

CAPTURE-RECAPTURE ANALYSIS OF A WINTERING BLACK-CAPPED CHICKADEE POPULATION IN CONNECTICUT, 1958-1993

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ABSTRACT.—We investigated the dynamics of a wintering population of Black-capped Chickadees (*Parus atricapillus*) using data from a long-term capture-recapture study. Goodness-of-fit and likelihood-ratio tests indicated that the standard Jolly-Seber model was inadequate for the data, so we explored different parameterizations of a model in which survival probability for new captures differed from that of previously marked birds. One possible explanation for the lower local survival rate of new captures is that some of the birds were transients that had no chance of being recaptured. Average survival probability over the entire period was 0.62, and the estimated fraction of transients among unmarked birds was 0.27. We found evidence that chickadee survival rates were lower in years immediately following establishment of the Tufted Titmouse (*Parus bicolor*) as a territorial species (after 1967) than during years immediately preceding this event. We found no evidence that chickadee survival rates were lower in the years immediately following establishment of territorial raptors (after 1984) than during preceding years. Evidence suggested a long-term decline in survival probability from 1959 to 1991. Received 3 September 1996, accepted 1 February 1997.

CHANGES IN BIRD ABUNDANCE are important to avian ecologists and conservation biologists, especially when viewed in the context of current rapid and large-scale changes in habitat on the earth's surface (Terborgh 1989). Many of our inferences about temporal changes in avian populations have been based on abundance estimates and indices (e.g. Robbins et al. 1989, Peterjohn et al. 1994), and associated inferences about causal factors responsible for such changes have been weak (James and McCullough 1995). Rates of reproduction, survival, emigration, and immigration are the main population parameters responsible for all changes in bird population size. Temple and Wiens (1989) have argued that inferences about causality and environmental effects that are based on these parameters are likely to be stronger than inferences based on changes in abundance. In general, we agree with this argument and focus our analysis primarily on survival rate. For a particular study population, we examined whether survival rates changed in association with (and possibly in response to) increases in abundance of potential competitors and predators. We also explored whether there was evidence of long-term change in annual survival rate.

In this paper, we analyze capture-recapture data from a long-term study of Black-capped

Chickadees (*Parus atricapillus*) wintering in Connecticut. From our previous analysis of data collected from these chickadees during 1958 to 1983, we concluded that the population fluctuated over the study period, but we provided no evidence of sustained trends (Loery and Nichols 1985). We found evidence of decreases in annual survival rate, recruitment, and population size following the establishment of Tufted Titmice (*Parus bicolor*) on the area, but these decreases were temporary. Here, we add 10 years of data to the original data set to further explore sources of variation in survival using a new analysis.

New capture-recapture models have been developed during the past decade (e.g. Nichols 1992, Lebreton et al. 1993), some of which were designed specifically for passerines. In addition to reassessing the influence of Tufted Titmice, we investigated an *a priori* hypothesis about possible effects of recent predation by raptors on the Black-capped Chickadee population. In 1985, a territorial Sharp-shinned Hawk (*Accipiter striatus*) and a territorial Cooper's Hawk (*Accipiter cooperii*) were found on the study area for the first time. Observations of hawks on the study area have increased and both species are now well established. We thus wanted to test for possible differences in de-

TABLE 1. Alternative parameterizations/interpretations of the survival probabilities for newly marked and previously marked animals under model 2 of Brownie and Robson (1983).

Parameter definitions	Survival probabilities (period i to $i + 1$)	
	Newly marked animals	Previously marked animals
Marking-effect model (Brownie and Robson 1983)		
ϕ_i = survival probability for previously marked animals	ϕ'_i	ϕ_i
ϕ'_i = survival probability for newly marked animals		
Transient model (Pradel et al. 1997)		
ϕ'_i = survival probability for residents	$(1 - \gamma_i)\phi'_i + \gamma_i\phi''_i = \gamma_i\phi'_i$	ϕ'_i
ϕ''_i = survival probability for transients (= 0)		
γ_i = probability that a newly marked animal is a resident		
Age-specific survival model		
ϕ''_i = survival probability for adult animals	$(1 - \gamma_i)\phi''_i + \gamma'_i\phi''_i$	ϕ''_i
ϕ''_i = survival probability for first-year animals		
γ'_i = probability that a newly marked animal is an adult		

mographic parameters (particularly survival) before and after 1985.

