

# Asymmetric exchange between populations differing in habitat quality: a metapopulation study on the citril finch

JUAN CARLOS SENAR<sup>1</sup>, MICHAEL J. CONROY<sup>2</sup> &  
ANTONI BORRAS<sup>1</sup>, <sup>1</sup>Museu de Zoologia, Barcelona, Spain, <sup>2</sup>USGS, Georgia  
Cooperative Fish and Wildlife Research Unit, University of Georgia, USA

**ABSTRACT** *The citril finch (Serinus citrinella) is a Cardueline finch restricted to the high mountains of western Europe. Since 1991 we have captured-recaptured about 6000 birds in two contrasting subpopulations located on the same mountain but separated by 5 km in distance. Citril finches, at the north-facing locality (La Vansa), rely more on Pine trees (Pinus uncinata) as their main food source, than birds at the south-facing locality (La Bofia), which rely more on herb seeds, which are of lower energetic content. Birds at La Vansa had higher body mass and fat score than those at La Bofia, suggesting that La Vansa was a site of higher-quality than La Bofia. By the use of a metapopulation approach and multistate models, we found that citril finches at the high-quality locality (La Vansa) showed higher survival rates than those at the low-quality one (La Bofia) (Vansa adults:  $\phi = 0.42 \pm 0.04$ , juveniles:  $\phi = 0.34 \pm 0.05$ ; Bofia adults:  $\phi = 0.35 \pm 0.04$ , juveniles:  $\phi = 0.28 \pm 0.05$ ). Dispersal was also asymmetric and higher for juvenile birds, with movement rates for juvenile citril finches from the low-quality to the higher-quality locality (Bofia to Vansa:  $\psi = 0.38 \pm 0.10$ ) higher than the reverse (Vansa to Bofia:  $\psi = 0.09 \pm 0.03$ ). We also investigated time-specific factors (e.g. meteorological data and fructification rate of Pinus) as potential predictors of overall mortality and dispersal patterns. The results do not allow strong conclusions regarding the impact of these factors on survival and movement rates. Patterns of movement found in the Citril Finch between localities document a new model for the dispersal of species from low to high quality habitats, which we label of 'sources and pools'. This contrasts with currently accepted models of 'sources and sinks', in which movement is from high to low quality habitats, and 'Ideal Free Distributions', in which there is a balanced dispersal between habitats of different quality.*

Correspondence: J. C. Senar, Museu Zoologia, P<sup>o</sup> Picasso s/n, Parc Ciutadella, 08003 Barcelona, Spain.  
E-mail: jcsenar@intercom.es

## 1 Introduction

Dispersal between subpopulations is a key topic in metapopulation ecology and evolution (Hanski, 1999). Three main theoretical models of dispersal have so far been proposed: (1) Random dispersal, in which organisms do a random walk through space (Slatkin, 1985); (2) The ideal free distribution, in which animals redistribute themselves until every animal has the same expected fitness (Fretwell & Lucas, 1970), which includes models of neutral (Payne, 1991) and balanced dispersal (Doncaster *et al.*, 1997); and (3) The ideal pre-emptive distribution, in which the first animal to use a reproductive site can pre-empt it, so that the reproductive surplus from high-quality habitats is ejected to low-quality areas (the 'source-sink' dynamics—Pulliam, 1988; Dias, 1996).

The availability of suitable statistical methodology has, until recently, limited the empirical study of dispersal (Pradel, 1996). Fortunately, multistratum models developed by Brownie *et al.* (1993) and others, and implemented in program MARK (White and Burnham, 1999) have bridged this gap. The aim of this paper is to take advantage of this improved methodology to investigate patterns of natal and breeding dispersal of the citril finch (*Serinus citrinella*).

The citril finch breeds in the boreal mountain zones of western temperate Europe (Cramp & Perrins, 1994), maintaining its higher densities in the Pyrenees mountains (Baccetti & Märki, 1997). In the Pyrenees, especially the oriental range, there is a high bioclimatic contrast between north and south facing slopes because of a Mediterranean influence (Gutiérrez, 1991). This permits the comparison of bird subpopulations that differ in habitat quality but that, given their geographic proximity, have a high potential for exchange of individuals. The citril finch is therefore an ideal organism to study dispersal in patchy habitats, a topic of high theoretical relevance (McPeck & Holt, 1992), via multistate models.

