

A COMPARISON OF RECAPTURE VERSUS RESIGHTING DATA IN A 15-YEAR STUDY OF SURVIVORSHIP OF THE BLACK-CAPPED CHICKADEE

BY WILLIAM H. ELDER AND DALE ZIMMERMAN

The abundance, ease of trapping, and widespread distribution of the Black-capped Chickadee (*Parus atricapillus*) have made it a popular subject for banding studies over the past half century (Odum 1942a, Speirs 1963, Smith 1967, and others cited below). No consensus has been reached concerning migration in this species. Since Van Tyne's early paper (1928), flock movements, invasions of new areas in winter (Lawrence 1958, Hussell and Stamp 1965), and withdrawal from winter range with onset of breeding season have been reported (Merritt 1978). Others are convinced that populations are strictly nonmigratory (Weise and Meyer 1979). Nearly all agree that there is a spring movement in the populations and that birds move north or expand their range locally at this season.

Mortality rates have been computed from disappearance of locally banded flock members at 40% (Wallace 1941) and 44% annually (Odum 1942b). Cumulative band-recovery data from the U.S. Fish and Wildlife Service have indicated annual mortality as 60.6% (Brewer 1963) and 49% (Henny 1972).

It is our purpose to (1) use sightings of live, color-banded birds to estimate mean annual survival rate; (2) to compare this survival rate with one derived from retrapping data; (3) to compare these rates with survival rates found in previous studies of band recoveries; (4) to compare life-table estimates and stochastic models; and (5) to record maximum longevities, apparent seasonal arrival times, and year-to-year philopatry as shown by one population in Missouri.

MATERIALS AND METHODS

This study was conducted at Elder's home at the southern edge of Columbia, Missouri, where a large feeding tray was maintained at the second-story level. Sunflower seeds were provided throughout the year but never ad libitum, due to squirrel competition. A few cups of seed were put out in the morning and again at noon, after which approximately one hour was frequently spent watching and recording individual birds seen (within 1 m). No record was kept of the total hours. This paper reports the results of these observations for the 15 years 1965-1979, inclusive.

Our banding year began 1 September, and data were recorded each week thereafter on all birds sighted. Trapping was usually conducted on weekends but not exclusively. It was terminated in spring when most birds departed for territories. All birds were marked with a FWS band on one leg and one or two color bands on the other so that each individual was identifiable at a glance. Each bird's presence was recorded

as observed on a weekly basis. Whenever an unbanded bird appeared, a Potter 2-cell trap was placed on the food tray and other foods restricted. Naive birds were usually caught within a few days of arrival. All recaptures were recorded to measure trapability and frequency of trap repeats. No record was made of total hours that traps were open. The birds were not weighed, measured, or sexed. Although Mosher and Lane (1972) provided a method by which they thought chickadees might be sexed by plumage differences, the validity of their technique could not be confirmed by Gochfeld (1977), nor could he recommend aging by wing chord (Odum 1943). Yunick (1980) found that some first-year chickadees showed complete skull pneumatization by the first week in October, indicating winter skulling of the species is unreliable.

At the end of the 15-year period, all data were tabulated and computer analyzed using the Statistical Analysis System, SAS Version 79.5 (Helwig and Council 1979) for analysis of survival, arrival and departure dates, trapability, length of stay, and transientness within the year, and constancy between years. Mean life span was calculated using equation 6a of Farner (1949).

RESULTS AND DISCUSSION

During the 15 years of study, 253 chickadees were trapped and banded. Resightings were recorded for 214 of these birds at least once after the week of banding. The other 39 birds (15%) were never seen again. These apparent transients were not concentrated; some arrived each week of December, January, and February; half (19) being taken in January.

Arrival and departure.—The first week in January was the most frequent arrival period (Fig. 1), but total new arrivals were also high in November, December, and February (94, 141, 74). Lawrence (1958) found November, January, and March were by far the most popular months of arrival in Ontario. Although much farther north, the major period of dispersal and therefore new arrivals was in January, as we found in Missouri. But in Massachusetts Wallace (1941) found February to be the month of greatest movement, and in New York Butts (1931) found an influx of birds in September with the peak in banding being reached in December.

As in Lawrence's study (1958), no recoveries and no foreign retraps were received in the 15 years of our study. A few of our color-banded birds were identified at other bird feeders in Columbia, but all were within 2 km of our banding station.

