

Estimation of long-term trends and variation in avian survival probabilities using random effects models

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ABSTRACT We obtained banding and recovery data from the Bird Banding Laboratory (operated by the Biological Resources Division of the US Geological Survey) for adults from 129 avian species that had been continuously banded for > 24 years. Data were partitioned by gender, banding period (winter versus summer), and by states/provinces. Data sets were initially screened for adequacy based on specific criteria (e.g. minimum sample sizes). Fifty-nine data sets (11 waterfowl species, the Mourning Dove and Common Grackle) met our criteria of adequacy for further analysis. We estimated annual survival probabilities using the Brownie et al. recovery model $\{S_t, f_t\}$ in program MARK. Trends in annual survival and temporal process variation were estimated using random effects models based on shrinkage estimators. Waterfowl species had relatively little variation in annual survival probabilities (mean CV = 8.7% and 10% for males and females, respectively). The limited data for other species suggested similar low temporal variation for males, but higher temporal variation for females (CV = 40%). Evidence for long-term trends varied by species, banding period and sex, with no obvious spatial patterns for either positive or negative trends in survival probabilities. An exception was Mourning Doves banded in Illinois/Missouri and Arizona/New Mexico where both males (slope = -0.0122, se = 0.0019 and females (slope = -0.0109 to -0.0128, se = 0.0018 - 0.0032) exhibited declining trends in survival probabilities. We believe our approach has application for large-scale monitoring. However, meaningful banding and recovery data for species other than waterfowl is very limited in North America.

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1 Introduction

In 1998, the Biological Resources Division of the United States Geological Survey issued a report on trends in biological resources in the United States (Mac *et al.*, 1998). This report contained information on long-term trends in population size of many vertebrate species, including birds. However, we think there were three problems in assessing the trends reported in Mac *et al.* (1998): (1) data for most avian species were based on population indices collected using questionable sampling schemes, such as roadside transects only (Robbins *et al.*, 1986); (2) long-term trends estimated from these data represented only the product of bird abundance and detectability near roads and not necessarily population size of avian species across their habitat (see Bystrak, 1981); and, (3) while population size is a variable of interest, survival and recruitment are the reasons why populations change in size over time. Thus, studies of trends in the probability of survival are more fundamental, although much more difficult to conceptualize and implement.

In this paper, we apply methods for detecting long-term trends in annual survival probability based on the likelihood framework universally used as the basis for credible analysis of band-recovery and capture-recapture data. We used band recovery models to estimate annual survival probabilities from time-specific models and then used random effects models (also called empirical Bayes models; see Maritz & Lwin, 1989; Carlin & Louis, 1996) to estimate trends and variation in survival over time. The data used in band-recovery models are marked animals that are recovered dead. The parameters, in our case, were survival probability (S_t) and recovery probability (f_t) in year t . Random effects models are used in statistics, especially in conjunction with shrinkage estimators of individual parameters (here, conditional annual survival probabilities, S_t). Despite their advantages and long history, random effects models have not been applied to band-recovery or capture-recapture data (see Johnson, 1989, in relation to surveys of waterfowl abundance). Here, the correct interpretation of random effects is that 'true' annual survival probabilities do not fall exactly on any simple, smooth model; the deviation of estimates of annual survival probability from such models are treated as random. Estimates of annual survival probability are not treated as being randomly drawn from a larger sample of years to which inferences might be made. Therefore, trends in annual survival probabilities estimated from random effects models are still conditional on the specific set of years used in the analysis; no reliable statistical inferences can be made beyond the period of years in which the parameters are estimated.

In addition to estimating trends in survival probabilities, we were also interested in estimating the process variation ($\sigma_{\text{process}}^2$) in S_t over both time ($\sigma_{\text{temporal}}^2$) and space ($\sigma_{\text{spatial}}^2$). Process variation must be separated from sampling variation, $\text{var}(\hat{S}_t|S)$, the variation attributable to estimating a parameter from sample data (Box *et al.*, 1978). For example, the total estimated variation ($\hat{\sigma}_{\text{total}}^2$) in \hat{S}_t over time or space can be viewed as (Skalski & Robson, 1992):

$$\hat{\sigma}_{\text{total}}^2 = \hat{\sigma}_{\text{process}}^2 + \hat{\text{var}}(\hat{S}_t|S)$$

Theory on random effects models allowed us to estimate the separate process variation from the total variation in the unrestricted general estimates of annual survival probabilities. Given estimated process variation, proper unconditional inference can be made about trends in survival probabilities and about actual individual annual survival probabilities. Current models and methods in use are all

restricted to conditional inference based only on sampling variation, and are thus theoretically not a suitable basis for valid inference on long-term trends.

The feasibility of using existing data for monitoring life-history parameters, such as survival, was demonstrated by Wotawa (1993) using band-recovery models on a single set of recovery data. Wotawa (1993) examined a 26-year data set (1964-1989) on Mallard ducks (*Anas platyrhynchos*) banded in eastern Colorado, and they found a long-term, negative linear trend in survival where S decreased 9.6% for males and 7.7% for females over the 26 year period. Long-term monitoring through banding, combined with modern analytic methods, allowed a very slow rate of decline in survival probability (0.3% per year) to be identified in Wotawa (1993) because of the long-term nature of the data set, the large numbers banded each year, and high recovery rates. Such a trend would probably have been missed with a shorter-term data set of, say, only 5-10 years.

The results from Wotawa (1993) motivated us to ask whether similar trends in survival probabilities could be detected in other avian species in North America. The Bird Banding Laboratory (BBL; operated by the Biological Resources Division of the US Geological Survey) was the source of such recovery data because the BBL has served as the repository for bird banding data in North America. The BBL had records on 50-60 million banded birds with many areas having continuous banding programs for 30-40 years. In this project, we attempted to obtain all the long-term data (≥ 24 continuous years of banding) available from the BBL for avian species in North America and analyse the subset of those data satisfying *a priori* criteria for minimum sample sizes. Each individual data set that met our criteria was then analysed for trend and variation in annual survival probability using our analytical approach.

In summary, we present here an analytical framework for analysing long-term trends and variation in parameters of avian populations. While we used this approach to examine avian survival probabilities, we believe that our approach is equally applicable to other population parameters, such as population size and recruitment, and to other taxa.

2 Methods

2.1 Selection criteria for long-term data sets

Long-term bird banding data sets (both late-summer and winter banding) were obtained from the BBL. The initial criteria for data sets to use in our analysis were, first, to use data sets that had ≥ 24 years of continuous banding of a species at one general banding site. Secondly, data for a given species in a general banding site had to have a minimum of 50 birds banded each year with no gaps (or if a minimum of 200 birds per year were banded we accepted one instance of no birds banded in a single year). Thirdly, there had to be at least a total of 200 direct (i.e. first year after banding) and 200 indirect recoveries. Fourthly, we used only birds that had been banded since 1955. Fifthly, we included only recoveries of dead birds (no retraps, repeats or returns), and only wild birds that were caught, banded and released immediately with no auxiliary marks (e.g. no colour bands, wing tags, radio-transmitters, etc). Finally, we restricted this study to adults (including young of the year banded during their first winter) of known sex.

Selection of data sets for analysis was determined and finalized before any analyses were done. Once selected, a data set was not removed from the analysis.

This approach avoided any selection biases. Data sets for waterfowl species were subdivided into pre-season bandings (July-September) with associated recoveries in September-February and winter bandings (January-March) with associated recoveries in April-December and January-March of the year(s) subsequent to the year when banded. In general, birds banded in the pre-season were on their breeding grounds but were recovered on migratory and wintering grounds. Winter bandings were of waterfowl wintering in a given location; their breeding grounds could have been the same but also could have been several different sources. Therefore, inferences concerning survival were not to the strict location where birds were banded. Data sets for non-waterfowl species were subdivided into summer bandings (May-August) and winter bandings (January-March). The recovery period was the 8 months following August for summer banding and the 9 months following March for winter banding.

