

Analysis of individual- and time-specific covariate effects on survival of *Serinus serinus* in north-eastern Spain

MICHAEL J. CONROY¹, JUAN CARLOS SENAR² &
JORDI DOMÈNECH², ¹USGS, Georgia Cooperative Fish and Wildlife Research
Unit, University of Georgia, USA and ²Museu de Zoologia, Barcelona, Spain

ABSTRACT We developed models for the analysis of recapture data for 2678 serins (*Serinus serinus*) ringed in north-eastern Spain since 1985. We investigated several time- and individual-specific factors as potential predictors of overall mortality and dispersal patterns, and of gender and age differences in these patterns. Time-specific covariates included minimum daily temperature, days below freezing, and abundance of a strong competitor, siskins (*Carduelis spinus*) during winter, and maximum temperature and rainfall during summer. Individual covariates included body mass (i.e. body condition), and wing length (i.e. flying ability), and interactions between body mass and environmental factors. We found little support of a predictive relationship between environmental factors and survival, but good evidence of relationships between body mass and survival, especially for juveniles. Juvenile survival appears to vary in a curvilinear manner with increasing mass, suggesting that there may exist an optimal mass beyond which increases are detrimental. The mass-survival relationship does seem to be influenced by at least one environmental factor, namely the abundance of wintering siskins. When siskins are abundant, increases in body mass appear to relate strongly to increasing survival. When siskin numbers are average or low the relationship is largely reversed, suggesting that the presence of strong competition mitigates the otherwise largely negative aspects of greater body mass. Wing length in juveniles also appears to be related positively to survival, perhaps largely due to the influence of a few unusually large juveniles with adult-like survival. Further work is needed to test these relationships, ideally under experimentation.

Correspondence: M. J. Conroy, USGS, Georgia Cooperative Fish and Wildlife Research Unit, University of Georgia, Athens, GA, 30602, USA.

1 Introduction

Prolonged snow cover, low temperature, frost or storms have all been shown to reduce survival and population density in several bird species (e.g. Trautman *et al.*, 1939; Slagsvold, 1975; Karlsson & Källander, 1977; Balen, 1980; Ekman, 1984; Clobert *et al.*, 1987; Baillie, 1990; Greenwood & Baillie, 1991; Hollands & Yalden, 1991; Newton *et al.*, 1993; Peach *et al.*, 1995; Smith, 1995). The effect of hard winters and other meteorological regional severity on regulating population numbers is therefore widely recognized, especially at high latitudes (Lack, 1966; Elkins, 1983; Newton, 1998). At lower latitudes, summer drought can also affect population numbers by reducing the amount of wetland available to waterfowl (Batt *et al.*, 1989), and arid-land species may be highly limited by annual variation in rainfall through its effect on plant growth and the consequent variation in bird food-supplies (Newton *et al.*, 1993; Peach *et al.*, 1991; Bryant & Jones, 1995; Møller, 1989; Baillie & Peach, 1992). However, prolonged severe weather is typically associated with hard winters, and although the effect of droughts is recognized, it is mostly associated with arid areas (Newton, 1998). Mediterranean areas are intermediate between these two extreme climates. Severe winters are sporadic, so that increased winter mortality should occur infrequently (Senar & Copete, 1995). In contrast, severe summer droughts may be common, and thus may be expected to increase mortality risk more frequently than does winter severity (Nager & Wiersma, 1996; Blondel & Aronson, 1999). Thus, our first aim was to study survival rates of a typically Mediterranean species, the serin, and to test which period and meteorological variables may be limiting for the species.

Weather losses are not random through a population. When extreme events occur, they eliminate vulnerable individuals and, in short-lived species, sometimes lead to measurable morphological change in the population (Newton, 1998). Hence, some sex- and age-groups may be affected more than others, and individuals of a particular size die in greater proportions than others. Bumpus (1899) provided one of the first examples of analysing how House Sparrows *Passer domesticus* found dead after a severe storm, differed in weight and measurements from those that survived. Studies on finches on Galapagos islands have become a classic work by showing how climatic events such as severe droughts changed the morphology of the species (Grant, 1986). More recently, Bryant & Jones (1995) have shown how in the Sand Martin *Riparia riparia*, drought years were followed by reductions in mean body size and wetter years by increases. These data are important because selective mortality provides one of the bases for the action of natural selection (Futuyma, 1998). Therefore, our second aim in this work was to test if weather effects on mortality may differ according to the sex, age and morphology of individuals. We examined these questions using captures and recaptures of serins, a small granivorous finch typical of the Mediterranean region (Newton, 1972).

2 Methods

2.1 Study population and field methods

Serins were trapped from 1985 to 2000 in the suburban area of Barcelona in north-eastern Spain. The study area consisted of orchards, small woods dominated by pine (*Pinus halepensis*) and gardens. Birds were trapped at least weekly at baited feeders using platform traps, clap-nets and mist-nests, and marked with numbered aluminium rings (Senar, 1988; Conroy *et al.*, 1999). For each bird we recorded

sex and age (see below). At first capture we also measured body mass using a 100 g electronic balance (accurate to 0.01 g) and wing-length, defined as maximum chord to the nearest 0.5 mm (Svensson, 1992).

2.2 General statistical model

We grouped the data by two capture periods: October–March (migration and wintering), and April–September (breeding and postbreeding), and excluded juvenile birds from analysis until these were recaptured as subadults or adults (second or later years of life), when sex can be determined (Conroy *et al.*, 1999). In our analyses to follow we also defined the calendar year as beginning in October rather than in March, so that in the first period (Oct–Mar) each year both subadults and adults were captured, with all subadults by definition becoming adults in the second period (Apr–Sep); this convention resulted in further model simplification, while retaining some ability to model age effects as well as sex and individual covariate effects. We developed a CJS model that included variation with respect to age (adult—after April in the year after hatching; or subadult—Oct–Dec in the hatching year and before April in the year after hatching), sex, and time (calendar year). The parameters of this general model included $\phi_{s,t}^{(v)}$, the probability of survival from the midpoint of each 6-month ringing period t to the midpoint in period $t + 1$, for birds of sex $s = 1$ (male), 2 (female), of age $v = 0$ (subadult), $v = 1$ (adult), and $t = 1, \dots, 28$. Similarly, capture probabilities were modelled by $p_{s,t}$, $s = 1, 2$; $t = 2, \dots, 29$. The probability of recapture during year t for marked birds in sex s ; capture probabilities were not age-specific because all recaptures were, by definition, of adults. This general model, denoted $\phi(\text{sex} \star \text{age} \star t) p(\text{sex} \star t)$ contained $k = 168$ parameters (112 sex-, age-, and time-specific survival rates and 56 sex- and time-specific recapture probabilities). The above model was generalized slightly to allow for short-term covariate effects (see Section 2.4) and possible temporary survival and movement effects in the first period following initial marking and release (e.g. due to a transient effect). This more general model, denoted as $\phi^*(\text{sex} \star \text{age} \star t) p(\text{sex} \star t)$ included the parameters

$$\phi_{s,t}^{(1)*} \quad s = 1, 2; t = 1, \dots, 28$$

modelling temporary (transient) effects, and time- and age-specific survival rates

$$\phi_{s,t}^{(0)} \quad s = 1, 2; t = 2, \dots, 28$$

$$\phi_{s,t}^{(0)*} \quad s = 1, 2; t = 1, \dots, 28$$

and

$$p_{s,t} \quad s = 1, 2; t = 2, \dots, 29$$

for 222 parameters (166 sex-, age-, and time-specific survival rates and 56 sex- and time-specific recapture probabilities).