## 2 Methods

### 2.1 Study population and field methods

Citril finches were captured and recaptured at two sites approximately 5 km apart, in the Pre-Pyrenees, approximately 100 km northwest of Barcelona. Both sites are at approximately 2000 m elevation, and are on opposite slopes of a 2378 m mountain; La Bofia faces south and La Vansa faces north (Fig. 1). The sites differ with respect to environmental conditions, with La Bofia being generally drier and sunnier, and La Vansa moister and cooler. Differences also exist in the abundance of the mountain pine (*Pinus uncinata*), an important food source for citril finches (Borras & Junyent, 1993), with abundance higher at La Vansa. Birds were ringed at La Bofia from 1986 to 1999, and at La Vansa from 1991 to 1999, with most (approximately 99%) captures and recaptures occurring between 1 April and 30 October. We captured a total of 5674 citril finches, obtaining 1383 recaptures (Vansa 3038/668, Bofia 2636/715). We have used the entire data set for the analysis of biometrical patterns, but for the analysis of capture-recapture data we have used birds captured from 1991 on, since in that period birds were simultaneously sampled at both localities.

Birds were captured with mist nets at drinking vessels and when picking up minerals at mountain huts. Birds were marked with numbered aluminium rings on capture. Sex and age were determined according to Svensson (1992); we defined juveniles as hatching year birds (EURING 3J and 3), and adults as after hatching

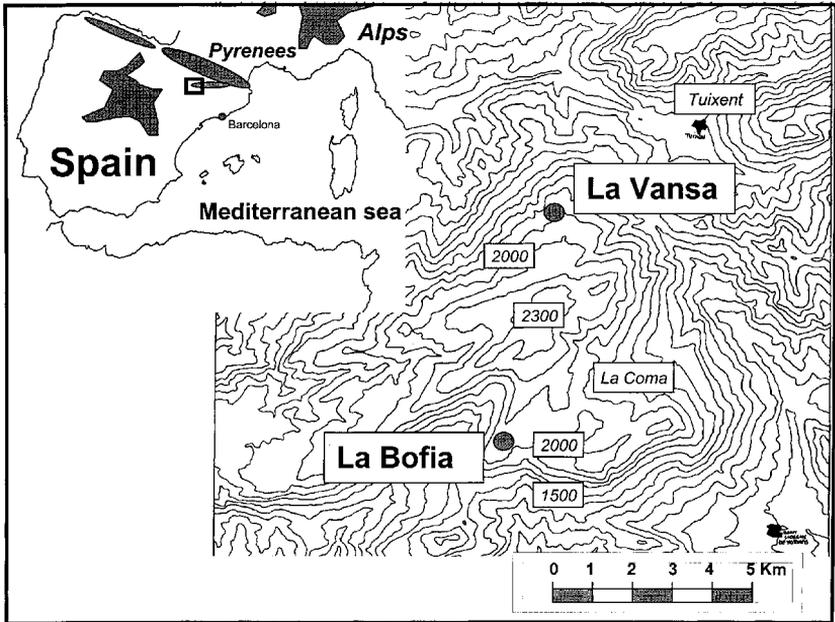


FIG. 1. Location of study areas and topographic relief (100 m contour lines).

year (EURING 5 & 6) (McClure, 1984; Pinilla, 2000). This allows differentiation of natal from breeding dispersal (Greenwood & Harvey, 1982) in that the birds abandon mountainous areas during the winter, to return in the spring (Borras & Junyent, 1993). For the analysis of biometric differences we differentiated yearlings (EURING 5) from true adults (EURING 6). We measured mass to the nearest 0.1 g and fat score according to a 6 grades scale (Ceballos *et al.*, 1984) averaging interclavicular and belly areas. We additionally assessed gut-contents, which provides an unbiased picture of the diet of the birds, by blowing aside the feathers on the neck so that the latest meal can be seen through the skin (Newton, 1972). Since diet in this species varies seasonally (personal observation), we split data in two different periods: Vernal period, from April to May, and Estival period, from June to July. We provide means  $\pm$  SE.

## 2.2 Preliminary analyses of survival and capture probability

Prior to developing multistate models for estimation, we conducted preliminary analyses using Cormack-Jolly-Seber (CJS) models, taking into account the two sites as strata in the estimation of survival and capture probabilities. Specifically, we developed a 'global model' that included variation with respect to area (La Bofia or La Vansa), age (adult, i.e. after hatching year or juvenile, i.e. hatching year), sex, and time (calendar year). The parameters of this general model included:

$$\phi_{a,ss,t}^{(v)}$$

the probability of survival from the midpoint of the ringing period (approximately 1 July) in year  $t$  to the midpoint in year  $t + 1$ , for birds in area  $a = 1$  (La Bofia), 2

(La Vansa), of sex  $s = 1$  (male), 2 (female), and of  $v = 0$  (juvenile), 1 (adult). Similarly, capture probabilities were modelled by

$$p_{a,s,t}$$

the probability of recapture during year  $t$  for marked birds in area  $a$ , and of sex  $s$ ; capture probabilities were not age-specific because all recaptures were, by definition, of adults.