Clearly, the study of long-term trends in survival probability could have taken other routes to the selection and analysis of banding and recovery data. We tried to emphasize large, clean data sets where there was continuous banding of large numbers of individuals of a species over relatively small (i.e. homogeneous) areas. Other strategies are certainly appropriate, but present more difficult analysis strategies, such as various meta-analysis methods (Hedges and Olkin, 1985).

2.2 Analytical approach

Basic models used in the analysis of these data were band recovery models outlined in Brownie *et al.* (1985) with two types of parameters, S_t (the conditional probability that a bird alive at time t survives one calendar year to the time of next banding) and f_t (the conditional probability that a banded bird alive at time t will be retrieved dead and its band reported during the next season). The conditional (annual) probabilities S and f were modelled as time-dependent $\{S_t, f_t\}$ within the product multinomial framework on time (t in years) using an identity link (see Lebreton *et al.*, 1992). Thus, S and f were modelled without any transforming link function, unlike the analysis performed by Wotawa (1993) where a logit link was used. We used an identity link so that estimates of σ were on the same scale as S ; use of a link function other than the identity link would have required back-transformation to achieve an appropriate scaling of $\hat{\sigma}^2$. Sexes were analysed separately within each species/location data set.

An alternative formulation of band recovery models is available (White & Burnham 1999) where a reporting probability (r ; the conditional probability that a band is reported, given that the bird has died) is used instead of f . The advantage of using the f parameterization is that there are no boundary problems with estimating S under the identity link. Under the $\{S, r\}$ formulation:

$$r_t = \frac{f_t}{1 - S_t}.$$

When S is bounded $0 \leq S \leq 1$ (e.g. using a logit or sine link function in the S, r formulation) and approaches 1, then numerical sampling variances for S become extremely biased (i.e. they approach 0). If S is not bounded (e.g. using an identity link function) and $\hat{S} > 1$, then negative estimates of r can result with associated problems in estimating sampling variances for \hat{S} . The disadvantage of using the $\{S, f\}$ parameterization is that the recovery probabilities (f) are a function of both

survival probabilities and reporting probabilities; modelling a covariate for f is not always clear compared with the r parameterization. However, we modelled S and f only with time-dependent models (see Section 2.3) and did not constrain either parameter using covariates.

Therefore, once annual estimates of S and f were obtained for a given data set, we used random effects models to obtain estimates (with their sampling variances) of average survival over time (\hat{S}), and temporal process variation ($\hat{\sigma}_{\text{temporal}}^2$), using an intercept-only model, and the slope parameter ($\hat{\beta}_1$) for S over time, using a linear trend model. The $\hat{\beta}_1$ were then compared within species and between locations within species to estimate spatial process variation in trends.

2.3 Analysis of $\{S_t, f_t\}$ models

We computed ML estimates of annual S and f under the identity link (a $\{S_t, f_t\}$ model using notation in Lebreton *et al.*, 1992). Estimates of the variance-covariance matrix were available to construct inference based on a random effects model. The latter was useful because the scope of inference is thereby changed from being conditional on the unknown (but estimated) annual survival rates to being an unconditional inference about possible trends (see Random Effects Modeling section). Likelihood-based fitting of the models was done with program MARK (White & Burnham, 1999; White *et al.*, 2001), a computer program for comprehensive analysis of band-recovery and capture-recapture data. MARK is an outgrowth of programs SURVIV (White, 1983) and RELEASE (Burnham *et al.*, 1987) and it has the greatest capabilities for analysis of band-recovery data. In this manner, we were able to obtain annual estimates of survival probability, with the associated covariance matrix, for each data set.

We computed a measure of overdispersion (\hat{c} ; Lebreton *et al.*, 1992) for each data set based on observed deviance divided by its degrees of freedom (Burnham *et al.*, 1987). This estimate was used to adjust the covariance matrix for the annual estimates of S for any overdispersion (see Wedderburn, 1974; Lebreton *et al.*, 1992).

2.4 Random effects modeling

We will focus on the estimates of linear trend effect, β_1 , based on random effects models using the ML estimates of S from model $\{S_t, f_t\}$ at this stage of the analysis. An alternative approach would have embedded a linear trend in the likelihood estimation of S in program MARK (a $\{S_T, f_t\}$ model). However, the standard error of $\hat{\beta}_1$ would have then been based only on sampling variation; hence, that standard error would be too low as compared to a direct regression on the true S_t (which we cannot do because the true S_t are not known). The random effects approach solves this problem and effectively allows a valid regression on the S_t .

We have recently developed the theory for the random effects model using annual survival rates from models based on S_t estimated from band-recovery models using an identity link. Moreover, those analyses have been incorporated (i.e. fitting trend models, estimation of process variation in the S_t and computing shrinkage estimates of annual survival rates) into program MARK. Because the random effects theory (Carlin & Louis, 1996; Longford, 1993) used here is not in the literature, we give a brief technical summary below (see also Burnham & White, this issue).

The basic model assumed is that $\hat{S}|\underline{S}$ has conditional mean vector \underline{S} and conditional covariance matrix W , and \underline{S} has an unconditional mean vector $E(\underline{S}) = X\beta$ and a simple unconditional dispersion matrix as $\sigma^2 I$. For a study with k years of banding, \underline{S} is a $k - 1$ by 1 vector of S_1, \dots, S_{k-1} , which are considered as exchangeable random variables (β is an r by 1 vector of parameters, X is $k - 1$ by r). The residuals, $\underline{S} - X\beta$, are thus ‘random effects’, hence the model name (Casella, 1995). The matrix X codes the structural model form assumed for the annual survival probabilities (such as a linear time trend, in which case $r = 2$). The model for \underline{S} is just a standard regression model. But we do not measure \underline{S} , rather we have only \hat{S} which is subject to sampling variation (a type of ‘measurement error’). Both \hat{S} and W come from model $\{S_t, f_t\}$ fitted to the data with MARK. However, β and σ^2 are unknown and σ^2 is not estimable from standard banding methods (σ^2 is process variation; W is sampling variation).

The unconditional model for \hat{S} is that \hat{S} has mean vector $X\beta$ and dispersion matrix $D = \sigma^2 I + W$. Standard likelihood methods will produce an estimator of β , but its standard error is then only based on W , not D , which is incorrect if there is real process variation (which there will be). In this context such ‘process variation’ can be interpreted as lack of fit to the assumed model structure with respect to the conditional analysis (but it is not lack of fit with respect to the unconditional model). It is then very important to incorporate this ‘lack of fit’ into test statistics and standard errors used for inference. If we had the true \underline{S} , W would be a matrix of all zeros, so then any value at all of $\beta \neq 0$ would be judged statistically significant in a conditional analysis. But if we had true \underline{S} , we would judge trends based directly on σ^2 estimated from residuals about the fitted model structure, rather than incorrectly judging trends based on W .

Theoretically, a likelihood-based analysis with banding models is possible under the random effects model; a Bayesian analysis is also possible. However, the required calculations for a likelihood-based analysis are not currently feasible. Therefore, we used a method of moments analysis described as follows. Given a value of σ^2 we have

$$\hat{\beta}(\sigma^2) = (X'D^{-1}X)^{-1}X'D^{-1}\hat{S}.$$

The unconditional covariance matrix of this $\hat{\beta}$ is

$$VC(\hat{\beta}) = X'D^{-1}X)^{-1}.$$

A one-dimensional search is used to find the estimate of σ^2 from

$$k - 1 - r = (\hat{S} - X\hat{\beta}(\sigma^2))'D^{-1}(\hat{S} - X\hat{\beta}(\sigma^2)).$$

A confidence interval on σ^2 can be computed; $\hat{\sigma}^2$ may be 0 or even negative; negative estimates were truncated to 0.