STUDY AREA AND CAPTURE METHODS

The study was conducted on the property of the White Memorial Foundation, a 1,600-ha sanctuary in Litchfield County, Connecticut (41°42'N, 73°12'W). The elevation is 305 m, and the habitat is primarily second-growth deciduous woods interspersed with red pine (*Pinus resinosa*) plantations and a small plantation of spruce (Loery and Nichols 1985). All of the red pines have now died, and most have been cut.

Chickadees were captured in single- and three-celled Potter traps baited with suet and sunflower seeds. The traps and food supply were available year-round, and the traps were tied open when not in use, permitting birds to enter and exit freely. The capture-recapture data analyzed were restricted to November, December, and January. Age of birds could not be determined at that time of year, so all birds were used in the analysis. First-year birds included in the analysis were at least five months old. The sampling period denoted as year i corresponds to November and December of calendar year i and January of year $i + 1$.

STATISTICAL METHODS

JOLLY-SEBER MODEL

Initially, we analyzed the data using program JOLLY (Brownie et al. 1986), which we also used in our previous analysis (Loery and Nichols 1985). Under the cell-pooling rules of program JOLLY, one component of the goodness-of-fit test is equivalent to the test developed by Brownie and Robson (1983) for a difference between survival of newly marked versus

previously marked animals (Pollock et al. 1985). The full goodness-of-fit test indicated that the Jolly-Seber model (Jolly 1965; Seber 1965, 1982; Pollock et al. 1990) did not fit the 1958–1993 data adequately, and the Brownie-Robson test statistic provided evidence that the primary reason for this was a survival difference between newly marked and previously marked animals (see Results).

BROWNIE-ROBSON MODEL

At least three reasons are possible for differences in survival probabilities of newly marked and previously marked animals, and capture-recapture models have been developed to deal with each of them (Table 1).

Trap response.—First, the initial handling and marking of an animal may affect its survival during the subsequent year. Brownie and Robson (1983) developed a special case of the models of Robson (1969) and Pollock (1975) to model this situation (Table 1). This model (denoted as model 2 in JOLLY; Pollock et al. 1990) includes time-specific survival parameters for newly marked (ϕ'_i) and previously marked (ϕ_i) animals.

Transients.—The second possible reason involves the existence of transients (Table 1). Some animals may pass through an area and be exposed to sampling efforts but are not likely to return to the area (e.g. Peach 1993). Pradel et al. (1997) developed a model to deal with transients and noted that it was structurally equivalent to model 2 of Brownie and Robson (1983). Pradel et al. (1997) wrote the survival probability for newly marked animals as:

$$\phi'_i = (1 - \gamma_i)\phi'_i + \gamma_i\phi''_i \quad (1)$$

where γ_i denotes the probability that a newly marked animal is a resident, and ϕ'_i and ϕ''_i are the annual sur-

vival probabilities for transients and residents, respectively. The survival probability for residents is the same parameter used to model survival of previously marked animals (the ϕ_i of Brownie and Robson 1983). By the operational definition of transient, the transient survival probability is 0. Thus, the weighted average survival rate for newly marked residents and transients becomes $\gamma_i \phi_i$, and the proportion of transients in the sample of unmarked animals can be estimated. Pradel et al. (1997) developed estimators and associated software for this model, and we use a version of their model incorporated into program SURVIV (White 1983).

Age.—The third possible reason for different survival probability of newly marked and previously marked animals involves age-specific differences in survival probability, coupled with the inability to determine age of animals upon initial capture (Table 1). Under this model, we envision one survival parameter for first-year animals and another that applies to all "adults" (i.e. >1 year old). Under this model, the survival probability for a newly marked animal is:

$$\phi'_i = (1 - \gamma'_i) \phi^y + \gamma'_i \phi^a, \quad (2)$$

where ϕ^y and ϕ^a denote the survival probabilities for newly marked first-year and older animals, respectively, and γ'_i specifies the probability that a newly marked animal is an adult. Thus, the survival probability for newly marked animals is a weighted mean of survival probabilities for young and adult animals, but unlike the case with the transient model, the value of ϕ^y is not known, and hence neither ϕ^y nor γ'_i can be estimated. This model is structurally equivalent to model 2 of Brownie and Robson (1983) and the transient model of Pradel et al. (1997), but it does not permit estimation of all model parameters. Instead, the data can be analyzed using model 2 of Brownie and Robson (1983). The resulting survival estimate for newly marked animals, ϕ'_i , can be interpreted as a weighted mean of survival rates for adults and young (in unknown proportion in the sample). We can analyze data using the equivalent transient model of Pradel et al. (1997) and interpret the estimate, $\hat{\gamma}_i$, as reflecting the degree to which survival of the mixed group of adults and young differs from the survival of adults only.