We assessed the adequacy of fit of the global model by two methods. First, we conducted an initial evaluation for adults only (stratified by sex) using the RELEASE tests in program MARK (White & Burnham, 1999). We also used RELEASE to test for possible transient effects as recommended by Pradel *et al.* (1997). For the global models described above, we examined goodness of fit statistics produced by program MARK, principally the ratio of the deviance-based chi square statistic to its degrees of freedom:

$$\hat{c} = \chi^2/\text{df}$$

Deviation of this statistic from 1 indicates lack of fit. However, this and other lack of fit statistics are known to be unreliable for sparse mark-recapture data sets such as ours. Therefore, we also conducted a number of bootstrap simulations, in which recapture data were generated under an assumed global model, given our sample sizes of released birds in each age-sex category, in each period, and used to estimate model parameters and compute \hat{c} . This process was repeated > 500 times and then used to compute

$$\hat{c}^* = \frac{\hat{c}_e}{\hat{c}_b}$$

where \hat{c}_e is the statistic for the model fitted to our data, and \hat{c}_b is the mean from the bootstrap simulations (where the global model is the true underlying model). This value was taken as a more reliable estimate of fit, and was used to adjust variances, confidence intervals, and likelihood statistics as recommended by Burnham & Anderson (1998).

We then formed a number of submodels in which the parameters of the global model were constrained under plausible hypotheses about sex-, age-, and time-specific parameter variation. For instance, sex-specific survival differences might be small (i.e. not detectable in our study), leading to a model in which survival rates were constrained to be equal between sexes. Likewise, although it is unlikely that survival or capture rates actually were constant between seasons and years, nonetheless the magnitude of temporal variation might be small in comparison to other differences of interest (e.g. sex-specific), thus leading to a model in which these parameters were constrained to be equal over time. Prior to considering the impact of covariates, we also constructed a number of additive or ‘parallelism’ models, in which the effects of age, sex, or other factors are assumed to operate, but not to interact with time. This type of model is reasonable under scenarios in which, for example, males have higher survival rates than females in any given time period, but respond in a similar fashion as females to environmental variation.

2.3 Environmental covariates

We obtained daily and monthly climatic data from the weather service offices at Observatori Fabra in Barcelona. Data were grouped according to the two periods each year over which survival rates were estimated, 1 Jan-1 Jul and 1 Jul-1 Jan, corresponding to the intervals between the midpoints of the Oct-Mar and Apr-Sep capture periods. For each period we wished to develop predictive models based on environmental covariates most likely to be limiting, particularly during the early part of the survival interval. For the first (Jan-Jul) period we selected average minimum daily temperature and numbers of days with temperature < 0°C during Jan-Mar. For the second (Jul-Jan) period we selected total rainfall (mm) and average daily maximum temperature during Jul-Sep. However, we were not especially interested in the expected, large seasonal (winter to summer) variation in these variables, but rather in identifying periods with exceptionally milder or stronger conditions than average, taking into account the time of year. Therefore, we standardized each of the environmental covariates by

$$w_{t(s)} = \frac{(y_{t(s)} - \bar{y}_s)}{s_s}$$

design effect) for the opposite season. We also constructed models in which time was modelled first by a seasonal effect, (winter or summer) and then by a covariate effect, to ascertain if survival differences were explainable by a general seasonal effect not attributable to our environmental covariate, or if additional variation was explained by the covariate. Season by covariate interactions were not considered, as the covariates by definition were confined to a particular season. The above model could be compared to a generalization with a seasonal effect, to which is added a year effect (i.e. year-to-year variation, unexplained by covariate predictors), for example denoting a season + year effect. This last readily extends to the generalized CJS, i.e. a general period-to-period effect is equivalent to season + year + season \times year.

2.4 Individual bird covariates

As noted earlier, we were interested in testing whether heterogeneity among birds was predictive of survival and, more importantly, whether individual bird attributes such as condition and body size interact with climatic variables in influencing seasonal survival. However, we anticipated *a priori* that both mass and wing length would vary among identifiable age and sex classes, and in the case of mass in particular, at different times of the year. We thus standardized body measurements using the estimated mean and standard deviation for individuals of the same age and sex, and trapped during the same 6-month trapping period (but irrespective of year), to eliminate effects induced by age- or sex-specific differences in these attributes, and to eliminate possible seasonal effects. A standardized value was computed as

$$z_{i(a)} = \frac{(x_{i(a)} - \bar{x}_a)}{s_a}$$

where $x_{i(a)}$ is the attribute value (e.g. body mass) for the i th individual in the a th age-sex-season stratum and \bar{x}_a , s_a are the estimated mean and standard deviation of the attribute for individuals in the a th stratum. Effectively these transformed values represented an individual's deviation from the average of otherwise similar birds (i.e. trapped at the same time of year, and of the same age and sex class), with large negative values representing unusually low values of the attribute (e.g. wing length), values close to zero representing 'average' birds, and large positive values representing unusually large attribute values. Incorporation of mass as a covariate is complicated by the fact that mass (even on a standardized or relative scale) may not be a permanent attribute of an animal, but rather is a transitory state. Unfortunately, in most cases body mass was not remeasured on individuals upon recapture, and of course was measured not at all for animals not recaptured. We thus had no way to assess whether mass was transitory, or to build appropriate models for survival and capture probability based on changing weight. Therefore, we incorporated mass as a covariate only to predict survival in the period immediately following first capture ($\phi_{s,t}^{(1)*}$ for adults, $\phi_{s,t}^{(0)}$ for subadults, $s = 1, 2$).