Improved estimates of the annual survival probabilities can be computed as the classical shrinkage estimates (it is the residuals that are shrunk):

$$\tilde{S} = \hat{\sigma}D^{(-1/2)}(\hat{S} - X\hat{\beta}) + X\hat{\beta},$$

with the covariance matrix of \tilde{S} estimated following Burnham & White (this issue).

All of the calculations needed for the random effects model analyses (including results not given here) were performed in program MARK. Thus for each data set, we were able to obtain a weighted mean estimate of \bar{S} ($\hat{\hat{S}}$), its appropriate standard error, and an estimate of temporal process variation ($\hat{\sigma}_{\text{temporal}}^2$) by using the annual estimates of S (from model $\{S_t, f_t\}$) in an intercept-only random-effects model

(i.e., X is a $k - 1 \times 1$ vector of 1s). Estimates of the time trend in $S(\hat{\beta}_1)$ and its appropriate standard error were obtained by using the annual estimates of S (from model $\{S_t, f_t\}$) in a linear-trend random effects model (i.e. X is a $k - 1 \times 2$ matrix with 1s in the first column and $t = 1, 2, \dots, k - 1$ in the second).

After the individual random effects analyses of each data set, we performed a preliminary meta-analysis using a components of variation analysis (Burnham *et al.*, 1987) on the estimates of $\hat{\sigma}^2$ and $\hat{\beta}_1$ from the linear-trend random effects model imposed on the ML estimates from the $\{S_t, f_t\}$ model. This allowed us to evaluate spatial process variation ($\sigma_{\text{spatial}}^2$) in the trend estimates by species.

3 Results and discussion

3.1 Data set selection

There were band-recovery data available for 926 species from the BBL, representing 50 481 425 birds banded and 3 043 226 birds recovered. Of these, data on 129 species (35 waterfowl and 94 non-waterfowl) had been collected over sufficiently long time periods and had sufficient numbers of total birds banded and recovered to warrant further investigation in this study (Appendix 1). A total of 68 data sets (58 waterfowl and 10 non-waterfowl) finally met all of our criteria for selection of data sets. These final data sets included 11 waterfowl species: Mallard (*Anas platyrhynchos*), American Black Duck (*Anas rubripes*), American Wigeon (*Anas americana*), Green-wing Teal (*Anas crecca*), Blue-wing Teal (*Anas discors*), Northern Pintail (*Anas acuta*), Wood Duck (*Aix sponsa*), Redhead (*Aythya americana*), Canvasback (*Aythya valisineria*), Greater Scaup (*Aythya marila*) and Canada Goose (*Branta canadensis*); and five non-waterfowl species: Mourning Dove (*Zenaida macroura*), White-winged Dove (*Zenaida asiatica*), European Starling (*Sturnus vulgaris*), Common Grackle (*Quiscalus quiscula*) and Evening Grosbeak (*Coccothraustes vespertinus*). These data sets were distributed across most of North America with the exception of the extreme south-east and Pacific north-west of the United States and Canada (Fig. 1). Each data set was analysed separately by gender. We were unable to obtain results for five data sets because numerical solution methods for finding ML estimates failed to converge and for six data sets because the matrix D in the random effects modelling was not always positive definite. In some cases, we were unable to obtain estimates for both sexes in a given data set. Therefore, we were able to obtain results for 59 data sets from the 11 waterfowl species and only two of the five non-waterfowl species (Mourning Dove and Common Grackle).

The theory underlying the product multinomial models for band recovery data is based on the assumption of independent fates of banded birds (Brownie *et al.*, 1985). Some overdispersion was seen in all data sets where an overdispersion parameter could be estimated (Table 1). While it seems likely that this parameter (c) is slightly overestimated (Cooch & White 2001), there was strong evidence that birds did not have independent fates, which was not unexpected in real biological populations. The lack of independence was relatively low; only for 17% of the 107 cases was $\hat{c} > 1.8$. Estimates of overdispersion (\hat{c}) ranged from 1.13 to 2.37 (Table 1), which suggested the need for inflation of the sampling variances and covariances (as was done in Tables 2-4) to account for partial dependence in fates of banded birds and other sources of heterogeneity.

In spite of the large numbers shown for many avian species, relatively few species

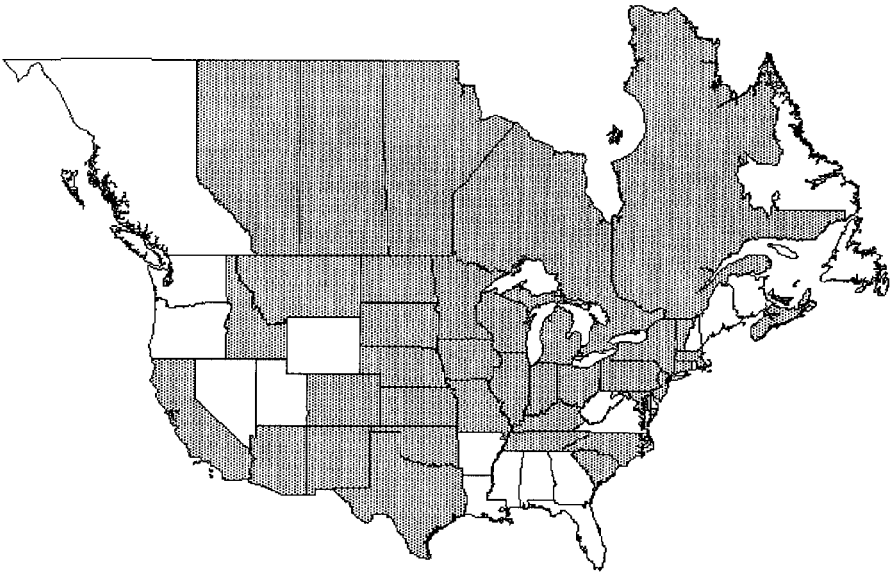


FIG. 1. Geographical distribution of 68 data sets for 16 species used in random effects analysis.

were represented by continuous, long-term banding, even at the level of a political state or province (Appendix 1). Most species were represented by relatively few numbers banded per year and most had a very low ($f < 0.01$) annual recovery probability. These limitations allowed a careful analysis of only a small fraction of the avian species (Table 1). In several cases we combined data over 2-5 geographic areas in order to have enough data for analysis of non-waterfowl species and some of the waterfowl species. For example, data for 10 states were pooled for the Common Grackle; analyses of these data must be considered only approximate due to the heterogeneity introduced by such extensive pooling of the data sets. Clearly, the retrospective estimation of trends in survival using band recovery models will remain impossible for most avian species. For example, the total probability of recovery for the Myrtle Warbler was only 0.0009 and the annual recovery probability was considerably less than this value.

3.2 Estimated mean survival

In general, ducks exhibited strong sexual differences in average survival (\hat{S}) over the time period (Table 2) whereas the Canada Goose did not. Data for non-waterfowl species were too sparse to allow such generalizations. In general, waterfowl species did not exhibit highly variable survival probabilities over time based on the coefficient of temporal process variation; males averaged similar coefficients of temporal process variation ($\bar{CV} = 0.087$, range = 0.000 - 0.477, $n = 55$) to females ($\bar{CV} = 0.100$, range = 0.000 - 0.364, $n = 47$) (Table 2). Although limited, males of the non-waterfowl species exhibited similar coefficients of temporal process variation to waterfowl species ($\bar{CV} = 0.109$, range = 0.006 - 0.212, $n = 2$) whereas females of the non-waterfowl species exhibited much higher coefficients of temporal process variation ($\bar{CV} = 0.402$, range =

0.000 – 0.971, $n = 3$) (Table 2). However, data were much more limited for the non-waterfowl species.