The mean interval between banding and first recapture was 3.9 weeks ($n = 105$), suggesting that many birds avoided traps after their initial contact. Some birds came back the next day to become regular visitors to traps, often learning to avoid stepping on the trip bar and thereafter entering repeatedly without being captured again.

Chickadees remained at our feeding station for a mean of 13 weeks

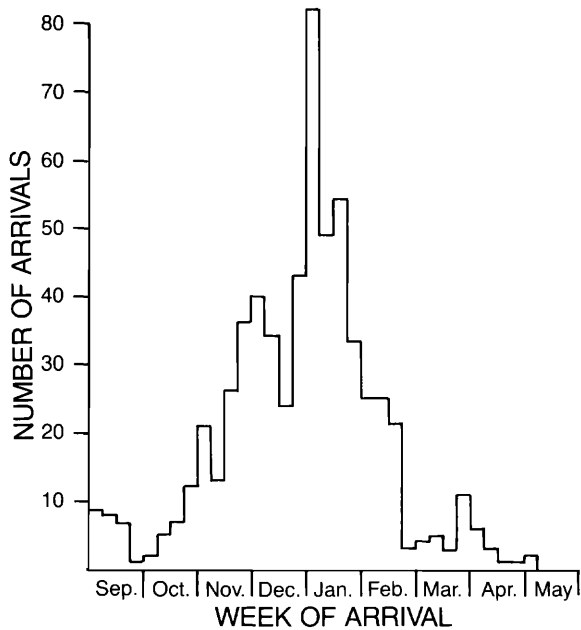


FIGURE 1. Week of arrival ($n = 616$) of Black-capped Chickadees. (Some individuals provided data for several years.)

($n = 457$); some were observed nearly every day, others irregularly or only during severe weather. While the modal length of their absence was only 1 week, the mean was 5.4 weeks. Of 136 chickadees that first arrived in December and were seen again, 82% remained through January. Of 192 birds arriving in January and seen again, 58% remained through February. The mean departure date ($n = 457$) was during the last week of March when birds started moving out to territories. Some new birds were taken during the April and May spring movement period (Fig. 1)—a phenomenon found by others (Bowdish 1938, Odum 1941, Blake 1952, Tanner 1952).

Annual survival as indicated by recaptures.—A composite dynamic life table of the type used by Deevey (1947) and Hickey (1952) was constructed from recapture data for all cohorts for which data were essentially complete (1964–1972, inclusive). From this (Table 1) an annual survival rate of 55% was determined.

When a stochastic model (Brownle et al. 1978) was constructed for the recapture data, the annual survival rate indicated was 55%, in agreement with the life-table method. The mean life span was slightly shorter than indicated by the life-table method (Table 2).

Annual survival as indicated by resightings.—A composite dynamic life table was then constructed from data supplied by resightings, whether

TABLE 1. A comparison of life tables for the Black-capped Chickadee based on recapture data and resighting data from color-banded birds.

x ¹	Recapture data				Resighting data			
	l _x	d _x	q _x	p _x	l _x	d _x	q _x	p _x
0-1	120	71	0.592	0.408	120	36	0.300	0.700
1-2	49	10	0.204	0.796	84	26	0.309	0.691
2-3	39	17	0.436	0.564	58	20	0.345	0.655
3-4	22	5	0.227	0.773	38	13	0.342	0.658
4-5	17	5	0.294	0.706	25	10	0.400	0.600
5-6	12	7	0.583	0.417	15	9	0.600	0.400
6-7	5	4	0.800	0.200	6	3	0.500	0.500
7-8	1	1	1.000	0	3	2	0.667	0.500
8-9	0				1	1	1.000	0

¹ x = age in years; l_x = survivorship to age x; d_x = number of deaths during age x; q_x = mortality during age x; p_x = survivorship during age x.

or not the birds were recaptured (Table 1). Results of this analysis revealed an estimated survival rate of 66%, or considerably higher than that provided by recaptures alone; this was confirmed by the stochastic model (Table 2). The difference was undoubtedly due in part to marked birds being exposed to observation more hours and on more days than they were to trapping. It also reflects that many birds become trap shy or trap wise—learning to steal seed without being caught; 46% were never recaptured, 15% were never resighted. Our findings suggest that survival rates are not truly shown by either recaptures or recoveries. Brewer (1963) used a life table to find a mean survival rate of 39.4% for 1276 banded birds, and Henny's (1972) report of a stochastic model of recoveries from over 100,000 bandings of Black-capped Chickadees provided an estimate of mean adult mortality of 0.49% or a survival of 51%; both are markedly lower than our estimate of 66% based on ob-

TABLE 2. A comparison of survival rates and mean life span of Black-capped Chickadees as shown by two methods of computation (years 1964-1972 included).