We constructed models in which survival on the logit scale was predicted as a quadratic function of the individual attributes, to allow for non-monotonic survival effect (e.g. survival increases with mass for very light birds but decreases for extremely heavy birds). As with the environmental covariates we used the general form

$$\mathbf{Y} = \mathbf{X}\beta$$

where

$$Y_i = \log\left(\frac{\phi_i(\mathbf{z})}{1 - \phi_i(\mathbf{z})}\right)$$

where survival is now a function of a vector of $k = 1, \dots, n$ individual attributes (i.e. covariates)

$$\mathbf{z}' = [I_1(i)z_1, I_2(i)z_2, \dots, I_n(i)z_n]$$

where z_k is the attribute of animal k , $k = 1, \dots, n$ and $I_k(i)$ is an indicator variable assuming 1 if the capture history for animal k is associated with the appropriate sex- age- time category (row of the design matrix) and 0 otherwise. Taking the previous example of three periods of survival for males and females, the CJS model is augmented by the individual covariate effects (e.g. body mass) for the individuals of the appropriate sex and time categories as defined by the animal's capture history. Thus

$$\mathbf{X} = \begin{bmatrix} 1 & 1 & 1 & 0 & 1 & 0 & \mathbf{z} & \mathbf{z} \\ 1 & 1 & 0 & 1 & 0 & 1 & \mathbf{z} & \mathbf{z} \\ 1 & 1 & 0 & 0 & 0 & 0 & \mathbf{z} & \mathbf{z} \\ 1 & 0 & 1 & 0 & 0 & 0 & \mathbf{z} & 0 \\ 1 & 0 & 0 & 1 & 0 & 0 & \mathbf{z} & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 & \mathbf{z} & 0 \end{bmatrix}$$

$$\phi' = [\phi_{m1}, \phi_{m2}, \phi_{m3}, \phi_{f1}, \phi_{f2}, \phi_{f3}]$$

$$\beta' = [\beta_0, \beta_1, \beta_2, \beta_3, \beta_4, \beta_5, \beta_6, \beta_7]$$

where $\beta_1 - \beta_5$ represent sex, time and sex \times time interaction effects, β_6 represents the additive (on a logit or other scale as determined by the model link function) effect of the covariate, and β_7 represents sex \times covariate interactions.

As noted earlier, we were particularly interested in whether individual attributes might interact with environmental conditions. In particular, we hypothesized that birds in better condition (higher body mass) might react differently to harsh environmental conditions or competitors, than birds in poorer condition (Lower mass). We therefore constructed models in which survival in the period following first capture was predicted by the interaction of a time-specific factor in that period and the body mass of the individual, again measured upon capture immediately before the period. For example, taking the earlier, hypothetical vector of environmental covariates, and the above individual covariate example, we would obtain

$$\mathbf{X} = \begin{bmatrix} 1 & 1 & 1 & 0 & 1 & 0 & 0.6\mathbf{z} \\ 1 & 1 & 0 & 1 & 0 & 1 & 0.4\mathbf{z} \\ 1 & 1 & 0 & 0 & 0 & 0 & 0.2\mathbf{z} \\ 1 & 0 & 1 & 0 & 0 & 0 & 0.6\mathbf{z} \\ 1 & 0 & 0 & 1 & 0 & 0 & 0.4\mathbf{z} \\ 1 & 0 & 0 & 0 & 0 & 0 & 0.2\mathbf{z} \end{bmatrix}$$

where the last column represents the interaction between the time- and individual-specific factors, indicating that the individual covariate (\mathbf{z}) operates at a different intensity depending on the level of the environmental factor (0.6, 0.4 or 0.2), and vice-versa.

2.5 Estimation and model selection

We used program MARK (White & Burnham, 1999) to estimate parameters and compare and select the ‘best’ models for inference, using the capture histories (sequence of mark, release, and recaptured or not recapture on each time occasion) and time- and individual-specific covariates described above. Our approach generally followed that described by Burnham & Anderson (1998). First, we delineated a ‘global model’ thought to capture important sources of temporal and individual variation in survival and capture probabilities consistent with the biology of our study organism, the characteristics of our study area and the limitations of our design. We then constructed plausible submodels, as described in Section 2.1. For example, additive models are reasonable under scenarios in which, for example, males have higher survival rates than females in any given time period, but respond in a similar fashion as females to environmental variation. To these we added the time- and individual-specific covariate models as described in Sections 2.3 and 2.4.

We used Akaike Information Criterion (AIC; Burnham & Anderson, 1998) to rank candidate models in our model set. We adjusted AIC for small effective sample sizes and for lack of fit by \hat{c} to form QAIC_C (Burnham & Anderson, 1998, pp. 51–53). The candidate models (global and submodels) were ranked by QAIC_C to calculate ΔQAIC_C (always zero for the best model). A model weight for a candidate model in the model set was then computed as

$$w_i = \frac{e^{(-\Delta\text{AIC}_i/2)}}{\sum_{j=1}^R e^{(-\Delta\text{AIC}_j/2)}}$$

where R is the number of models in the set of candidate models.

Generally we sought to identify the most plausible model as that model with the lowest QAIC_C value (equivalently, highest model weight). However, several models were frequently close competitors ($\Delta\text{QAIC}_C < \text{approximately } 2$) and had similar weights. In such cases we considered all ‘close’ models as equally plausible, and estimated parameters for each. In all cases, however, we incorporated model uncertainty into the estimation of variances and confidence intervals of parameters. If inference was based on a single ‘best’ model we reported the parameter estimates for that model, but calculated variances and confidence intervals by computing an estimate of unconditional variance for each parameter (Burnham & Anderson, 1998, p. 134) as

$$\text{var}(\hat{\theta}) = \left[\sum_{i=1}^R w_i \sqrt{\text{var}(\hat{\theta}_i | M_i) + (\hat{\theta}_i - \hat{\theta}_a)^2} \right]^2$$

where θ is the parameter of interest (e.g. survival rate or coefficient in a covariate relationship),

$$\hat{\theta}_a = \sum_{i=1}^R w_i \hat{\theta}_i$$

is the weighted average estimate across models, and $\hat{\theta}_i$ and $\text{var}(\hat{\theta}_i|M_i)$ are the parameter estimate and conditional variance based on the i th model, for the R' models in which the parameter appears. If inference was based on multiple models we followed a similar procedure, but instead of a 'best' estimate we reported the weighted average estimate, where averaging is again across the R' models in which the parameter appears. In both cases, the weights w_i of the subset of models used were normalized to sum to 1.

In addition to obtaining the best possible estimates of survival rates, and investigating patterns of variation in these rates in relation to environmental and individual factors, we were interested in constructing predictive models of these relationships. Therefore, once we obtained a suitable subset of models based on information criteria, we constructed a predictive model based on the model-averaged estimates ($\hat{\beta}$) of the parameters contained among the several models. We then applied these parameters to a design matrix (\mathbf{X}_0) containing specified values for the predictor variables (sex, age, covariates, etc) and obtained predictions as

$$\hat{\mathbf{Y}} = \mathbf{X}_0 \hat{\beta}$$

with estimated variance-covariance structure of

$$v(\hat{\mathbf{Y}}) = \mathbf{X}_0 \mathbf{V} \mathbf{X}_0'$$

where \mathbf{V} is the estimated variance-covariance matrix of the model-averaged estimates (Searle, 1971, pp. 90-91). We estimated \mathbf{V} by first estimating the correlation matrix under the model containing all the parameters of interest, then estimating the unconditional parameter variances as described above, and finally applying the unconditional variance estimates to the correlation matrix to re-estimate the variance covariance matrix. Approximate 95% confidence intervals of $\hat{\mathbf{Y}}$ were obtained as

$$\hat{\mathbf{Y}} \pm 1.96 \times [D(\mathbf{V})]^{1/2}$$

where D is an operator producing a vector of elements from the diagonal of a square matrix. Finally, these were back-transformed to obtain predicted survival rates by

$$\hat{\mathbf{S}} = \text{logit}^{-1}[\hat{\mathbf{Y}}]$$

to obtain the predicted value and upper and lower confidence limits.