Where comparisons were possible, the mean of the estimated mean survival probability (i.e. averaging \hat{S} across states or provinces) showed good consistency between banding periods. For example, average survival probability for Mallards banded in the pre-season was 64.7% versus 65.1% for winter-banded birds, while the respective values for females were 53.4% versus 55.0%. Mallards banded in New York seemed to have lower survival probabilities during both banding periods than other areas (Table 1).

3.2 Estimated trends in avian survival

Time intervals for estimated trends in survival ranged from 24 to 42 years (Table 1). Estimates of trend ($\hat{\beta}_1$) were quite precise compared with the estimates of process variance. We found greater numbers of positive trends in survival probabilities in both males (19 negative, 36 positive) and females (19 negative, 28 positive) of waterfowl species (Table 3). However, all of the non-waterfowl species had negative trends ($n = 5$). We were not able to generalize much about non-waterfowl species because of the sparseness of the data. We examined the waterfowl more closely for patterns in the observed trends in survival probability over time.

Consistent negative trends were observed in Greater Scaup (both sexes) banded during the winter, female Mallards, Canvasback, and Canada Geese (Table 4). Interestingly, all of the populations showing consistent negative trends (based on 95% confidence intervals) were from birds banded during the winter period. Males of waterfowl species banded during the pre-season exhibited an overall positive trend with the lowest coefficient of spatial process variation whereas females of waterfowl species banded during the winter exhibited negative trends in survival with the next lowest coefficient of spatial process variation (Table 4). Females banded during the pre-season and males banded during the winter exhibited the highest coefficients of spatial process variation; they also exhibited trends in survival that were closer to zero based on their 95% confidence intervals (Table 4).

Consistent negative trends were observed for both male and female Greater Scaup banded during the winter period (Table 4). Female Mallards, Canvasbacks and Canada Geese banded during the winter period also showed substantial declines in survival probability. Male Black Ducks banded during the winter also indicated a decreasing survival probability (Table 4). Substantial increases in long-term survival probability were seen in several species banded during the pre-season period: male Mallards, Blue-winged Teal and Wood Duck, in addition to female Green-winged Teal and Wood Duck. The pattern suggested is decreasing survival probabilities for birds banded during the winter period and increasing survival probabilities for birds banded during the pre-season period.

The patterns seen in the mean estimates tend to be supported by the individual estimates in Table 3. For example, 11 of 12 of the estimates of slope ($\hat{\beta}_1$) for male Mallards banded during the pre-season period were positive, while 8 of the 11 estimates for female Mallards were positive. Negative trends in survival probability are indicated for most of the Mallard populations banded during the winter period: 7 of 10 areas for males and 7 of 8 areas for females have estimates that were negative (Table 3). Given the mixing of populations of Mallards on the breeding and wintering grounds, the differing sign of long-term survival trends does not appear to be a contradiction. Instead, our results seem to suggest increasingly

TABLE 1. Summary of time periods for each data set and estimates of over-dispersion ($\hat{\epsilon}$) used in the analysis of data sets. Missing values (denoted by '—') are for data sets where analysis failed to converge

Species	Season	State/Province	Years			$\hat{\epsilon}$	
			First	Last	No.	Males	Females
<i>Waterfowl species</i>							
Mallard	Pre	AB	1955	1996	42	1.42	1.54
Mallard	Pre	CA	1955	1996	42	1.34	1.61
Mallard	Pre	CO	1958	1984	27	1.28	—
Mallard	Pre	MB	1955	1996	42	1.39	1.45
Mallard	Pre	MI	1959	1996	38	1.35	1.42
Mallard	Pre	MN	1956	1996	41	1.50	1.51
Mallard	Pre	MT	1957	1996	40	1.19	1.70
Mallard	Pre	NY	1956	1996	41	1.30	1.72
Mallard	Pre	ND	1959	1996	38	1.39	1.68
Mallard	Pre	ON,PQ	1961	1996	36	1.47	1.81
Mallard	Pre	SK	1955	1996	42	1.43	1.31
Mallard	Pre	WI	1961	1996	36	1.45	1.84
Mean					39	1.38	1.60
Mallard	Winter	AR	1960	1989	30	1.19	—
Mallard	Winter	CA	1957	1988	32	1.27	1.49
Mallard	Winter	CO	1961	1989	29	1.85	1.45
Mallard	Winter	ID	1965	1988	24	1.33	1.32
Mallard	Winter	KS,NE	1955	1984	30	1.65	1.33
Mallard	Winter	MD	1957	1988	32	1.37	1.43
Mallard	Winter	NY	1958	1996	39	1.50	2.26
Mallard	Winter	NC,SC	1962	1989	28	1.22	1.49
Mallard	Winter	OK,TX	1962	1991	30	1.43	1.23
Mallard	Winter	TN	1959	1989	31	1.25	1.37
Mean					31	1.41	1.48
Black Duck	Pre	MI,ON	1955	1996	42	1.73	2.15
Black Duck	Pre	NS,PQ	1960	1996	37	1.68	1.88
Mean					40	1.70	2.02
Black Duck	Winter	MD	1956	1988	33	1.78	2.03
Black Duck	Winter	MA,NJ,NY	1955	1993	39	1.46	1.62
Black Duck	Winter	NC,SC,TN	1960	1989	30	1.67	1.46
Mean					34	1.64	1.70
Amer Wigeon	Winter	CA	1955	1978	24	1.27	—
GW Teal	Pre	CO	1958	1982	25	2.10	1.39
BW Teal	Pre	AB	1955	1996	42	1.44	2.03
BW Teal	Pre	MB,ON	1955	1996	42	1.65	1.70
BW Teal	Pre	SK	1955	1996	42	1.49	1.94
Mean					42	1.52	1.89
Pintail	Pre	AB	1955	1996	42	1.51	1.51
Pintail	Pre	CA	1955	1980	26	1.66	1.55
Pintail	Pre	CO	1958	1981	24	1.41	—
Pintail	Pre	MB	1967	1996	30	2.02	2.14
Pintail	Pre	ND	1973	1996	24	1.36	2.37
Pintail	Pre	SK	1955	1996	42	1.46	1.61
Mean					31	1.57	1.83
Pintail	Winter	CA	1955	1982	28	1.56	1.51

TABLE 1.—(Continued)

Species	Season	State/Province	Years			\hat{c}	
			First	Last	No.	Males	Females
Wood Duck	Pre	AR,MO	1958	1996	39	1.92	—
Wood Duck	Pre	IL,IN,IA,OH	1958	1996	39	1.49	1.81
Wood Duck	Pre	KY,NC,SC,TN	1960	1996	37	1.50	1.78
Wood Duck	Pre	MA,NY,ON,PA,VT	1955	1996	42	1.13	1.49
Wood Duck	Pre	MI,MN,WI	1959	1996	38	1.28	1.33
Mean					39	1.47	1.60
Redhead	Pre	AB,SK	1961	1996	36	1.91	1.68
Redhead	Winter	NY	1955	1991	37	1.54	1.54
Canvasback	Winter	MD	1956	1995	40	1.55	—
Canvasback	Winter	NY	1955	1982	28	1.21	1.92
Mean					34	1.38	—
Gr Scaup	Winter	NY	1955	1990	36	1.95	1.62
Canada Goose	Pre	MB	1968	1996	29	1.50	1.52
Canada Goose	Pre	MI,ON	1966	1996	31	1.60	1.60
Canada Goose	Pre	NY	1967	1996	30	1.69	1.51
Mean					30	1.60	1.54
Canada Goose	Winter	IL	1959	1989	31	1.45	—
Canada Goose	Winter	MD	1960	1990	31	1.30	1.29
Canada Goose	Winter	NC,TN	1958	1986	29	1.40	—
Mean					30	1.38	—
<i>Non-Waterfowl species</i>							
Mourning Dove	Summer	AZ,NM	1955	1994	40	—	1.74
Mourning Dove	Summer	IL,MO	1955	1992	38	1.54	1.61
Mean					39	—	1.67
Grackle	Summer	OH,IL,IN,IA,MI, MN,ON,WI,SD,ND	1955	1996	42	1.44	—
Grackle	Summer	MD,MA,NJ,NY,CT, PA	1955	1989	35	—	1.85
Mean					39	—	—

favourable survival probabilities for birds as they leave the breeding grounds, but once on certain wintering grounds they seem to face decreasingly favourable survival probabilities. The causes and implications of these results are not well understood and will require additional research. We do not think these results are the result of some methodological failure; however, this cannot be totally ruled out at this time.