REDUCED-PARAMETER MODELS

Model 2 of Brownie and Robson (1983), and its structural equivalents (transient model and age-specific model), contain a large number of parameters. Large numbers of parameters are sometimes consistent with biological reality, but they carry a cost in terms of estimator precision. More parameters translate to larger variances, so we would like to find a model that adequately describes the data using the smallest number of parameters (Burnham and Anderson 1992, Lebreton et al. 1992). Pradel et al. (1997)

wrote computer code to implement model 2 and associated reduced-parameter models in program SURVIV (White 1983), and we investigated the adequacy of various reduced-parameter models for the chickadee data using this software.

We denote our general model as $(\phi'_i, p'_i, \gamma_i)$, with the r superscripts indicating that the parameter applies to resident animals and the i subscripts indicating time-specific parameters. The reduced-parameter models of primary interest were those involving constancy of parameters over time. We indicate reduced-parameter models in which a parameter is constant over time by dropping the time (i) subscript from the parameter symbol. For example, we denote a model with time-specific survival and capture probabilities but constant probability that a newly marked animal is a transient ($\gamma_i = \gamma$, for all i) as (ϕ'_i, p'_i, γ) .

MODEL SELECTION

We evaluated the adequacy of the different models in describing the data using goodness-of-fit tests. The goodness-of-fit tests implemented in JOLLY (tests of Brownie and Robson 1983 and Pollock et al. 1985) were used for model 2 and the Jolly-Seber model. Fit of reduced-parameter versions of model 2 was obtained by summing the goodness-of-fit χ^2 statistic for model 2 and the likelihood-ratio χ^2 statistic from the test comparing model 2 and the reduced-parameter model. In addition to their use in constructing goodness-of-fit statistics, likelihood-ratio tests were used to test between nested models (Lebreton et al. 1992). In such tests, the model with fewer parameters served as the null hypothesis, and the model with more parameters served as the alternative hypothesis. Selection of the most appropriate model for estimation purposes was based primarily on Akaike's Information Criterion (AIC; Akaike 1973, Burnham and Anderson 1992, Lebreton et al. 1992). AIC combines information on the ability of the model to fit the data and the number of model parameters.

TESTS FOR VARIATION IN SURVIVAL

Hypotheses concerning the influence of Tufted Titmice (hypothesized competitors) and raptors (hypothesized predators) on chickadee survival were tested using survival estimates and their estimated variances and covariances in conjunction with program CONTRAST (Hines and Sauer 1989, Sauer and Williams 1989). Because our *a priori* prediction was that chickadee survival rates would decrease after establishment of titmice and raptors, we used one-tailed tests. In addition to these tests using year-specific survival estimates, we developed reduced-parameter models with one survival parameter for the years preceding the event of interest (establishment of titmice or hawks) and another for the years following the event. As a methodological detail, we re-

tained a separate parameter for ϕ_{ss} because of the poor sample size for that year and because ϕ_i cannot be estimated for the first year of a study (Pradel et al. 1997). Consequently, the survival parameter for the period preceding the event of interest covered years beginning with and subsequent to 1959. Tests of such survival models against a model with constant survival over all years provide a test for possible effects of the event of interest. Tests of models with year-specific survival parameters against these "event" models address the question of additional year-to-year variation in survival beyond that explained by the event.

Some of the tests associated with titmouse and hawk establishment led to the inference that survival rates in later years differed from those in earlier years. We thus developed an additional model in which survival (ϕ_i denotes the probability of surviving the interval between sampling periods i and $i + 1$) was modeled as a linear-logistic function of the sampling period (where 1959 was denoted sample period 2, 1960 was denoted period 3, and so on):

$$\phi_i = \frac{e^{(a+bi)}}{1 + e^{(a+bi)}} \tag{3}$$

where i denotes the sample period and a and b are model parameters to be estimated. With respect to model notation, we label the survival element of models with year-specific survival as ϕ_i and the survival portion of models using the linear-logistic relation in equation 3 as ϕ_i^r .

ABUNDANCE ESTIMATION AND TESTS

We were also interested in estimating size of the wintering population. Different approaches to this estimation are indicated, depending on which of the parameterizations in Table 1 best describes the biological situation. We chose to estimate population size of all birds (not just residents under the transient model, and not just adults under the age-specific model). In order to do this, we assumed that all birds (both transients and residents under the transient model and both young and adult under the age-specific model) exhibited the same capture probability (e.g. under the transient model, $p_i^r = p_i^t$), i.e. that estimated from the data on previously caught birds.