3 Results

3.1 General analysis

We conducted a preliminary analysis of birds captured as adults and, performed tests in program RELEASE. The combined results of TEST 2 and TEST 3 from RELEASE provide no evidence of lack of model fit for the sex-stratified CJS model ($\chi^2 = 68.82$, $df = 94$, $P = 0.98$). In particular, these tests provided no indication of a transient or temporary capture effect. We thence proceeded with the development of global age-, sex-, and time-specific models as described in Section 2.1, and estimated parameters of model $\phi(\text{sex}^* \text{age}^* t)p(\text{sex}^* t)$, as well as the more general $\phi^*(\text{sex}^* \text{age}^* t)p(\text{sex}^* t)$. The fit of the more general model ($\hat{c}_e = 22.857$) was worse than that of $\phi(\text{sex}^* \text{age}^* t)p(\text{sex}^* t)$ ($\hat{c}_e = 14.247$), and had many parameters that were poorly estimated (e.g. very large standard errors). Therefore, $\phi(\text{sex}^* \text{age}^* t)p(\text{sex}^* t)$ was taken as the provisional global model, and subjected to further

evaluation using bootstrapping. The average from $n = 576$ bootstrap samples was $\hat{c}_b = 11.338$ (95th percentile = 9.937), both of which exceeded \hat{c}_e . We took this as evidence of moderate extra-binomial variation, lack of fit, or both, and following the recommendations of Burnham & Anderson (1998) used $\hat{c}^* = 14.247/11.338 = 1.26$ to adjust variances, confidence intervals, and AIC values in subsequent estimation and model comparisons (Table 1). These results were used with model averaging to obtain the sex-, age-, and time-specific estimates of ϕ in Fig. 1. These indicate a small sex-specific difference in survival (males higher than females) but consistently higher adult than juvenile survival rates. Survival exhibited great year-to-year variability, particularly for adults, but only a minor apparent seasonal effect.

3.2 Covariates analyses

Time specific and individual covariate values are summarized in Tables 2 and 3. Table 2 generally confirms the mildness of the Mediterranean climate, with a fairly narrow range in winter and summer temperatures and days below freezing in winter. In contrast, there was a wide range in numbers of wintering siskins captured (0 to > 3000) and in Jul-Sep rainfall (78–329 mm). These data and those of the individual covariates summarized in Table 3 were used as predictors in the covariate models (Table 1) after standardization as described in Sections 2.3 and 2.4.

The models in Table 1 were grouped into four categories: (1) those containing no covariates (individual or time-specific); containing only (2) time or (3) individual covariates; and (4) containing both types of covariates, in particular, interactions between individual and time-specific factors. Our first conclusion based on the rankings displayed was that category (2) models were universally poor in performance, with $\Delta\text{QAIC}_C > 74$ and $w_i \approx 0$ for all models in this category. We therefore removed these models from further consideration, and concentrated on categories (1), (3) and (4). We were particularly interested in (4), as these models related to our *a priori* ideas about birds in different condition. The ‘best’ model overall ($w_i = 0.25$) was of this type, including a term involving the interaction between mass and winter abundance of siskins. Several other of the category (3) and (4) models were reasonable contenders for further consideration (w_i approaching 0.10, $\Delta\text{QAIC}_C < 2$); virtually none of the category (1), and none of the category (2) models approached these criteria. We therefore examined the best category (1) model and two best category (2) models, all meeting the above criteria, to determine the subset of predictor variable for further estimation and predictive modelling. Based on this, we obtained model-averaged estimates for the parameters listed in Table 4, where again averaging was done separately for each parameter, across models in which that parameter appears. These estimates were then used to develop predictions for the specific set of covariate and other factors shown in Figs 2–4. There is an apparent optimum for body mass of juveniles, with the maximum predicted survival at approximately 1 SD below the average juvenile mass, and declining thereafter; there was little effect of mass on survival except at very high (> 2 SD above the mean) masses (Fig. 2). However, there appears to be a pronounced interaction between siskin abundance and mass in affecting Jan-Jul survival (Fig. 3). At average levels of siskins the relationship is nearly identical to that depicted in Fig. 2 (Fig. 3(b)). However, at low siskin abundance the effect of increasing mass on survival is monotonically negative (Fig. 3(a)) whereas at high siskin abundance the reverse is true (Fig. 3(c)).

TABLE 1. Model selection criteria for serins ringed as adults and subadults and recaptured in Barcelona, 1986–1999