The estimated decline in survival probability of Mallards in eastern Colorado was the motivation for this study, thus we will examine this area in more detail. The decreasing survival probability for male Mallards is clear: $\hat{\beta}_1 = -0.0052$, with $\hat{se}(\hat{\beta}_1) = 0.0011$, giving a Wald statistic of -4.7 . There is less evidence for female Mallards where $\hat{\beta}_1 = -0.0037$, with $\hat{se}(\hat{\beta}_1) = 0.0029$, giving a Wald statistic of -1.3 . Here, the estimated slope for females is less than that for males and the standard error is substantially greater, primarily due to fewer females banded and lower female recovery rates.

Perhaps the most striking evidence of a decline in survival probability is for the

TABLE 2. Estimates of mean survival (\hat{S}), temporal process variation (represented as the standard deviation $\hat{\sigma}_{\text{temporal}}$) and the coefficient of temporal process variation (CV) for avian survival data sets. All estimates are based on the shrinkage means model $\{S_t, f_t\}$

Species	Season	State/Province	Males			Females				
			\hat{S}	$\text{se}(\hat{S})$	$\hat{\sigma}_{\text{temporal}}$	CV ¹	\hat{S}	$\text{se}(\hat{S})$	$\hat{\sigma}_{\text{temporal}}$	CV ¹
<i>Waterfowl species</i>										
Mallard	Pre	AB	0.681	0.006	0.031	0.045	0.550	0.018	0.083	0.151
Mallard	Pre	CA	0.629	0.014	0.081	0.128	0.547	0.013	0.063	0.115
Mallard	Pre	CO	0.629	0.012	0.044	0.069	—	—	—	—
Mallard	Pre	MB	0.667	0.007	0.037	0.055	0.554	0.016	0.076	0.138
Mallard	Pre	MI	0.670	0.007	0.034	0.051	0.561	0.016	0.073	0.131
Mallard	Pre	MN	0.648	0.009	0.041	0.063	0.558	0.011	0.040	0.072
Mallard	Pre	MT	0.635	0.017	0.096	0.151	0.487	0.016	0.000	0.000
Mallard	Pre	NY	0.608	0.011	0.043	0.070	0.489	0.023	0.107	0.219
Mallard	Pre	ND	0.675	0.009	0.043	0.064	0.555	0.012	0.012	0.022
Mallard	Pre	ON,PQ	0.608	0.011	0.049	0.081	0.511	0.009	0.000	0.000
Mallard	Pre	SK	0.692	0.007	0.042	0.061	0.581	0.010	0.034	0.059
Mallard	Pre	WI	0.628	0.007	0.000	0.000	0.525	0.725	0.067	0.128
Mallard	Winter	AR	0.681	0.008	0.032	0.047	—	—	—	—
Mallard	Winter	CA	0.613	0.017	0.083	0.135	0.543	0.014	0.010	0.019
Mallard	Winter	CO	0.683	0.012	0.055	0.080	0.611	0.021	0.095	0.155
Mallard	Winter	ID	0.645	0.016	0.065	0.101	0.559	0.032	0.129	0.230
Mallard	Winter	KS,NE	0.678	0.005	0.000	0.000	0.570	0.030	0.138	0.242
Mallard	Winter	ND	0.628	0.008	0.000	0.000	0.545	0.012	0.000	0.000
Mallard	Winter	NY	0.588	0.020	0.097	0.165	0.435	0.022	0.000	0.000
Mallard	Winter	NC,SC	0.645	0.012	0.049	0.076	0.559	0.010	0.000	0.000
Mallard	Winter	OK,TX	0.691	0.009	0.035	0.051	0.577	0.024	0.099	0.172
Mallard	Winter	TN	0.660	0.009	0.036	0.055	0.547	0.012	0.032	0.058
Black Duck	Pre	MI,ON	0.617	0.011	0.000	0.000	0.463	0.020	0.000	0.000
Black Duck	Pre	NS,PQ	0.595	0.015	0.032	0.053	0.485	0.026	0.083	0.170
Black Duck	Winter	MD	0.649	0.012	0.000	0.000	0.554	0.020	0.000	0.000
Black Duck	Winter	MA,NJ,NY	0.690	0.007	0.030	0.043	0.581	0.008	0.000	0.000
Black Duck	Winter	NC,SC,TN	0.685	0.007	0.000	0.000	0.560	0.014	0.035	0.062
Amer Wigeon	Winter	CA	0.628	0.020	0.082	0.130	—	—	—	—
GW Teal	Pre	CO	0.523	0.024	0.000	0.000	0.240	0.039	0.000	0.000
BW Teal	Pre	AB	0.584	0.013	0.000	0.000	0.433	0.024	0.000	0.000
BW Teal	Pre	MB,ON	0.549	0.020	0.082	0.148	0.460	0.018	0.000	0.000

TABLE 2.—(Continued)

Species	Season	State/Province	Males			Females				
			\hat{S}	$\hat{se}(\hat{S})$	$\hat{\sigma}_{\text{temporal}}$	CV ¹	\hat{S}	$\hat{se}(\hat{S})$	$\hat{\sigma}_{\text{temporal}}$	CV ¹
BW Teal	Pre	SK	0.608	0.009	0.000	0.000	0.479	0.017	0.000	0.000
Pintail	Pre	AB	0.677	0.010	0.030	0.045	0.550	0.019	0.079	0.143
Pintail	Pre	CA	0.708	0.014	0.060	0.084	0.562	0.021	0.054	0.097
Pintail	Pre	CO	0.709	0.025	0.088	0.124	—	—	—	—
Pintail	Pre	MB	0.589	0.045	0.155	0.263	0.364	0.036	0.071	0.195
Pintail	Pre	ND	0.686	0.023	0.000	0.000	0.570	0.036	0.000	0.000
Pintail	Pre	SK	0.704	0.014	0.069	0.098	0.556	0.014	0.000	0.000
Pintail	Winter	CA	0.673	0.023	0.110	0.163	0.582	0.045	0.212	0.364
Wood Duck	Pre	AR,MO	0.511	0.026	0.110	0.207	—	—	—	—
Wood Duck	Pre	IL,IN,IA,OH	0.563	0.021	0.115	0.204	0.465	0.018	0.073	0.157
Wood Duck	Pre	KY,NC,SC,TN	0.571	0.009	0.000	0.000	0.481	0.014	0.000	0.000
Wood Duck	Pre	MA,NY,ON,PA,VT	0.531	0.013	0.064	0.120	0.502	0.028	0.171	0.341
Wood Duck	Pre	MI,MIN,WI	0.548	0.009	0.040	0.072	0.442	0.013	0.000	0.000
Redhead	Pre	AB,SK	0.540	0.022	0.000	0.000	0.436	0.039	0.150	0.345
Redhead	Winter	NY	0.741	0.012	0.060	0.080	0.619	0.013	0.034	0.055
Canvasback	Winter	MD	0.732	0.022	0.117	0.160	—	—	—	—
Canvasback	Winter	NY	0.667	0.055	0.269	0.403	0.526	0.034	0.120	0.229
Gr Scaup	Winter	NY	0.727	0.010	0.016	0.022	0.599	0.028	0.131	0.219
Canada Goose	Pre	MB	0.754	0.013	0.045	0.060	0.750	0.021	0.093	0.124
Canada Goose	Pre	MI,ON	0.716	0.012	0.038	0.053	0.705	0.022	0.097	0.138
Canada Goose	Pre	NY	0.603	0.022	0.087	0.145	0.662	0.012	0.000	0.000
Canada Goose	Winter	IL	0.779	0.012	0.047	0.061	—	—	—	—
Canada Goose	Winter	MD	0.750	0.068	0.358	0.477	0.763	0.022	0.108	0.142
Canada Goose	Winter	NC,TN	0.739	0.008	0.000	0.000	—	—	—	—
<i>Non-Waterfowl species</i>										
Mourning Dove	Summer	AZ,NM	—	—	—	—	0.266	0.046	0.258	0.971
Mourning Dove	Summer	IL,MO	0.361	0.021	0.077	0.212	0.259	0.023	0.061	0.235
Grackle	Summer	OH,IL,IN,IA,MI,MN, ON,WI,SD,ND	0.607	0.015	0.003	0.006	—	—	—	—
Grackle	Summer	MD,MA,NJ,NY,CT,PA	—	—	—	—	0.552	0.027	0.000	0.000