	Life table method	Stochastic method
	<u>Resighting data</u>	
Mean survival rate ¹	65%	67 ± 3%
Mean life span ²	2.4 years*	2.6 ± 0.28 years
	<u>Recapture data only</u>	
Mean survival rate	55%	54%
Mean life span	1.71 years*	1.6 ± 0.13 years

¹ Average survival rate = $1 - \frac{D_1 + D_2 + D_3 + \dots}{D_1 + 2D_2 + 3D_3 + 4D_4 + \dots}$ (Caughley 1977:105).

² Calculated with equation 6a of Farner (1949).

TABLE 3. Maximum longevity of Black-capped Chickadees.

Authority	Area	Sample size	Oldest bird
Butts 1931	NY	50	7 yr
Harding 1932	MA	Not given	7 yr, 6 mo
Baldwin 1935	MA	Not given	8 yr
Wallace 1941	MA	3500	8 yr plus
Cooke 1950	Manitoba	Not given	8 yr, 8 mo
Lawrence 1958	Ontario	340	9 yr
Brewer 1963	KS to NJ	1276	8 yr plus
Downs 1964	VT	Not given	10 yr, 3 mo
Kennard 1964	NH	Not given	10 yr, 8 mo
Smiley 1964	NY	Not given	9 yr, 5 mo
Smith 1964	MA	Not given	9 yr, 3 mo
Wharton 1964	MA	Not given	9 yr, 4 mo
Henny 1972	Entire range	100,783	7-8 yr
This study	MO	253	9 yr

servations. Our figure also exceeds that of 40-60% given by Ricklefs (1973) for temperate passerines in general.

Longevity.—Although the mean life span of this population of chickadees was only 2.5 years, some birds lived to surprising old age for so small a species. Other studies of the species have revealed that individuals may live to be 9 years and rarely 10 (Table 3).

A comparison of the rates of shrinkage in cohorts showing birds known to be alive each year after banding as shown in Table 1 reveals that resightings are better than recaptures alone, primarily because they are much more numerous. These tables also show that among 253 chickadees banded, one lived to be 8 years old. One has since been seen in its ninth year. Ages are based on the assumption that most birds were banded within the first year of life (their first winter, HY and AHY).

Examination of Table 3 will show that the maximum longevity in this species is not entirely related to sample size. In our study, 23 birds exceeded 5 years of age (12%) while only 16 of 3500 birds reported by Wallace (1941) reached this age. This suggests regional differences may be real or that our birds survived better because an artificial food source was available to them during periods of severe winter stress (heavy snows and ice storms). This is further indicated by the fact that Brewer's (1963) sample of 1276 FWS Black-capped Chickadee band reports revealed only two birds over 8 years of age.

Philopatry.—Not all birds remaining alive returned every year to our station; in fact, 12% of the chickadees skipped one or more years. The frequency with which this occurred was: 1 year (21 times), 2 years (6), 3 years (2), 4 years (3). Years missed were either alternate or sequential and totaled 51 of the 616 bird-year observations (8%). Many banders have recorded individual chickadees that have been absent 1 year and returned the next, and Kluijver (1951) found this true of the Great Tit (*Parus major*).

