates in excess of 60 percent per annum, i.e. their *average* length of life is less than one year.

Equation (2) and Tables 2 and 3 show the age distribution which we might expect to find in adult populations with various mortality rates. From these it will be seen that we should expect to find a few passerines up to eight or ten years of age in any large series of band returns.

Table 4 suggests that the first year mortality of chickadees must be about 89 percent, i.e. the chance of a given chickadee egg hatching and surviving to become part of the reproductive population is not much greater than one in ten.

The correspondence of the actual survival of color-banded chickadees with the calculated survival rates is good enough to suggest that it would be worth while to accumulate more data from color-banded chickadees. The author would appreciate data of this sort for chickadees which include both the date of banding and the date when the banded bird was last seen. It would help to know the degree of coverage for intervening dates, especially if any long periods of absence of the observer might influence the data.

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