¹ CV = $\hat{\sigma}_{\text{temporal}}/\hat{S}$; note that values of $\hat{\sigma}_{\text{temporal}}$ and \hat{S} in this table were rounded to the third decimal place and may not produce the same CV values as reported in this table; the CV reported was based on non-rounded values of $\hat{\sigma}_{\text{temporal}}$ and \hat{S} .

TABLE 3. Estimates of linear trends ($\hat{\beta}_i$) for avian survival data sets. All estimates are based on the shrinkage linear model $\{S_i, f_i\}$

Species	Season	State/Province	Males		Females	
			$\hat{\beta}_i$	$\hat{se}(\hat{\beta}_i)$	$\hat{\beta}_i$	$\hat{se}(\hat{\beta}_i)$
<i>Waterfowl species</i>						
Mallard	Pre	AB	0.0016	0.0006	0.0029	0.0017
Mallard	Pre	CA	0.0032	0.0010	0.0036	0.0010
Mallard	Pre	CO	0.0029	0.0021	—	—
Mallard	Pre	MB	0.0019	0.0007	0.0052	0.0013
Mallard	Pre	MI	0.0014	0.0007	0.0049	0.0015
Mallard	Pre	MN	0.0021	0.0007	0.0021	0.0009
Mallard	Pre	MT	0.0022	0.0015	0.0015	0.0014
Mallard	Pre	NY	0.0025	0.0009	0.0009	0.0021
Mallard	Pre	ND	0.0016	0.0008	-0.0028	0.0012
Mallard	Pre	ON,PQ	0.0024	0.0011	-0.0021	0.0010
Mallard	Pre	SK	0.0014	0.0006	0.0004	0.0010
Mallard	Pre	WI	-0.0004	0.0007	-0.0033	0.0012
Mallard	Winter	AR	-0.0005	0.0012	—	—
Mallard	Winter	CA	0.0031	0.0019	0.0022	0.0019
Mallard	Winter	CO	-0.0052	0.0011	-0.0037	0.0029
Mallard	Winter	ID	-0.0028	0.0027	-0.0044	0.0057
Mallard	Winter	KS,NE	-0.0004	0.0009	0.0072	0.0710
Mallard	Winter	MD	-0.0012	0.0012	-0.0050	0.0018
Mallard	Winter	NY	0.0058	0.0016	-0.0011	0.0022
Mallard	Winter	NC,SC	-0.0023	0.0016	0.0000	0.0016
Mallard	Winter	OK,TX	-0.0020	0.0014	-0.0057	0.0033
Mallard	Winter	TN	0.0004	0.0013	-0.0029	0.0017
Black Duck	Pre	MI,ON	0.0020	0.0013	0.0003	0.0019
Black Duck	Pre	NS,PQ	-0.0041	0.0015	-0.0089	0.0027
Black Duck	Winter	MD	0.0007	0.0018	-0.0050	0.0027
Black Duck	Winter	MA,NJ,NY	0.0009	0.0008	0.0003	0.0010
Black Duck	Winter	NC,SC,TN	0.0003	0.0013	0.0010	0.0021
Amer Wigeon	Winter	CA	-0.0008	0.0035	—	—
GW Teal	Pre	CO	-0.0034	0.0052	0.0164	0.1041
BW Teal	Pre	AB	0.0022	0.0011	0.0043	0.0022
BW Teal	Pre	MB,ON	0.0000	0.0022	0.0005	0.0020
BW Teal	Pre	SK	0.0011	0.0008	-0.0008	0.0016
Pintail	Pre	AB	0.0029	0.0008	-0.0010	0.0018
Pintail	Pre	CA	0.0041	0.0018	0.0082	0.0029
Pintail	Pre	CO	-0.0010	0.0046	—	—
Pintail	Pre	MB	-0.0043	0.0060	-0.0167	0.0041
Pintail	Pre	ND	0.0005	0.0043	0.0077	0.0060
Pintail	Pre	SK	0.0031	0.0010	0.0003	0.0015
Pintail	Winter	CA	0.0010	0.0035	0.0023	0.0051
Wood Duck	Pre	AR,MO	0.0034	0.0020	—	—
Wood Duck	Pre	IL,IN,IA,OH	0.0012	0.0009	0.0019	0.0013
Wood Duck	Pre	KY,NC,SC,TN	0.0014	0.0009	0.0022	0.0013
Wood Duck	Pre	MA,NY,ON,PA,VT	0.0027	0.0011	0.0015	0.0016
Wood Duck	Pre	MI,MN,WI	0.0023	0.0008	0.0034	0.0014
Redhead	Pre	AB,SK	0.0042	0.0024	0.0040	0.0039
Redhead	Winter	NY	-0.0005	0.0014	0.0008	0.0017
Canvasback	Winter	MD	0.0016	0.0021	—	—
Canvasback	Winter	NY	-0.0096	0.0064	-0.0149	0.0038
Gr Scaup	Winter	NY	-0.0048	0.0015	-0.0060	0.0029
Canada Goose	Pre	MB	-0.0041	0.0013	-0.0039	0.0027
Canada Goose	Pre	MI,ON	0.0005	0.0018	0.0053	0.0026
Canada Goose	Pre	NY	0.0021	0.0029	-0.0024	0.0017

TABLE 3.—(Continued)

Species	Season	State/Province	Males		Females	
			$\hat{\beta}_1$	$\hat{se}(\hat{\beta}_1)$	$\hat{\beta}_1$	$\hat{se}(\hat{\beta}_1)$
Canada Goose	Winter	IL	-0.0001	0.0018	—	—
Canada Goose	Winter	MD	-0.0070	0.0083	-0.0091	0.0022
Canada Goose	Winter	NC,TN	0.0014	0.0017	—	—
<i>Non-Waterfowl species</i>						
Mourning Dove	Summer	AZ,NM	—	—	-0.0128	0.0032
Mourning Dove	Summer	IL,MO	-0.0112	0.0019	-0.0109	0.0018
Grackle	Summer	OH,IL,IN,IA,MI, MN,ON,WI,SD,ND	-0.0020	0.0018	—	—
Grackle	Summer	MD,MA,NJ,NY,CT, PA	—	—	-0.0007	0.0034

Mourning Dove. Pooling banding and recovery data for Illinois and Missouri resulted in $\hat{\beta}_1 = -0.0122$, with $\hat{se}(\hat{\beta}_1) = 0.0019$, giving a Wald statistic of -5.9 for males and $\hat{\beta}_1 = -0.0109$, with $\hat{se}(\hat{\beta}_1) = 0.0018$, giving a Wald statistic of -4.0 for females. Pooling of data for Arizona and New Mexico resulted in $\hat{\beta}_1 = -0.0128$, with $\hat{se}(\hat{\beta}_1) = 0.0032$, giving a Wald statistic of -6.1 for females (Table 2). These estimates suggest a precipitous decline in the probability of survival and would seem to warrant a more intensive analysis of the banding and recovery data on the Mourning Dove. In particular, meta-analysis methods (e.g. Cook *et al.*, 1992; Arnqvist & Wooster, 1995; Franklin & Shenk, 1995) would be appropriate for the analysis of these data without the need arbitrarily to pool data across large geographic areas.