Unfortunately, it was not possible to estimate all parameters of the above model, because of limitations in our field sampling procedures. In particular, juveniles could not be sexed unless subsequently recaptured following moult, from September on and usually in the following year when they were defined as adults. Because birds that were not recaptured, and therefore may have died, could not be sexed, it was not possible to obtain estimates of sex-specific survival for juveniles, or to combine the parameters for the juvenile data (ambiguous with regard to sex) with those for the adult data. Therefore, we first conducted a CJS analysis of only adults, including birds originally captured as juveniles but later recaptured as adults; for these latter birds, the first capture as adult was used as the initial capture, i.e. all previous captures for the bird were discarded. This allowed us to test for evidence of sex-specificity in survival and capture for adults. Our reasoning was that if these parameters were not sex-specific, we could then conduct an age-specific analysis, pooled across sexes.

For both analyses (adults only, sex-specific and juveniles only, age-specific) the general CJS model contained a large number of parameters, and we constructed a number of models under simplifying assumptions of constancy of parameters over time, between sites, and between sexes and ages. We also constructed several models allowing for 'parallelism', in which the effects of area, age, or sex, or other factors are assumed to operate, but not to interact with time. These types of models are reasonable under scenarios in which, for example, adults have higher survival rates than juveniles in any given time period, but respond in a similar fashion as females to environmental variation over time. All models were evaluated and compared, and estimates obtained, as described in Section 2.5.

### 2.3 Development of a multistate model

We modelled survival, movement, and capture as first-order Markov processes, based on the idea that the area of each bird at time  $t + 1$  is a 'state', and is a stochastic function of its state (i.e. area) at time  $t$ . Animals are allowed either to remain in a given state (e.g. survive and stay in a given area), or transit to a different state (e.g. survive and move to a different area). Reverse transition is also allowed; that is, ordinarily animals that move from area A to area B are allowed to return to area A. This type of transition is thus distinct from that which occurs in age-specific CJS models, in which transition occurs from younger to older age classes, but not the reverse. The basic model structure, known as the Arnason-Schwarz model (Schwarz & Arnason, 1990; Brownie *et al.*, 1993; Schwarz *et al.*, 1993) is a multistate analogue of the CJS model. The data structure involves the usual series of individual or summarized capture histories, but instead of '1' or '0' to denote 'captured' or 'not captured', the notation is augmented to identify the location of capture. For example, in our study, the capture history

would denote that an individual was first captured in year 1 in La Bofia, was next recaptured in year 4 in La Vansa, recaptured again in La Bofia in year 7, and not subsequently recaptured. Capture histories of this type were further classified into the age and sex of the individual birds, allowing the creation of summary records for input into program MARK (White & Burnham, 1999) for analysis. The following parameters are defined in the multistate model

$\gamma_i^{rs}$  the probability of being alive and in area  $s$  at time  $t + 1$ , for marked birds alive and in area  $r$  at time  $t$ .

$p_i^r$  the probability that an animal alive in area  $r$  at time  $t$  is captured,

$r = 1$  (La Bofia),  $2$  (La Vansa). The probabilities  $\gamma_i^{rs}$  are, in turn, a product of the biological parameters of interest, namely the probability of annual survival, and the conditional probability of movement, given that the animal has survived from  $t$  to  $t + 1$ . That is

$$\gamma_i^{rs} = \phi_i^r \psi_i^{rs}$$

where  $\phi_i^r$  is the probability of survival over  $[t, t + 1]$  for a bird alive in area  $r$  year  $t$ , and  $\psi_i^{rs}$  is the probability of movement from area  $r$  to area  $s$  for birds that survive the interval and do not permanently emigrate from the entire study area. By definition, movement to any other area (i.e. not La Vansa or La Bofia) is off the study, so that  $\psi_i^{11} = 1 - \psi_i^{12}$ ,  $\psi_i^{22} = 1 - \psi_i^{21}$ , and so only estimation of  $\psi_i^{12}$ ,  $\psi_i^{21}$  is required. As with the CJS models in Section 2.1, this model is generalized to include age and sex effects, with the parameter of the global model including area, age, sex-, and time-specific survival ( $\phi_{sit}^{r(v)}$ ) and movement ( $\psi_i^{rs(v)}$ ), and area-, sex-, and time-specific capture ( $p_{sit}^r$ ) probabilities.