Covariates ^a	Model ^{b,c}	k^d	ΔQAIC_c^e	w_i^f
Individual*time	$\phi(\text{sex} + \text{age} + \text{wt} * \text{sisk} + \text{wng} + \text{wng}^2 + \text{age} * \text{wng} + \text{seas} * \text{wng} + \text{t})$	61	0.00	0.2538
Individual*time	$\phi(\text{sex} + \text{age} + \text{wt} * \text{frz} + \text{wng} + \text{wng}^2 + \text{age} * \text{wng} + \text{seas} * \text{wng} + \text{t})$	61	2.56	0.0706
Individual*time	$\phi(\text{sex} + \text{age} + \text{wt} * \text{tmax} + \text{wng} + \text{wng}^2 + \text{age} * \text{wng} + \text{seas} * \text{wng} + \text{t})$	61	2.63	0.0681
Individual*time	$\phi(\text{sex} + \text{age} + \text{wt} * \text{tmin} + \text{wng} + \text{wng}^2 + \text{age} * \text{wng} + \text{seas} * \text{wng} + \text{t})$	61	3.00	0.0566
Individual*time	$\phi(\text{sex} + \text{age} + \text{wt} * \text{rain} + \text{wng} + \text{wng}^2 + \text{age} * \text{wng} + \text{seas} * \text{wng} + \text{t})$	61	4.07	0.0332
Individual*time	$\phi(\text{sex} + \text{age} + \text{wt} + \text{wt}^2 + \text{age} * \text{wt} + \text{seas} * \text{wt} + \text{wt} * \text{sisk} + \text{t})$	61	4.36	0.0287
Individual*time	$\phi(\text{sex} + \text{age} + \text{wt} + \text{wt}^2 + \text{age} * \text{wt} + \text{seas} * \text{wt} + \text{wt} * \text{frz} + \text{t})$	61	5.11	0.0197
Individual*time	$\phi(\text{sex} + \text{age} + \text{wt} + \text{wt}^2 + \text{age} * \text{wt} + \text{seas} * \text{wt} + \text{wt} * \text{tmin} + \text{t})$	61	5.67	0.0149
Individual*time	$\phi(\text{sex} + \text{age} + \text{wt} + \text{wt}^2 + \text{age} * \text{wt} + \text{seas} * \text{wt} + \text{wt} * \text{tmax} + \text{t})$	61	6.21	0.0114
Individual*time	$\phi(\text{sex} + \text{age} + \text{wt} + \text{wt}^2 + \text{age} * \text{wt} + \text{seas} * \text{wt} + \text{wt} * \text{rain} + \text{t})$	61	6.48	0.0099
Individual*time	$\phi(\text{sex} + \text{age} + \text{wt} + \text{wt}^2 + \text{age} * \text{wt} + \text{seas} * \text{wt} + \text{wt} * \text{weather})$	70	10.28	0.0015
Individual	$\phi(\text{sex} + \text{age} + \text{wng} + \text{wng}^2 + \text{age} * \text{wng} + \text{seas} * \text{wng} + \text{t})$	60	1.56	0.1162
Individual	$\phi(\text{sex} + \text{age} + \text{wt} + \text{wt}^2 + \text{seas} * \text{wt} + \text{t})$	59	1.96	0.0951
Individual	$\phi(\text{sex} + \text{age} + \text{wt} + \text{wt}^2 + \text{t})$	59	2.26	0.082
Individual	$\phi(\text{sex} + \text{age} + \text{wng} + \text{wng}^2 + \text{seas} * \text{wng} + \text{t})$	59	3.17	0.0519
Individual	$\phi(\text{sex} + \text{age} + \text{wt} + \text{wt}^2 + \text{age} * \text{wt} + \text{seas} * \text{wt} + \text{t})$	60	3.96	0.0351
Individual	$\phi(\text{sex} + \text{age} + \text{wng} + \text{wng}^2 + \text{t})$	58	8.58	0.0035
None	$\phi(\text{sex} * \text{age} + \text{t})$	57	4.81	0.0229
None	$\phi(\text{sex} + \text{age} + \text{t})$	56	5.18	0.0190
None	$\phi(\text{age} + \text{t})$	55	7.58	0.0057
None	$\phi(\text{sex} * \text{age} * \text{t})$	116	26.78	0.0000
None	$\phi(\text{sex} * \text{age} * \text{t})p(\text{sex} * \text{t})$ (global model)]	142	61.47	0.0000
None	$\phi(\text{sex} + \text{age} + \text{seas} + \text{age} * \text{seas} + \text{year})$	44	69.74	0.0000
None	$\phi * (\text{age} + \text{t})$	57	71.63	0.0000
None	$\phi * (\text{sex} * \text{age} + \text{t})$	59	72.54	0.0000
None	$\phi * (\text{sex} * \text{age} + \text{t})p(\text{sex} + \text{t})$	60	73.86	0.0000
None	$\phi * (\text{sex} * \text{age} * \text{t})p(\text{sex} * \text{t})$	173	87.01	0.0000
None	$\phi(\text{sex} + \text{age} + \text{seas} + \text{age} * \text{seas})$	32	95.27	0.0000
None	$\phi(\text{sex} * \text{age} + \text{t})p(\text{sex} * \text{t})$	84	107.98	0.0000
None	$\phi * (\text{sex} * \text{age} + \text{t})p(\text{sex} * \text{t})$	86	111.99	0.0000
None	$\phi * (\text{sex} * \text{age})$	34	158.06	0.0000
Time	$\phi(\text{sex} + \text{age} + \text{seas} + \text{age} * \text{seas} + \text{rain} + \text{tmax} + \text{sisk} + \text{frz} + \text{tmin} + \text{age} * \text{weath})$	42	74.76	0.0000
Time	$\phi(\text{sex} + \text{age} + \text{seas} + \text{age} * \text{seas} + \text{sisk} + \text{frz} + \text{tmin})$	35	84.60	0.0000
Time	$\phi(\text{sex} + \text{age} + \text{seas} + \text{age} * \text{seas} + \text{rain} + \text{tmax} + \text{sisk} + \text{frz} + \text{tmin})$	37	88.50	0.0000
Time	$\phi(\text{sex} + \text{age} + \text{seas} + \text{age} * \text{seas} + \text{rain} + \text{tmax})$	34	98.90	0.0000
Time	$\phi(\text{sex} + \text{age} + \text{rain} + \text{tmax} + \text{sisk} + \text{frz} + \text{tmin})$	35	124.90	0.0000

^aModels grouped by covariate type (individual, time-specific, or both) and sorted by descending model weight (w_i) within group.

^bCovariates: sisk = counts of siskins at serin trapping sites during Jan-Mar; frz = number of days with temperature < 0°C during Jan-Mar; tmin = average minimum daily temperature during Jan-Mar; tmax = average daily maximum temperature during Jul-Sep; rain = total rainfall (mm) during Jul-Sep; weath = all weather covariates in the model, e.g. age*weath in model $\phi(\text{sex} + \text{ages} + \text{rain} + \text{tmax} + \text{tmin} + \text{age} * \text{weath})$ denotes interaction terms age*rain, age*tmax, and age*tmin; wt = body mass, wng = wing length.

^cCovariate effects included in linear logistic model of survival; all models include a time but no other effect for recapture (p).

^d k = number of model parameters

^e ΔQAIC_c = difference above lowest corrected QAIC value; Variance inflation factor $\hat{c} = 1.26$;

^f w_i = model weight based on ΔQAIC_c ; model weight is based on models in all covariate groups.

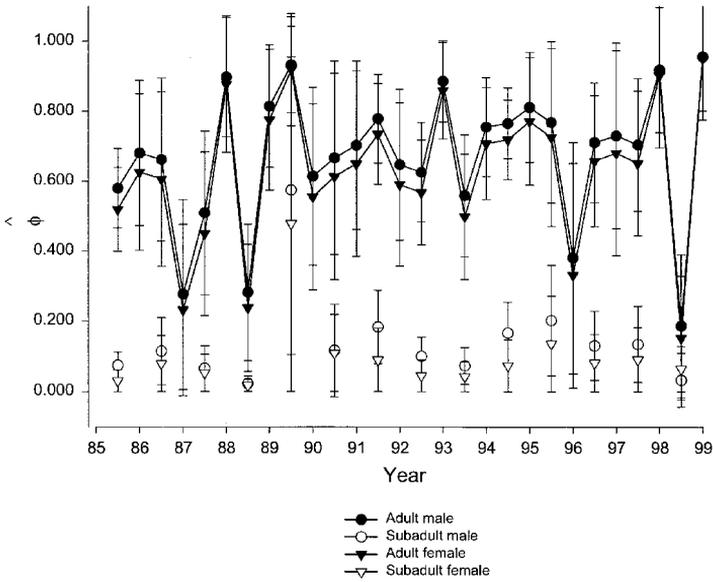


FIGURE 1. Model-averaged estimates and approximate 95% confidence intervals of time-, age-, and sex-specific survival. Tick marks correspond to Apr-Sep of corresponding year (1985-99), midpoint between ticks to Oct-Mar of each year.