3.3 Variation in true survival probability

Estimates of the year-to-year variation in the true survival probabilities are presented in Table 2 as a standard deviation and are best understood as a coefficient of variation (CV). The data for Mallards are most informative due to the large sample sizes and the large number of areas where birds have been banded over long time frames. The CV for male Mallards was 6.6% for birds banded in the pre-season and 7.1% for winter-banded birds. The corresponding estimates for female Mallards were 9.4% and 9.7%, respectively. These estimates are in good agreement between the two banding periods, but suggest that survival probability may vary somewhat more in female Mallards. Patterns for the other species are more difficult to detect or interpret because far less data are available.

4 Conclusion

We believe that understanding long-term trends in demographic parameters is a goal worthy of attention because of the potential to better understand overall trends in animal populations. Unfortunately, the data were not available for retrospective analyses of long-term trends in avian populations, except for 16 of the 926 species and subspecies for which data were deposited in the BBL. Francis (1995) also found that current data collection by the BBL was inadequate for monitoring survival in most avian species in North America. In at least one case, our data

TABLE 4. Estimates of mean linear trends ($\hat{\beta}_1$), spatial process variation (represented as standard deviation $\hat{\sigma}_{\text{spatial}}$) and coefficients of spatial process variation in males and females for 11 species of waterfowl banded in two seasons (pre-season and winter). The number of separate populations is denoted by n

Species	Season	n	$\hat{\beta}_1$	Males				Females				
				95% CI for $\hat{\beta}_1$				95% CI for $\hat{\beta}_1$				
				Lower	Upper	$\hat{\sigma}_{\text{spatial}}$	CV ¹	Lower	Upper	$\hat{\sigma}_{\text{spatial}}$	CV ¹	
Mallard	Pre	12	0.0017	0.0012	0.0022	0.0005	0.266	0.0012	-0.0006	0.0029	0.0027	2.301
Mallard	Winter	10	-0.0006	-0.0066	0.0054	0.0027	4.758	-0.0016	-0.0032	0.0000	0.0015	0.916
Black Duck	Pre	2	-0.0010	-0.0026	0.0006	0.0041	4.082	-0.0041	-0.0132	0.0050	0.0063	1.539
Black Duck	Winter	3	0.0007	0.0004	0.0011	0.0000	0.000	-0.0007	-0.0044	0.0031	0.0026	3.892
American Widgeon	Winter	1	-0.0008	-0.0076	0.0061	—	—	—	—	—	—	—
Green-winged Teal	Pre	1	-0.0033	-0.0135	0.0068	—	—	0.0164	0.0028	0.0300	—	—
Blue-winged Teal	Pre	3	0.0014	0.0005	0.0022	0.0000	0.000	0.0011	-0.0018	0.0040	0.0018	1.630
Pintail	Pre	6	0.0011	-0.0018	0.0040	0.0018	1.630	-0.0004	-0.0090	0.0082	0.0092	20.842
Pintail	Winter	1	0.0010	-0.0057	0.0078	—	—	0.0024	-0.0076	0.0123	—	—
Wood Duck	Pre	5	0.0019	0.0013	0.0026	0.0000	0.000	0.0023	0.0015	0.0031	0.0000	0.000
Redhead	Pre	1	0.0042	-0.0005	0.0088	—	—	0.0040	-0.0037	0.0117	—	—
Redhead	Winter	1	-0.0005	-0.0034	0.0023	—	—	0.0008	-0.0025	0.0041	—	—
Canvasback	Winter	2	-0.0024	-0.0129	0.0081	0.0063	2.657	-0.0150	-0.0224	-0.0075	—	—
Greater Scaup	Winter	1	-0.0048	-0.0078	-0.0018	—	—	-0.0060	-0.0117	-0.0003	—	—
Canada Goose	Pre	3	-0.0010	-0.0047	0.0026	0.0026	2.489	-0.0004	-0.0059	0.0050	0.0042	9.729
Canada Goose	Winter	3	0.0006	-0.0013	0.0024	0.0000	0.000	-0.0091	-0.0134	-0.0047	—	—
All Species	Pre	33	0.0016	0.0010	0.0022	0.0012	0.754	0.0009	-0.0008	0.0025	0.0041	4.583
All Species	Winter	22	-0.0005	-0.0016	0.0007	0.0020	4.266	-0.0026	-0.0046	-0.0006	0.0034	1.306

¹ CV = $\hat{\sigma}_{\text{spatial}}/\hat{\beta}_1$; note that values of $\hat{\sigma}_{\text{spatial}}$ and $\hat{\beta}_1$ in this table were rounded to the fourth decimal place and may not produce the same CV values as reported in this table; the CV reported was based on non-rounded values of $\hat{\sigma}_{\text{spatial}}$ and $\hat{\beta}_1$.

selection criteria eliminated a long-term data set that used colour-banded birds (Francis *et al.*, 1992). Thus, some of our *a priori* criteria for data set selection could be relaxed to encompass more long-term data sets. However, the number of additional data sets yielding credible results would still be small relative to the large number of species for which the BBL maintains banding data.

An important consideration is that monitoring of trends in survival probabilities alone will not completely elucidate factors affecting overall population trends in a species nor are they necessarily reflective of trends in population size. For example, declining trends in survival probabilities could be a density-dependant response to increasing population size. Therefore, estimation of long-term trends in survival is only one piece of the puzzle. Ideally, data on recruitment rates and overall population size for a given species would be available for analysis using a random effects model as we proposed here. Although long-term data on recruitment and population size are available for some species (e.g. waterfowl; see Padding *et al.*, 2000; US Fish and Wildlife Service, 2000), for most avian species in North America such data are lacking.

However, monitoring survival can help identify which demographic parameter may be responsible for population changes. For example, > 20-year population declines have been observed in Mourning Doves in Missouri and parts of Arizona (Reeves *et al.*, 1993; Schultz *et al.*, 1996). The cause for these declines is largely unknown (Schultz *et al.*, 1996). Our results strongly suggest that declining survival may be responsible for Mourning Dove population declines and that research should focus on understanding potential factors responsible for declines in survival.

The analytical framework we have outlined here is appropriate for monitoring trends in recruitment and population size and is a first step in developing a complete picture in long-term trends in avian populations. Further refinements to our approach would incorporate non-linear trend models, in addition to the linear models we employed, into the random effects modelling approach. We were unable to include non-linear models because there was no objective manner to select non-linear models over a linear model in the random-effects framework. Thus, there is a need to incorporate model selection procedures in the random effects modelling approach (see Burnham & White, this issue).

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Appendix 1.

Avian species that met the initial criteria of sufficient number of bandings, recoveries and length of time for analysis in this study.