We estimated population size and its conditional standard error as:

$$\hat{N}_i = n_i / \hat{p}_i^r \tag{4}$$

and

$$SE(\hat{N}_i) = \left[\left(\frac{n_i}{\hat{p}_i^r} \right)^2 \left(\frac{\widehat{var}(\hat{p}_i^r)}{(\hat{p}_i^r)^2} \right) \right]^{0.5} \tag{5}$$

respectively, where n_i is the total number of birds

caught in year i , N_i is the number of birds in the wintering population, and \hat{p}_i^r and $\widehat{var}(\hat{p}_i^r)$ are the estimated capture probability and its estimated variance. These latter two estimates are obtained from the capture-recapture model selected for use in estimation. We used simple linear regression of $\ln(\hat{N}_i)$ versus time (i) to test for a population increase or decrease over this period of study. Under the assumption of a constant rate of population change, the slope of the regression (b) estimates the instantaneous rate of population change, and e^b estimates the finite rate of population change. The use of this regression approach to test for population increases or decreases over time is strictly correct only when the error terms of the regression model show no serial correlation. Virtually all sampling correlations among the \hat{N}_i were negligible under the selected model, but this did not eliminate the possibility of a correlation among the underlying true values, N_i . We tested for serial correlation using the Durbin-Watson d statistic (Durbin and Watson 1951).

RESULTS

INITIAL MODEL SELECTION

Capture-recapture data for nearly 2,000 chickadees banded in winter are summarized in Table 2. The goodness-of-fit test of program JOLLY provided strong evidence that the Jolly-Seber model (ϕ_i, p_i) did not fit the data well (Table 3). The likelihood-ratio test of the Jolly-Seber model versus Brownie-Robson model 2 ($\phi_i^r, p_i^r, \gamma_i$) provided strong evidence that survival probabilities of newly marked chickadees differed from those of previously marked birds ($\chi^2 = 111.3$, $df = 33$, $P < 0.01$). We thus retained the general structure and investigated models with time constraints on all three types of parameters (Table 3). The likelihood-ratio test of model (ϕ_i^r, p_i^r, γ) versus the general model ($\phi_i^r, p_i^r, \gamma_i$) provided no evidence of time-specificity of γ ($\chi^2 = 41.3$, $df = 33$, $P = 0.15$). This constant- γ model (ϕ_i^r, p_i^r, γ) had the lowest AIC of all models tested (Table 3), indicating its appropriateness for this data set.

The likelihood ratio test for constant annual survival probability ($[\phi_i^r, p_i^r, \gamma]$ vs. $[\phi_i^r, p_i^r, \gamma_i]$) provided evidence of temporal variation ($\chi^2 = 75.7$, $df = 33$, $P < 0.01$). This result indicates the necessity of modeling annual survival probability as a year-specific parameter and provides motivation for investigating possible causes of year-to-year variation in survival.

Sampling effort changed over time, reaching high levels that were maintained for the last 20

TABLE 3. Goodness-of-fit test statistics and Akaike's Information Criterria (AIC) for some models investigated with Black-capped Chickadee data.

Model name and parameterization	Goodness-of-fit test			AIC
	χ^2	df	P	
(ϕ_i, p_i, γ) (Brownie-Robson model 2, transient parameterization)	13.1	14	0.52	792.1
(ϕ_i, p_i, γ)	54.1	47	0.22	767.4
$(\phi_i, p_{i < 74}, p_{i \geq 74}, \gamma)^a$	127.9	65	<0.01	804.9
$(\phi_i, p_{i < 74}, p_{i \geq 74}, \gamma)^b$	218.5	79	<0.01	867.5
(ϕ_i, p_i, γ)	130.1	80	<0.01	777.1
(ϕ_i, p_i, γ)	520.3	114	<0.01	1,099.3
(ϕ_i, p_i) (Jolly-Seber model)	133.3	56	<0.01	835.9

^a Model includes year-specific survival parameters (ϕ_i), a single parameter for the probability that a new animal is a resident (γ), year-specific capture probabilities prior to 1974 (p_i for $i < 74$; $p_{i \geq 74}$), and a single capture probability parameter for the years 1974–1992 ($p_{\geq 74}$).

^b Model includes year-specific survival parameters (ϕ_i), a single parameter for the probability that a new animal is a resident (γ), and 2 capture parameters, 1 for years prior to 1974 ($p_{i < 74}$) and another for years after and including 1974 ($p_{i \geq 74}$).