TABLE 2. Time-specific covariates used in analysis of survival rates for serins recaptured in Barcelona, 1986-1999

Period	Variable	\bar{x}	SD	<i>n</i>	min	max
Jan-Mar	Min temp °C	6.60	0.75	14	5.60	8.00
	Days < 0C	1.86	2.21	14	0.00	7.00
	<i>n</i> siskins captured	474.86	923.89	14	0.00	3105.00
Jul-Sep	Rain (mm)	160.48	72.31	14	77.70	329.30
	Max. temp °C	27.07	0.94	14	25.40	28.73

TABLE 3. Individual covariates used in analysis of survival rates for serins recaptured in Barcelona, 1986-1999

Sex	Age	Period	Mass					Wing				
			\bar{x}	SD	<i>n</i>	min	max	\bar{x}	SD	<i>n</i>	min	max
Male	Adult	Oct-Mar	11.25	1.00	333	9.0	14.5	71.92	3.99	333	70.0	78.0
		Apr-Sep	11.00	0.67	294	8.9	13.0	71.44	1.54	294	68.5	76.5
	Subadult	Oct-Mar	11.54	1.03	810	8.9	16.5	71.40	1.71	810	65.0	77.0
Female	Adult	Oct-Mar	11.24	0.98	201	8.8	15.5	69.08	1.88	201	61.5	76.0
		Apr-Sep	11.30	1.10	304	9.3	15.0	68.81	1.54	304	63.5	72.5
	Subadult	Oct-Mar	11.39	1.72	736	9.0	18.0	68.77	1.72	736	61.0	75.0
Total			2678					2678				

TABLE 4. Model-averaged estimates of individual and time-specific covariate effects for serins

Parameter	$\hat{\theta}_a$	$SE(\hat{\theta}_a)$	95% Confidence interval	
			Lower	Upper
Intercept	7.5811	73.8130	-137.0925	152.2546
Sex	0.2370	0.1175	0.0067	0.4674
Age	2.5476	0.2919	1.9754	3.1197
Wt	2.6507	1.8853	-1.0445	6.3459
Wt ²	-2.8681	1.9261	-6.6432	0.9070
Age*wt	-0.0216	0.2392	-0.4904	0.4473
Seas*wt	-0.1749	0.2588	-0.6823	0.3324
Wt*sisk	0.4319	0.2478	-0.0538	0.9177
Wng	-0.1006	0.4326	-0.9486	0.7473
Wng ²	0.6178	0.4333	-0.2314	1.4671
Age*wng	-0.2688	0.1593	-0.5811	0.0435
Seas*wng	-0.5371	0.1821	-0.8939	-0.1802

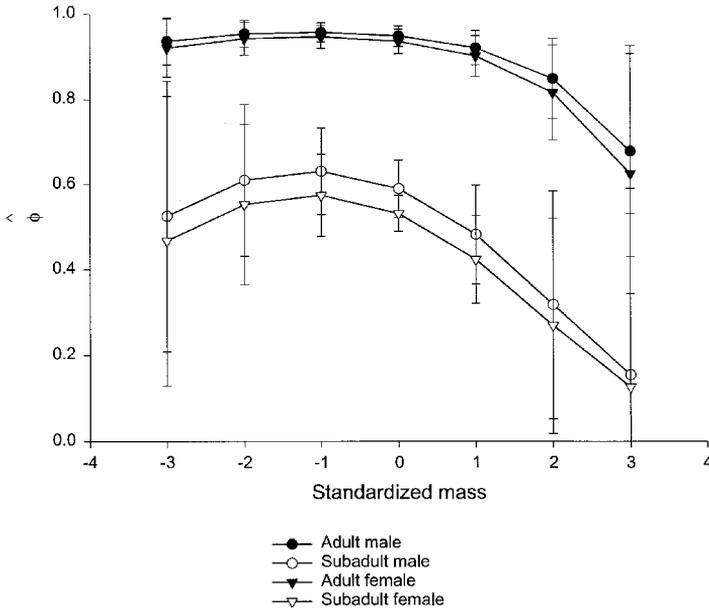


FIGURE 2. Predicted survival of serins in relation to body mass, averaged between 6-month survival periods. Error bars represent 95% confidence intervals of predicted survival after back transformation from linear logistic model, using weighted average estimates of coefficients (Table 4).

Predicted survival of subadults increased with wing length, so that unusually large subadults (> 3 SD above the mean) were predicted to survive at nearly the same rate as adults. In contrast, adult survival was virtually unaffected by changes in body mass (Fig. 4). Interpretation of these results should take into account that adult and juvenile wing lengths are very similar and that the ranges in size overlap very much (Table 2). In addition, of course, on average juvenile survival is much lower than adult survival. Therefore, the effects apparent in Fig. 4 may be largely due to a few unusually large individuals, which have very high (adult-like) survival.

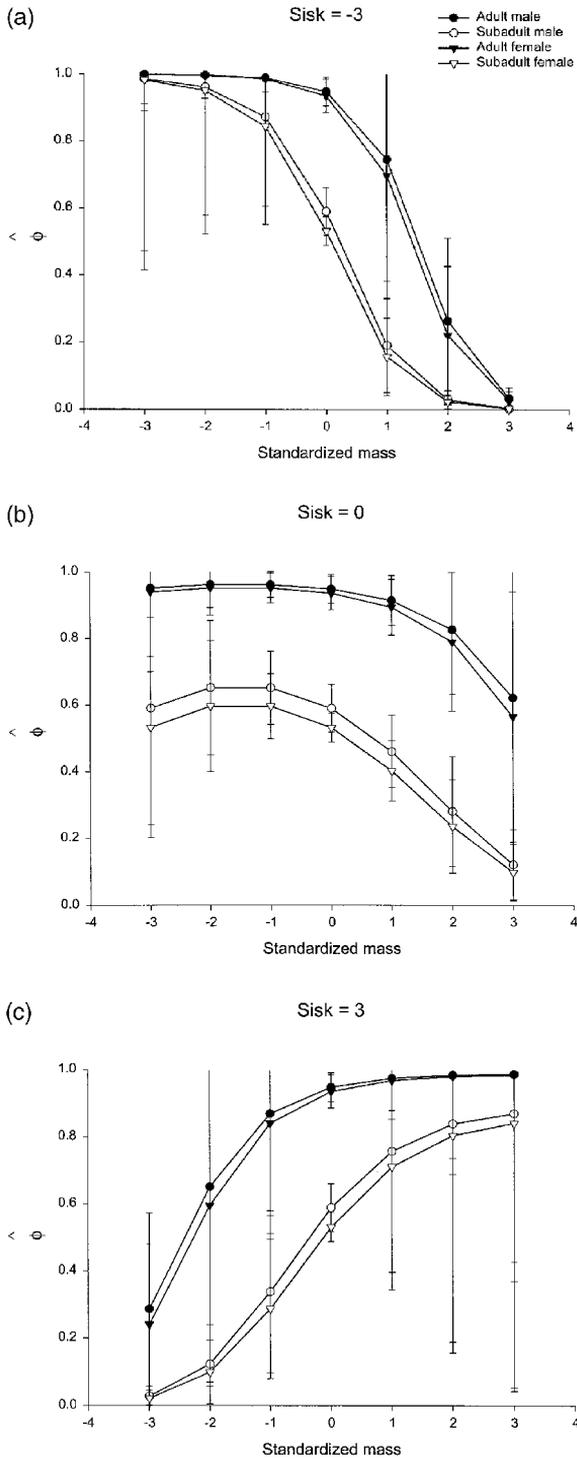


FIGURE 3. Predicted survival of serins in relation to body mass during Jan-Jul, at different levels of standardized abundance of siskins: (a) -3 (3 SD units below average) (b) 0 (average), and (c) 3 (3 SD units above average). Error bars represent 95% confidence intervals of predicted survival after back transformation from linear logistic model, using weighted average estimates of coefficients (Table 4).