Species	Number banded	Number recovered	First year	Last year	Number of years
Common Tern	741 895	92 666	1971	1996	26
Black Skimmer	42 221	1 301	1968	1993	26
Leach's Storm-Petrel	97 779	2 472	1956	1996	41
Hooded Merganser	4 700	422	1947	1997	50
Mallard	5 318 068	773 276	1920	1997	77
Mallard × Black Duck Hybrid	21 812	2 944	1930	1997	67
American Black Duck	898 636	149 666	1917	1997	80
Mottled Duck	31 608	2 772	1948	1996	48
Gadwall	80 093	9 971	1922	1997	75
American Wigeon	204 459	25 485	1923	1997	74
American Green-winged Teal	376 695	25 755	1921	1997	76
Blue-winged Teal	1 193 755	56 382	1920	1997	77
Cinnamon Teal	30 430	1 783	1926	1997	71
Northern Shoveler	45 460	4 318	1925	1997	72
Northern Pintail	1 216 485	137 165	1922	1997	75
Wood Duck	1 015 659	96 979	1924	1997	73
Redhead	241 563	51 418	1923	1997	74
Canvasback	154 248	23 024	1928	1997	69
Greater Scaup	46 945	5 797	1948	1997	49
Lesser Scaup	322 922	27 510	1920	1997	77
Ring-necked Duck	144 321	19 957	1920	1997	77
Common Goldeneye	14 873	1 959	1934	1997	63
Barrow's Goldeneye	17 194	2 373	1947	1996	49
Bufflehead	18 028	1 794	1932	1997	65
Common Eider	19 746	2 668	1947	1997	50
Ruddy Duck	9 921	496	1926	1996	70
Lesser Snow Goose (White phase)	352 751	62 507	1947	1997	50
Lesser Snow Goose (Blue phase)	154 648	23 507	1945	1997	52
Greater Snow Goose	30 121	4 067	1962	1996	34
Ross' Goose	26 266	3 466	1951	1997	46
Greater White-fronted Goose	97 990	16 702	1947	1996	49
Canada Goose	2 181 748	491 092	1921	1997	76
Cackling Goose	40 143	5 278	1948	1996	48
Small Canada Goose	155 553	31 415	1948	1997	49
Atlantic Brant	23 983	4 263	1965	1995	30
Black Brant	88 781	8 281	1958	1996	38
Mute Swan	1 829	507	1961	1997	36
Whistling Swan	11 668	5 566	1947	1997	50
Trumpeter Swan	6 248	1 154	1948	1997	49
American Coot	150 785	7 365	1923	1997	75
American Woodcock	97 047	5 277	1948	1997	50
Semipalmated Sandpiper	197 833	1 513	1960	1997	38
Piping Plover	6 555	405	1956	1990	35
Band-tailed Pigeon	111 231	8 174	1951	1997	47
Mourning Dove	1 931 513	89 137	1920	1997	78
White-winged Dove	250 460	11 686	1953	1996	44
Northern Harrier	16 810	601	1955	1997	43
Sharp-shinned Hawk	294 711	3 488	1955	1997	43
Cooper's Hawk	51 650	1 465	1955	1997	43
Northern Goshawk	18 767	738	1955	1997	43
Red-tailed Hawk	114 042	5 763	1955	1997	43

Species	Number banded	Number recovered	First year	Last year	Number of years
Red-shouldered Hawk	11 370	627	1955	1997	43
Swainson's Hawk	15 887	610	1960	1996	37
Ferruginous Hawk	16 697	597	1959	1996	38
Golden Eagle	7 453	610	1957	1997	41
Bald Eagle	20 959	2 766	1964	1997	34
Prairie Falcon	14 781	704	1955	1997	43
Peregrine Falcon	28 572	2 038	1955	1997	43
Merlin	21 971	537	1955	1997	43
Osprey	30 310	2 197	1961	1996	36
Barn Owl	34 456	1 909	1955	1997	43
Northern Saw-whet Owl	56 247	917	1955	1997	43
Eastern Screech-Owl	21 847	985	1955	1997	43
Great Horned Owl	30 820	2 842	1955	1996	42
Hairy Woodpecker	24 458	902	1955	1997	43
Downy Woodpecker	120 033	3 840	1955	1997	43
Red-bellied Woodpecker	15 903	449	1955	1997	43
Yellow-shafted Flicker	54 070	876	1955	1996	42
Blue Jay	453 901	23 299	1955	1997	43
Western Scrub-Jay	11 721	682	1955	1997	43
European Starling	648 705	24 518	1955	1997	43
Brown-headed Cowbird	834 539	14 148	1955	1997	43
Yellow-headed Blackbird	111 652	666	1955	1997	43
Red-winged Blackbird	729 819	12 345	1955	1997	43
Baltimore Oriole	82 331	748	1955	1997	43
Brewer's Blackbird	20 723	1 038	1955	1997	43
Common Grackle	681 270	36 814	1955	1997	43
Boat-tailed Grackle	16 712	678	1955	1996	42
Evening Grosbeak	603 061	16 987	1955	1997	43
Purple Finch	723 063	20 192	1955	1997	43
House Finch	780 571	9 779	1955	1997	43
Common Redpoll	321 593	668	1955	1997	43
American Goldfinch	952 162	5 833	1955	1997	43
Pine Siskin	556 338	2 181	1955	1997	43
Vesper Sparrow	19 222	446	1955	1996	42
Savannah Sparrow	97 720	550	1955	1997	43
Harris' Sparrow	56 281	621	1955	1996	42
White-crowned Sparrow	227 840	3 901	1955	1997	43
Gambel's White-crowned Sparrow	137 872	5 748	1955	1997	43
Nuttall's White-crowned Sparrow	10 839	929	1967	1996	30
Golden-crowned Sparrow	68 778	6 414	1955	1997	43
White-throated Sparrow	988 316	8 645	1955	1997	43
American Tree Sparrow	404 923	12 751	1955	1996	42
Chipping Sparrow	209 257	7 208	1955	1997	43
Field Sparrow	142 704	2 038	1955	1997	43
Slate-colored Junco	1 359 116	15 198	1955	1997	43
Oregon Junco	157 949	2 199	1955	1997	43
Gray-headed Junco	18 576	506	1956	1996	41
Song Sparrow	616 651	16 502	1955	1997	43
Fox Sparrow	98 665	736	1955	1997	43
Eastern Towhee	120 062	3 697	1955	1997	43
Spotted Towhee	24 938	1 233	1955	1997	43
California Towhee	11 014	1 826	1960	1997	38
Northern Cardinal	356 639	10 787	1955	1997	43
Rose-breasted Grosbeak	83 946	1 358	1955	1997	43
Black-headed Grosbeak	15 517	401	1955	1997	43
Purple Martin	124 985	1 182	1955	1997	43

Species	Number banded	Number recovered	First year	Last year	Number of years
Cliff Swallow	188 962	6 856	1955	1997	43
Barn Swallow	174 277	1 157	1955	1997	43
Tree Swallow	446 653	3 811	1955	1997	43
Bank Swallow	194 932	1 482	1955	1996	42
Cedar Waxwing	141 399	1 233	1955	1997	43
Yellow Warbler	172 254	434	1955	1997	43
Myrtle Warbler	733 442	679	1955	1997	43
Audubon's Warbler	55 997	550	1955	1997	43
Common Yellowthroat	323 048	645	1955	1997	43
House Sparrow	388 003	1 671	1955	1997	43
Northern Mockingbird	52 909	1 440	1955	1997	43
Gray Catbird	579 461	8 340	1955	1997	43
Brown Thrasher	97 481	4 657	1955	1997	43
Carolina Wren	39 432	583	1955	1997	43
House Wren	189 459	2 374	1955	1997	43
White-breasted Nuthatch	71 582	3 114	1955	1997	43
Eastern Tufted Titmouse	116 664	4 562	1955	1997	43
Black-capped Chickadee	497 620	14 724	1955	1997	43
Carolina Chickadee	70 334	1 481	1955	1997	43
Wood Thrush	101 870	1 098	1955	1997	43
American Robin	432 185	14 322	1955	1997	43
Eastern Bluebird	349 578	2 195	1955	1997	43