#### 2.4 Evaluation of environmental covariates

Meteorological data were available from two stations: La Coma, located nearly between La Vansa and La Bofia and at 1700 m elevation, and therefore most representative of weather conditions at either site, and Tuixent, a small village at about 1400 m elevation at 3.5 km from La Vansa (Fig. 1). Previous work on citril finches in the Alps (Brandl & Bezel, 1988; Bezel *et al.*, unpublished data) suggested a correlation between June temperatures and survival. Unfortunately, weather data were not available for La Coma for June for 1994 and 1995, but they were available for Tuixent for these years. We examined the correlation between weather measurement at these two stations over 1986-1999 and found strong correlations for maximum monthly temperature ( $r = 0.91$ ,  $p = 0.001$ ), and total monthly precipitation ( $r = 0.77$ ,  $p = 0.01$ ), and days per month of precipitation  $r = 0.65$ ,  $p = 0.05$ ). We then used a linear regression model to predict the missing years of data for La Coma, using the values observed for Tuixent for those years. We calculated standardized values for the time-specific covariates using the means and standard deviations of each covariate estimated over years. The resulting values thus represented deviations from average values (over 1986-1999) for each of these covariates.

We also hypothesized that the productivity of pines, by affecting the food supply for citril finches, would affect temporal variation in survival rates, movement rates, or both. Cones of black pine (*Pinus nigra*) are used by citril finches during the end of winter and spring (February-April) while they are still on their wintering areas (Borras & Junyent, 1993). An index to regional black pine productivity was

computed as 0 (no cones observed anywhere), 1 (some cones, only in a few areas), 2 (high production in some areas), and 3 (high production in all areas) (Borras & Cabrera, 1996). In years in which level 3 production occurred we observed opportunistic breeding of citril finches (Borras & Senar, 1991). Cones from the mountain pine (*Pinus uncinata*) are used by citril finches during the spring (March-May) in high elevations (Borras & Junyent, 1993). For this species we used a different categorization, because cone production does not exhibit the dramatic crashes of black pines (Génard & Lescourret, 1987). For mountain pines the index was computed as 0 (no cones observed), 1 (average production) and 2 (high production). Because these are nominal categories of production rather than ratio measures, in our initial analyses we treated both black pine (BP) and mountain pine (MP) production as categorical predictors, in addition to analyses in which we used the index measures directly (0, 1, 2 and 3 for BP and 0, 1 and 2 for MP).

The general form of our covariate models was

$$\log\left(\frac{\theta_i}{1 - \theta_i}\right) = \sum_{j=1}^p \beta_j X_{i,j}$$

where  $\theta_i$  is a parameter of interest, e.g. survival ( $\phi$ ) or movement ( $\psi$ ) for the  $i$ th category (combination of site, age, sex and time);  $\beta_j$  is a parameter to be estimated,  $j = 1, \dots, k$ ; and  $X_{ij}$ ,  $i = 1, \dots, n$ ,  $j = 1, \dots, k$  is an element of a design matrix containing either 0s or 1s. For example, the model

$$Y = X\beta'$$

where

$$Y_i = \log\left(\frac{\psi_i}{1 - \psi_i}\right), \quad i = 1, \dots, 7$$

$$\psi' = [\psi_1^{12(1)}, \psi_2^{12(1)}, \psi_3^{12(1)}, \psi_1^{12(0)}, \psi_2^{12(0)}, \psi_3^{12(0)}]$$

describes the parameterization of age- and time-specific movement rates (e.g. from La Bofia to La Vansa) for three years. The design matrix

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

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

which describe age ( $\beta_1$ ), time ( $\beta_2, \beta_3$ ) and age  $\times$  time interactions ( $\beta_4, \beta_5$ ) in determining movement rates. An alternative model might substitute a vector of standardized weather covariates (e.g. temperature) for separate estimation of movement rates each year. For example, if standardized temperatures over periods 1, 2 and 3 are  $[-0.6, 0.4, 0.2]$  then

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

$$\beta^T = [\beta_0, \beta_1, \beta_2, \beta_3]$$

### 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. 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. For citril finches, we could anticipate differences in survival, and possibly capture, related to the bird’s sex and age, and varying with time because of varying environmental conditions. In addition, we had *a priori* reasons to suspect differences in survival rates, capture rates, and movement rates between La Bofia and La Vansa, because of the differing environmental and habitat conditions on these sites, noted earlier.