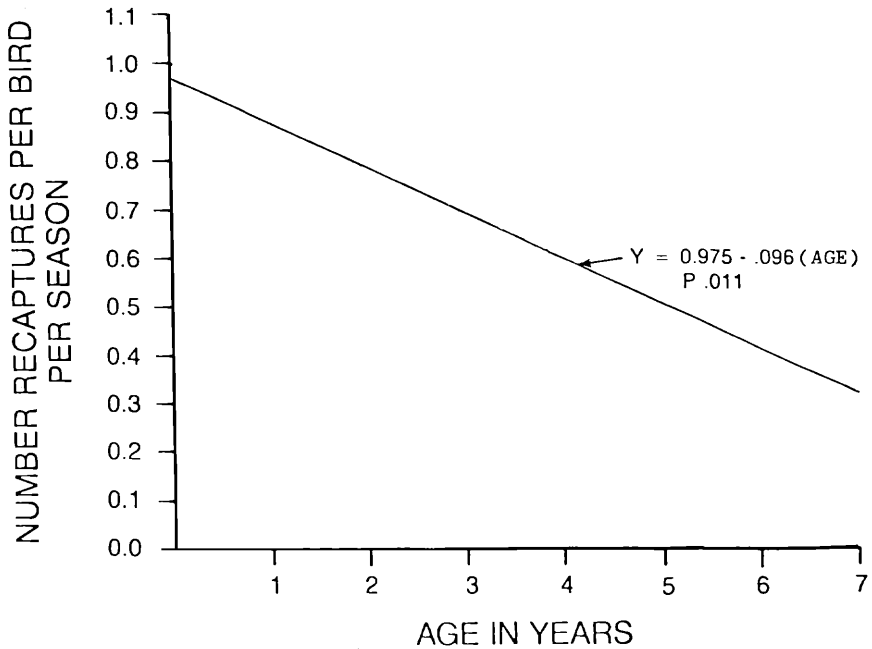


FIGURE 2. Relationship of age to frequency of recapture in Black-capped Chickadees ($n = 105$).

Influence of age.—Although the exact age of birds was not known, years-after-banding provided a scale of relative age and permitted analysis of age-related phenomena. Figure 2 shows that birds became trap wise—the mean number of recaptures per bird per season decreased as birds grew older. When we plotted number of resightings against relative age, no change was found with increasing age. There was no trend in either arrival or departure date as birds aged, nor was there any trend in the number of weeks a bird was absent during its winter stay—transientness does not increase or decrease with age, whether measured in weeks absent or in entire years skipped. Finally, the interval between first and second captures in any 1 year did not change with age.

In some years of our study (4) all birds that were newly banded were also resighted repeatedly, while in some other years as many as 5–9 were not seen again after being banded. When tabulated by age, they were seen to be roughly proportional to the number of that age cohort still alive (Table 4).

We then asked whether or not these transients were seasonal in appearance, but tabulation showed them to appear as follows: December—5, January—19, February—11, March—2, April—2. There seems no evidence here of migrational movement.

TABLE 4. Distribution in time of chickadees that appeared only once in any particular year.

Years after banding	Same year	1	2	3	4	5	6	7	8
Number of chickadees	39	21	17	13	3	5	1	0	1

SUMMARY

Survivorship among 253 Black-capped Chickadees was studied by trapping, color banding, and weekly recording of sightings for 15 years at a single station in Columbia, Missouri. Recapture data provided an estimate of 54% annual survival and 1.6 years mean life span when analyzed with a stochastic model and 1.7 years with a composite dynamic life table. Resightings gave an estimated annual survival of 66% with a life table and 67% with a stochastic model—both significantly higher than indicated by trapping data alone. The mean life span revealed by resightings was 2.42 years by the life table method and 2.56 years by the stochastic model. The conclusions are biased by the fact that observations were made on more days than trapping was conducted, but trapping was done on 8-hour days and observations were but 1–2 hours per day. Maximum longevity was at least 9 years; during which 12% disappeared for 1–4 years before returning. Trapability declined with age of birds. New birds arrived in numbers from November through February and peaked in early January.

ACKNOWLEDGMENTS

We gratefully acknowledge James N. Burroughs for many helpful suggestions in accomplishing our computer analyses and Terry Finger and J. J. Hickey for critical review.

LITERATURE CITED

- BALDWIN, D. A. 1935. Percentages of surviving chickadees of different ages. *Bird-Banding* 6:69–70.
- BLAKE, C. H. 1952. A population balance for the Black-capped Chickadee. *Bird-Banding* 23:165–168.
- BOWDISH, B. S. 1938. Chickadee movements at Demarest, New Jersey. *Bird-Banding* 9: 159.
- BREWER, R. 1963. Ecological and reproductive relationships of Black-capped and Carolina chickadees. *Auk* 80:9–47.
- BROWNLE, C., D. R. ANDERSON, K. P. FURNHAM, AND D. S. ROBSON. 1978. Statistical inference from band recovery data: a handbook. U.S. Fish Wildl. Serv. Resour. Publ. 131.
- BUTTS, W. K. 1931. A study of the chickadee and White-breasted Nuthatch by means of marked individuals. II. The chickadee. *Bird-Banding* 2:1–26.
- CAUGHLEY, G. 1977. Analysis of vertebrate populations. John Wiley and Sons, London.
- COOKE, M. T. 1950. Returns from banded birds. *Bird-Banding* 21:11–18.
- DEEVEY, E. S., JR. 1947. Life tables for natural populations. *Q. Rev. Biol.* 22:238–314.