TABLE 4. Annual survival rate estimates for Black-capped Chickadees under the Jolly-Seber model (ϕ_i, p_i) and a best fit reduced-parameter version of the Brownie-Robson model (transient parameterization [ϕ_i, p_i, γ]).

Year	Jolly-Seber		Brownie-Robson	
	ϕ_i	$\widehat{SE}(\phi_i)$	ϕ_i	$\widehat{SE}(\phi_i)$
1958	0.90	0.315	0.95	0.319
1959	0.64	0.143	0.77	0.164
1960	0.83	0.160	0.90	0.159
1961	0.62	0.116	0.71	0.123
1962	0.55	0.082	0.63	0.091
1963	0.64	0.091	0.72	0.096
1964	0.59	0.084	0.66	0.088
1965	0.51	0.074	0.58	0.083
1966	0.69	0.119	0.68	0.112
1967	0.49	0.067	0.59	0.196
1968	0.61	0.090	0.65	0.086
1969	0.53	0.091	0.56	0.090
1970	0.52	0.070	0.64	0.083
1971	0.43	0.055	0.48	0.060
1972	0.76	0.081	0.82	0.080
1973	0.54	0.051	0.64	0.058
1974	0.49	0.042	0.56	0.048
1975	0.50	0.053	0.54	0.057
1976	0.67	0.065	0.72	0.068
1977	0.51	0.047	0.60	0.149
1978	0.48	0.044	0.56	0.050
1979	0.62	0.054	0.66	0.056
1980	0.55	0.048	0.65	0.053
1981	0.46	0.047	0.50	0.051
1982	0.53	0.044	0.62	0.189
1983	0.43	0.055	0.50	0.062
1984	0.48	0.062	0.53	0.266
1985	0.37	0.056	0.43	0.063
1986	0.46	0.060	0.54	0.146
1987	0.62	0.053	0.71	0.126
1988	0.54	0.044	0.66	0.168
1989	0.53	0.071	0.56	0.070
1990	0.36	0.047	0.43	0.055
1991	0.60	0.079	0.70	0.085
Mean	0.56	0.012	0.62	0.019

years. We thus investigated models in which capture probability was modeled as a constant after 1973, but in all cases models parameterized with time-specific capture probabilities were preferred (see Table 3). Thus, we retained time-specificity of survival and capture probabilities and modeled only γ as a constant. All further estimation and testing were based on this model with the lowest AIC (ϕ_i, p_i, γ).

PARAMETER ESTIMATES

Estimates of annual survival probability under the Jolly-Seber model and the low-AIC transient model are presented in Table 4. As explained above, the Jolly-Seber model is inappropriate for these data, and neither point estimates nor estimated standard errors are valid. We present survival estimates under this model only for comparative purposes, because our initial analysis of these data (Loery and Nichols 1985) used this model. The estimates of resident survival under the transient model typically are larger than the survival estimates under the Jolly-Seber model. This is expected, because transients (which are never seen again) contribute to estimation of survival probability under the Jolly-Seber model but not under the transient model.

The estimated constant probability that a new bird is a resident is $\hat{\gamma} = 0.73$ (SE = 0.027). Thus, we estimate that over a quarter of the new, unmarked birds trapped each winter are transients with virtually no chance of being re-trapped on the study area.

TABLE 5. Results of testing the null hypothesis that resident chickadee survival rates differed during selected periods before and after the establishment of (1) Tufted Titmice and (2) Sharp-shinned and Cooper's hawks on the study area.

Period A: before establishment	Period B: after establishment	Survival estimates (SE)		Test statistic ^a		
		A	B	χ^2	df	P ^b
Tufted Titmouse						
1966	1967	0.68 (0.112)	0.59 (0.196)	0.2	1	0.35
1962-66	1967	0.66 (0.031)	0.59 (0.196)	<0.1	1	0.38
1962-66	1967-71	0.66 (0.031)	0.59 (0.035)	1.6	1	0.10
1959-66	1967-91	0.71 (0.028)	0.59 (0.022)	10.7	1	<0.01
Sharp-shinned and Cooper's hawks						
1983	1984	0.50 (0.062)	0.53 (0.266)	<0.1	1	0.60
1979-83	1984	0.59 (0.044)	0.53 (0.266)	<0.1	1	0.41
1979-83	1984-91	0.59 (0.044)	0.57 (0.049)	<0.1	1	0.39
1959-83	1984-91	0.64 (0.018)	0.57 (0.049)	1.8	1	0.09

^a Computed using program CONTRAST (Hines and Sauer 1989).