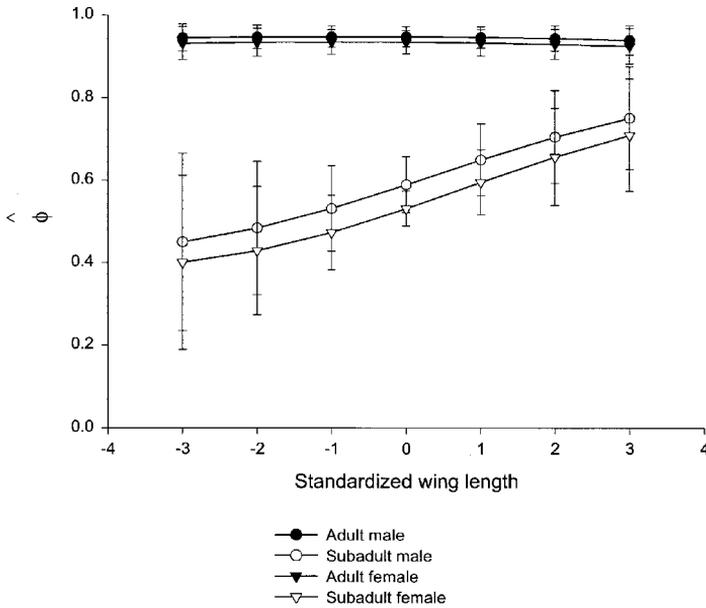


FIGURE 4. Predicted survival of serins in relation to wing length, averaged between 6-month survival periods. Error bars represent 95% confidence intervals of predicted survival after back transformation from linear logistic model, using weighted average estimates of coefficients (Table 4).

Finally, the confidence intervals on the parameter estimates used in these predictions (Table 4) were quite wide, leading to high prediction variance as reflected in the error bars in Figs 2 and 3; thus, biological interpretation of these relationships must be made with caution.

4 Discussion

Our analysis failed to detect a predictive relationship between environmental covariates and survival, and neither does there seem to be a strong indication of seasonal variation in survival, as would be expected from the mild weather in the Mediterranean area. The general expectation of higher survival rates for adults compared with subadults was confirmed by our models and estimates. Similarly, there was, as expected, a higher survival of males compared to females (Breitwisch, 1989), although this difference was not as pronounced. We have evidence for a relationship between body mass (taken as an indicator of body reserves against starvation) and survival of both sexes. For juveniles there is evidence of a curvilinear mass-survival relationship, whereas for adults predicted survival declines with increasing mass. Both results are consistent with the suggestion by Witter & Cuthill (1993) that very heavy birds are disadvantaged by mass in survival; this is especially noticeable for juveniles.

In spite of the general lack of importance of environmental factors, at least one factor, the presence and relative abundance of siskins, appears to influence the body mass-survival relationship. At low and average levels of siskin abundance, survival generally decreases with mass but at high siskin levels the effect seems reversed, suggesting that the need to have more body stores to overcome competition with the more dominant siskins may compensate for the disadvantage of heavy

mass, as has been found in studies at the intraspecific level (Clark & Ekman, 1995; Ekman & Lilliendahl, 1993; Hafthorn, 1998; Hake, 1996). Subordinate individuals within a flock prefer to maintain high fat loads, which although increasing predation risk, allows the subordinate birds to overcome the more immediate risk of starvation because of competition with dominant flock companions. Our results therefore resemble those of Krams (1998) on mixed-species flocks of parids, but have the additional aspect of relating the body mass/competition relationship to survival. The positive mass-survival relationship at times when competition is strongest (i.e. when many siskins are present), and the apparent reversal of the relationship when siskins are absent (when the disadvantages of higher body mass may prevail; Witter & Cuthill, 1993), suggests that management of body reserves is related to overall fitness as summarized by survival.

Naturally, we cannot exclude the possibility that other environmental or other factors are operating to influence survival in serins. Nor, because of the observational nature of this study, can we exclude the possibility that our empirical results are the result of chance covariation among many factors, and do not represent causation. However, we believe that the study has the advantage over much previous work in starting with reasonable *a priori* hypotheses about environmental and individual covariate effect. Our application of rigorous analytical methods based on information criteria provide additional strength to the resulting inferences. At the least, our work is a good motivation for further, ideally, experimental tests of these questions.

Finally, we recognize that our study design and analysis has inherent limitations that must be taken into account in generalizing these results. An important limitation is that our estimates of the effects of environmental and individual covariates on survival are conditional on birds that have survived to subadult status, i.e. have survived their first winter of life. Further investigations into these questions should take into account the possibility that juveniles respond differently to these factors than do subadults and adults. These investigations may be facilitated by improvements in methods for determining the sex of juvenile birds, a major reason that this cohort was excluded from our analyses.

Acknowledgements

We are grateful to D. Bone and M. L. Arroyo for help in the field and laboratory. We gratefully acknowledge the support provided by the North Atlantic Treaty Organization through grant CRG 950147 to MJC and JCS, and by Dirección General de Investigación Científica y Técnica DGICYT from the Spanish Government through grants PB92-0044-C02 and BOS 2000-0141 to JCS. We thank the editor and two anonymous referees for helpful comments on earlier drafts. The Georgia Cooperative Fish and Wildlife Research Unit is jointly sponsored by the USGS Biological Resources Division, the University of Georgia, the Georgia Department of Natural Resources, and the Wildlife Management Institute.

REFERENCES

- BAILLIE, S. R. (1990) Integrated population monitoring of breeding birds in Britain and Ireland, *Ibis*, 132, pp. 151-166.
- BAILLIE, S. R. & PEACH, W. J. (1992) Population limitation in Palearctic-African migrant passerines, *Ibis*, 134 (Suppl. 1), pp. 120-132.