- DOWNES, J. R. 1964. Old chickadee. *Bird-Banding* 35:124.
- FARNER, D. S. 1949. Age groups and longevity in the American Robin: comments, further discussion, and certain revisions. *Wilson Bull.* 61:68-81.
- GOCHFELD, M. 1977. Plumage variation in Black-capped Chickadees: is there sexual dimorphism? *Bird-Banding* 48:62-66.
- HARDING, K. C. 1932. Age record of Black-capped Chickadee. *Bird-Banding* 3:118.
- HELWIG, J. T., AND K. A. COUNCIL (EDS.) 1979. SAS users guide, SAS Institute, Inc., Raleigh, N.C.
- HENNY, C. J. 1972. An analysis of the population dynamics of selected avian species: with special reference to changes during the modern pesticide era. U.S. Fish Wildl. Serv. Wildl. Res. Rep. 1.
- HICKEY, J. J. 1952. Survival studies of banded birds. U.S. Fish Wildl. Serv. Spec. Sci. Rep.-Wildl. 15.
- HUSSELL, D. J. T., AND R. W. STAMP. 1965. Movements of Black-capped Chickadees at Long Point, Ontario, during the spring of 1962. *Bird-Banding* 36:71-80.
- KENNARD, J. 1964. Old chickadee. *Bird-Banding* 35:124.
- KLUJVER, H. N. 1951. The population ecology of the Great Tit, *Parus m. major* L. *Ardea* 39:1-135.
- LAWRENCE, L. K. 1958. On regional movements of Black-capped Chickadees. *Auk* 75: 415-443.
- MERRITT, P. G. 1978. Characteristics of Black-capped and Carolina chickadees at the range interface in northern Indiana. *Jack-Pine Warbler* 56:171-179.
- MOSHER, J. I., AND S. LANE. 1972. A method of determining the sex of captured Black-capped Chickadees. *Bird-Banding* 43:139-140.
- ODUM, E. P. 1941. Annual cycle of the Black-capped Chickadee—I. *Auk* 58:314-333.
- . 1942a. Annual cycle of the Black-capped Chickadee—III. *Auk* 59:499-531.
- . 1942b. A comparison of two chickadee seasons. *Bird-Banding* 13:155-159.
- . 1943. Some physiological variations in the Black-capped Chickadee. *Wilson Bull.* 55:178-189.
- RICKLEFS, R. E. 1973. Fecundity, mortality and avian demography. Pp. 366-435 in *Breeding biology of birds*, D. S. Farner (ed.). Natl. Acad. Sci., Washington, D.C.
- SMILEY, D. 1964. Another nine-year-old chickadee. *Bird-Banding* 35:267.
- SMITH, C. L. 1964. Old chickadee. *Bird-Banding* 35:124.
- SMITH, S. M. 1967. Seasonal changes in the survival of the Black-capped Chickadee. *Condor* 69:344-359.
- SPEIRS, J. M. 1963. Survival and population dynamics with particular reference to Black-capped Chickadees. *Bird-Banding* 34:87-93.
- TANNER, J. T. 1952. Black-capped and Carolina chickadees in the southern Appalachian Mountains. *Auk* 69:407-424.
- VAN TYNE, J. 1928. A diurnal local migration of the Black-capped Chickadee. *Wilson Bull.* 40:252.
- WALLACE, G. J. 1941. Winter studies of color-banded chickadees. *Bird-Banding* 12: 49-67.
- WEISE, C. M., AND J. R. MEYER. 1979. Juvenile dispersal and development of site-fidelity in the Black-capped Chickadee. *Auk* 96:40-55.
- WHARTON, W. P. 1964. Nine-year-old chickadee. *Bird-Banding* 35:41.
- YUNICK, R. P. 1980. Timing of completion of skull pneumatization of the Black-capped Chickadee and the Red-breasted Nuthatch. *N. Am. Bird Bander* 5:43-46.

School of Forestry, Fisheries and Wildlife, University of Missouri, Columbia, Missouri 65211. Received 28 Dec. 1981; accepted 11 Feb. 1983.