^b One-tailed tests, with lower survival rates predicted for the more recent periods.

SOURCES OF VARIATION IN SURVIVAL

The estimates of annual survival rate from model (ϕ'_i, p'_i, γ) were used to test hypotheses about possible effects of the establishment of Tufted Titmice, Sharp-shinned Hawks, and Cooper's Hawks on chickadee survival. We used only resident survival rates in all of our tests.

Tests comparing 1967 survival of residents (extending from late 1967 to late 1968 and including the period during which titmice first nested on the area) with survival of residents in both the previous year (1966) and the previous 5-year period (1962 to 1966) showed no evidence of a difference (Table 5). The test of the five years before and after titmouse establishment provided some evidence of a difference (P

= 0.10). When we compared all of the study years before and after titmouse establishment (1959 to 1966 vs. 1967 to 1991), we found evidence of lower average survival rates of resident chickadees in the more recent years (Table 5).

Territorial Sharp-shinned and Cooper's hawks were first recorded on the study area in 1985. Tests involving single years and 5-year periods provided no evidence of a survival difference associated with hawk establishment (Table 5). Tests provided weak evidence for a difference between average survival rate for 1959 to 1983 (0.64) versus 1984 to 1991 (0.57; Table 5).

We developed models specifically to test for differences in survival before and after establishment of titmice and hawks. The model with different survival parameters before and after the establishment of titmice ($\phi'_{<67}, \phi'_{\geq 67}, p'_i, \gamma$) did not fit the data well ($\chi^2 = 111.8, df = 78, P < 0.01$). It did a significantly better job of explaining variation in the data than the constant-survival model (ϕ', p'_i, γ) but did not explain the data as well as the model permitting annual variation in survival (ϕ'_i, p'_i, γ ; Table 6). The AIC for the titmouse establishment model was lower (AIC = 763.1) than that for the constant-survival model (AIC = 777.1; Table 3). The survival probability estimates under this model were 0.68 (SE = 0.023) for the period before titmouse establishment and 0.59 (SE = 0.013) for the period after establishment.

The model with different survival paramete-

TABLE 6. Likelihood ratio tests involving models with survival constant over time (ϕ', p'_i, γ), different survival probabilities before and after titmouse establishment ($\phi'_{<67}, \phi'_{\geq 67}, p'_i, \gamma$) and hawk establishment ($\phi'_{<84}, \phi'_{\geq 84}, p'_i, \gamma$), linear-logistic change in survival as a function of time (ϕ'_i, p'_i, γ) and unspecified year-to-year variation in survival (ϕ'_i, p'_i, γ).

Models tested (H_0 vs. H_a)	Test statistic		
	χ^2	df	P
(ϕ', p'_i, γ) vs. $(\phi'_{<67}, \phi'_{\geq 67}, p'_i, \gamma)$	14.1	1	<0.01
(ϕ', p'_i, γ) vs. $(\phi'_{<84}, \phi'_{\geq 84}, p'_i, \gamma)$	7.9	1	<0.01
(ϕ', p'_i, γ) vs. (ϕ'_i, p'_i, γ)	17.6	1	<0.01
$(\phi'_{<67}, \phi'_{\geq 67}, p'_i, \gamma)$ vs. (ϕ'_i, p'_i, γ)	57.7	31	<0.01
$(\phi'_{<84}, \phi'_{\geq 84}, p'_i, \gamma)$ vs. (ϕ'_i, p'_i, γ)	63.9	31	<0.01
(ϕ'_i, p'_i, γ) vs. (ϕ'_i, p'_i, γ)	54.2	31	<0.01