- BALEN, J. H. V. (1980) Population fluctuations of the great tit and feeding conditions in winter, *Ardea*, 68, pp. 143-164.
- BATT, B. D. J., ANDERSON, M. G., ANDERSON, C. D. & CASWELL, F. D. (1989) The use of prairie potholes by North American ducks. In: A. V. VALK (Ed) *Northern Prairie Wetlands*, pp. 204-227 (Ames, Iowa, Iowa State University Press).
- BLONDEL, J. & ARONSON, J. C. (1999) *Biology and wildlife of the Mediterranean region* (Oxford, Oxford University Press).
- BREITWISCH, R. (1989) Mortality patterns, sex ratios, and parental investment in monogamous birds, *Current Ornithol.*, 6, pp. 1-50.
- BRYANT, D. M. & JONES, G. (1995) Morphological changes in a population of Sand Martins *Riparia riparia* associated with fluctuations in population size, *Bird Study*, 42, pp. 57-65.
- BUMPUS, H. (1899) The elimination of the unfit as illustrated by the introduced sparrow *Passer domesticus*, *Mar, Biol, Lab., Biol, Lect*, 1899, pp. 209-228.
- BURNHAM, K. P. & ANDERSON, D. R. (1998) *Model Selection and Inference* (New York, Springer).
- CLARK, C. W. & EKMAN, J. (1995) Dominant and subordinate fattening strategies—a dynamic game, *Oikos*, 72, pp. 205-212.
- CLOBERT, J., LEBRETON, J. D. & ALLAINE, D. A. (1987) A general approach to survival rate estimation by recaptures or resightings of marked birds, *Ardea*, 75, pp. 133-142.
- CONROY, M. J., SENAR, J. C., HINES, J. E. & DOMÈNECH, J. (1999) Development and application of a mark-recapture model incorporating predicted sex and transitory behavior, *Bird Study*, 46 (Suppl.), pp. 62-73.
- EKMAN, J. B. (1984) Density-dependent seasonal mortality and population fluctuations of the temperate-zone willow tit (*Parus montanus*), *Journal of Animal Ecology*, 53, pp. 119-134.
- EKMAN, J. B. & LILLIENDAHL, K. (1993) Using priority to food access-fattening strategies in dominance-structured willow tit (*Parus montanus*). *Behavioral Ecology*, 4, pp. 232-238.
- ELKINS, N. (1983) *Weather and Bird Behaviour*, pp. 239 (Calton, Poyser).
- FUTUYMA, D. J. (1998) *Evolutionary Biology* (Sunderland, Massachusetts, Sinauer Associates).
- GRANT, P. R. (1986) *Ecology and Evolution of Darwin's Finches*, pp. 458 (Princeton, Princeton University Press).
- GREENWOOD, J. J. D. & BAILLIE, S. R. (1991) Effects of density-dependence and weather on population changes of English passerines using a non-experimental paradigm, *Ibis*, 133, pp. 121-133.
- HAFTORN, S. (1993) Rank-dependent winter fattening in the willow tit (*Parus montanus*), *Ornis Fennica*, 77, pp. 49-56.
- HAKE, M. (1996) Fattening strategies in dominance-structured greenfinch (*Carduelis chloris*) flocks in winter, *Behavioural Ecology Sociobiology*, 39, pp. 71-76.
- HOLLANDS, P. K. & YALDEN, D. W. (1991) Population dynamics of Common Sandpipers *Actitis hypoleucos* breeding along an upland river system, *Bird Study*, 38, pp. 151-159.
- KARLSSON, J. & KÄLLANDER, H. (1977) Fluctuations and density of suburban populations of Blackbird *Turdus merula*, *Ornis Scandinavica*, 8, pp. 139-144.
- KRAMS, I. (1998) Rank-dependent fattening strategies of Willow Tit (*Parus montanus*) and Crested Tit (*P. cristatus*) mixed flock members, *Ornis Fennica*, 75, pp. 19-26.
- LACK, D. (1966) *Population Studies of Birds*, pp. 1-340 (Oxford, Clarendon Press).
- MÖLLER, A. P. (1989) Population dynamics of a declining Swallow *Hirundo rustica* population, *Journal of Animal Ecology*, 58, pp. 1051-1063.
- NAGER, R. G. & WIERSMA, P. (1996) Physiological adjustment to heat in Blue Tit *Parus caeruleus* nestlings from a Mediterranean habitat, *Ardea*, 84, pp. 115-125.
- NEWTON, I. (1972) *Finches*, pp. 288 (London, Collins).
- NEWTON, I. (1998) *Population Limitation in Birds*, pp. 597 (San Diego, Academic Press).
- NEWTON, I., WYLLIE, I. & ROTHERY, P. (1993) Annual survival of Sparrowhawks *Accipiter nisus* breeding in three areas of Britain, *Ibis*, 135, pp. 49-60.
- PEACH, W., BAILLIE, S. R. & UNDERHILL, L. (1991) Survival of British Sedge Warblers *Acrocephalus schoenobaenus* in relation to west African rainfall, *Ibis*, 133, pp. 300-305.
- PEACH, W., DUFEU, C. & MCMEEKING, J. (1995) Site tenacity and survival rates of Wrens *Troglodytes troglodytes* and Treecreepers *Certhia familiaris* in a Nottinghamshire wood, *Ibis*, 137, pp. 497-507.
- PRADEL, R., HINES, J. E., LEBRETON, J.-D. & NICHOLS, J. C. (1997) Capture-recapture survival models taking account of transients, *Biometrics*, 53, pp. 60-72.
- SEARLE, S. R. (1971) *Linear Models*, 532 pp. (Wiley, New York).
- SENAR, J. C. (1988) Trapping finches with the Yunick Platform Trap: the residency bias, *Journal Field Ornithology*, 59, pp. 381-384.

- SEÑAR, J. C. & COPETE, J. L. (1995) Mediterranean house sparrows (*Passer domesticus*) are not used to freezing temperatures: an analysis of survival rates, *Journal of Applied Statistics*, 22, pp. 1069-1074.
- SLAGSVOLD, T. (1975) Critical period for regulation of Great Tit (*Parus major* L.) and Blue Tit (*Parus caeruleus* L.) populations, *Norwegian Journal of Zoology*, 23, pp. 67-88.
- SMITH, S. M. (1995) Age-specific survival in breeding Black-capped Chickadees (*Parus atricapillus*), *Auk*, 112, pp. 840-846.
- SVENSSON, L. (1992) *Identification Guide to European Passerines*, pp. 368 (Stockholm, L. Svensson).
- TRAUTMAN, M. B., BILLS, W. E. & WICKLIFF, E. L. (1939) Winter losses from starvation and exposure of waterfowl and upland game birds in Ohio and other northern states, *Wilson Bulletin*, 51, pp. 86-104.
- WHITE, G. C. & BURNHAM, K. P. (1999) Program MARK—survival estimation from populations of marked animals, *Bird Study*, 46 (Suppl.), pp. 120-139.
- WITTER, M. S. & CUTHILL, I. C. (1993) The ecological costs of avian fat storage, *Philosophical Transactions of the Royal Society of London, Series B*, 340, pp. 73-92.