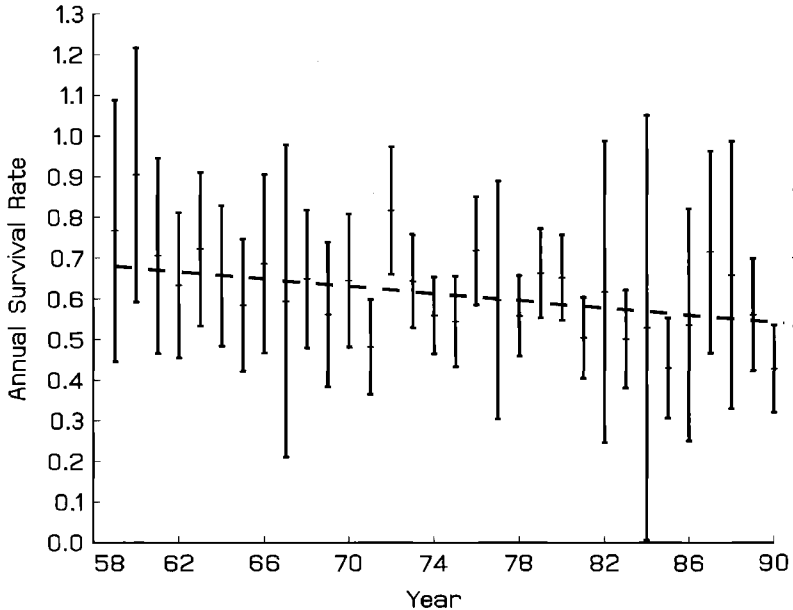


FIG. 1. Annual survival-rate estimates with approximate 95% confidence intervals for wintering Black-capped Chickadees in Connecticut, 1959 to 1992. Dashed line depicts the estimated linear-logistic decline in survival over time.

ters before and after establishment of Cooper's and Sharp-shinned hawks ($\phi'_{<84}$, $\phi'_{\geq 84}$, p'_i , γ) also did not fit the data well ($\chi^2 = 118.0$, $df = 78$, $P < 0.01$) but had a relatively low AIC (AIC = 769.3). This model explained the data better than the constant-survival model but not as well as the model permitting year-to-year variation in annual survival (Table 6). The estimated survival probabilities before and after hawk establishment were 0.62 (SE = 0.014) and 0.56 (SE = 0.023), respectively.

The model specifying annual survival probability as a linear-logistic function of sample period (ϕ'_i , p'_i , γ) did not fit the data well ($\chi^2 = 108.3$, $df = 78$, $P = 0.01$) but had the lowest AIC of all models tested (AIC = 759.6). This model explained the data better than the constant-survival model but not as well as the model permitting unspecified year-to-year variation in annual survival (Table 6). The estimates for the linear-logistic parameters were $\hat{a} = 0.79$ (SE = 0.105) and $\hat{b} = -0.019$ (SE = 0.0050). This linear-logistic function is plotted with the point estimates under model (ϕ'_i , p'_i , γ) in Figure 1.

ABUNDANCE

Estimates of population size and their approximate 95% confidence intervals are pre-

sented in Figure 2. The linear regression analysis of $\ln(\hat{N}_i)$ versus time (i) provided evidence of a population decline over the study period ($F = 6.6$, $df = 1$ and 30, $P = 0.02$). The Durbin-Watson statistic ($d = 1.55$) provided no evidence ($P > 0.05$) of serial correlation of the regression model error terms (Durbin and Watson 1951). The estimated slope ($\hat{b} = -0.012$, $\widehat{SE}[\hat{b}] = 0.0047$) translates to a finite rate of population change of $e^{\hat{b}} = 0.99$, indicating an approximate rate of decline in population size of 1% per year.

DISCUSSION

We rejected the Jolly-Seber model in favor of a model permitting different survival probabilities for newly marked versus previously marked birds. At least three alternative explanations exist for survival differences between newly marked and previously marked birds: (1) the effect of initial handling, (2) age-specific differences, and (3) the existence of transients. Because these models are structurally identical and cannot be distinguished solely on the basis of capture-recapture data, we need ancillary data (see Pradel et al. 1995) and/or biological

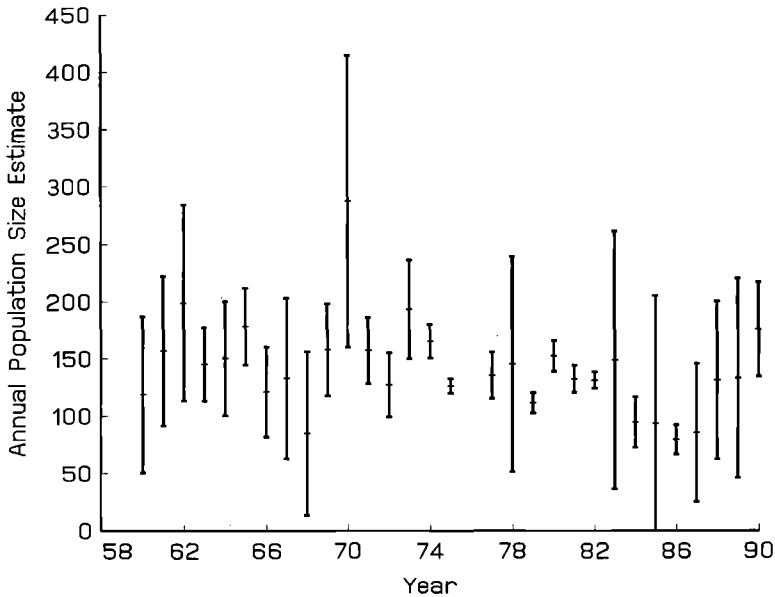


FIG. 2. Annual population-size estimates with approximate 95% confidence intervals for wintering Black-capped Chickadees in Connecticut, 1959 to 1993.

insight to choose among these alternative explanations.

In the case of chickadees, we believe that any difference between the response to initial and subsequent handling was unimportant to survival probabilities. Handling appears to be less stressful for chickadees than for many other species, and bait trapping seems to be less stressful than mist netting for most species. The age-specific and transient models are plausible, however. Loery et al. (1987) focused on age-specific differences in survival rates. Because newly marked birds are likely to include a large fraction of first-year birds, and because previously marked birds include only older birds (>1 year), age-specificity is a reasonable interpretation for survival differences between newly marked and previously marked birds. The magnitude of the difference, however, leads us to believe that transients also are a factor and may be the primary determinant.

Smith (1991) provided evidence of transients in a winter population of chickadees. These birds may include what she called "visiting migrants," which are young birds that arrive in October or November, stay all winter, and leave in late March or early April. We now have evidence of the destination of one of these migrants. A chickadee that we banded on 2 De-

ember 1990 and last recaptured on 4 March 1991 was found dead in Bridgewater, Vermont on 2 May 1994. This is the first of the 2,000 chickadees we have caught during our November/January sampling periods that has been recovered elsewhere. Bagg (1969) reported several other examples of chickadees that were banded in one of the midwinter months and have now been recovered elsewhere.

All three of the alternative explanations noted above for the estimated survival differences between newly marked and previously marked birds are adequately handled using our modeling approach (Brownie and Robson 1983, Pradel et al. 1997). Another possible explanation involves heterogeneous capture probabilities that can, in some situations, lead to biased estimates of survival for previously unmarked animals (Francis and Cooke 1993). We doubt that this was operating because our goodness-of-fit tests of transient models provided no evidence of heterogeneous capture probabilities.

As in our earlier analysis (Loery and Nichols 1985), we found evidence that survival rates decreased during the years immediately following titmouse establishment. We found little evidence that survival rates in the years immediately following establishment of Sharpshinned Hawks and Cooper's Hawks were

lower than in the previous years. However, long-term comparisons of all study years before and after either titmouse or raptor establishment indicated that chickadee survival rates were lower in the later years. We found evidence that both annual survival probability and abundance of chickadees declined from 1959 to 1991.

Several possible explanations exist for the decline in survival probability and population size. We believe that the most likely explanation is the gradual maturing of the surrounding forest habitat. All of the trees Smith (1991) listed as favorites for chickadee nesting, i.e. alder (*Alnus* spp.), birch (*Betula* spp.), poplar (*Populus* spp.), cherry (*Prunus* spp.), and willow (*Salix* spp.), are pioneer species. These taxa gradually are being replaced by maple (*Acer* spp.), oak (*Quercus* spp.), ash (*Fraxinus* spp.), and other more mature forest species in our area. It is more difficult for chickadees to excavate cavities in the latter tree species. Changes in northeastern forests also are relevant to changes in relative numbers of Black-capped Chickadees and Tufted Titmice. Titmice typically do not excavate their own nesting cavities. Maturation of northeastern forests is thus creating conditions less favorable for chickadees, but not for titmice.

Changes in weather patterns are another possible explanation for the decline in chickadees. Researchers at the National Climatic Data Center found a high index of extreme weather conditions since the late 1970s (Kerr 1995). However, previously we found no evidence of a relationship between chickadee survival rate and winter temperature (Loery and Nichols 1985). Therefore, we believe that changes in the composition of the surrounding forest have been the most important determinants of chickadee survival probabilities in our area over the last 33 years, with the establishment of a new potential competitor of only short-term significance and the establishment of new potential predators of little (or no) significance.

During the preparation of Loery and Nichols (1985), we were disappointed by the limited use of capture-recapture models for bird banding data and by the extensive use of *ad hoc* statistics such as return rate (see Martin et al. 1995). This situation has changed markedly during the last decade, and many students of avian population ecology now use probabilistic

capture-recapture models for data analysis. Our experience with avian capture-recapture data leads us to believe that transient models of the type used here and described by Pradel et al. (1997) will be useful in many other studies of marked birds (see DeSante et al. 1995). We urge those involved in studies of marked birds to consider such models in their analyses.

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