In all cases we examined the fit of the global model, initially using the deviance-based estimated of goodness of fit produced by program MARK (White & Burnham, 1999)

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

Deviation of this statistic from 1 indicates lack of fit (Burnham & Anderson, 1998; White & Burnham, 1999). However, this and other lack of fit statistics are known to be unreliable for sparse capture-recapture data sets such as ours. Therefore, for each global model we conducted  $n = 500$  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 they were used to estimate model parameters and they computed the  $\chi^2$  deviance statistic in MARK. We compared the distribution and average of the bootstrap deviances with that produced by the global model, and following the recommendations of Burnham & Anderson (1998) computed a variance inflation factor ( $c$ ) as

$$\hat{c}^* = \frac{\chi_c^2}{\chi_b^2}$$

where  $\chi_c^2$  is the statistic for the model fitted to our data, and  $\chi_b^2$  is the mean from the bootstrap simulations (where the global model is the true underlying model). This statistic was subsequently used in the computation of QAIC<sub>c</sub>, below.

We then formed a number of submodels in which the parameters of the global model were constrained under plausible hypotheses about site-, age-, sex- 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.

We used Akaike’s Information Criterion (AIC; Burnham & Anderson (1998)) as the basic metric of the plausibility of our alternative models. In most cases, AIC was adjusted for small effective sample sizes as described by Burnham & Anderson (1998, p. 51) to form  $AIC_c$ . Usually there was evidence of lack of fit of the global model, leading to further adjustment by a variance inflation factor to form  $QAIC_c$  (Burnham & Anderson, 1998, p. 53). The candidate models (global and submodels) were ranked by AIC ( $AIC_c$ ,  $QAIC_c$ ) to calculate  $\Delta AIC$  (always zero for the best model). A model weight for a candidate model in the model set was then computed as

$$w_i = \frac{e^{(-\Delta AIC_i/2)}}{\sum_{j=1}^R e^{(-\Delta AIC_j/2)}}$$

where  $R$  is the number of models in the set of candidate models. These calculations are performed automatically in MARK, but in some cases we made multiple runs (e.g. involving or not involving time-specific covariates), in which case the candidate models were combined and the above formula used to calculate model weight.

Generally, we sought to identify the most plausible model as that model with the lowest  $\Delta AIC$  value (equivalently, highest model weight). However, frequently several models were close competitors ( $\Delta AIC < \text{approximately } 2$ ) 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

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

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

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

which 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 report 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.

### 3 Results

#### 3.1 Characterization of the two subpopulations

The analysis of the diet of citril finches by crop inspection through the skin, revealed that although a seasonal effect was present, with birds relying more heavily on pine seeds versus herbs in the Vernal period than in the Estival one (Vernal 81%,  $N = 310$ , Estival 18%,  $N = 739$ ), birds differed in the use of pine seeds according to locality: citril finches at La Vansa included 40% ( $n = 687$ ) of pine seeds in their diet as compared to herbs, while birds at La Bofia included 29% of pine seeds ( $n = 362$ ) (three-way contingency table; Locality  $\times$  Diet:  $\chi^2 = 6.83$ ,  $P < 0.01$ , Season  $\times$  Diet:  $\chi^2 = 372.75$ ,  $P < 0.001$ ; Locality  $\times$  Season  $\times$  Diet:  $\chi^2 = 2.42$ ,  $P = 0.12$ ). When differentiating Dandelion *Taraxacum officinalis*, from other herbs, we found citril finches in La Vansa relying more on Dandelion (30% of 412 samples) than birds in La Bofia (9% of 256 samples) (three-way contingency table; Locality  $\times$  Herb Diet:  $\chi^2 = 31.40$ ,  $P < 0.001$ , Season  $\times$  Herb Diet:  $\chi^2 = 0.23$ ,  $P = 0.63$ ; Locality  $\times$  Season  $\times$  Herb Diet:  $\chi^2 = 4.32$ ,  $P = 0.04$ ).

Citril finches in La Vansa showed a higher body mass than birds in La Bofia (Vansa:  $12.70 \pm \text{SE}0.02$ ,  $N = 2115$ , Bofia:  $12.56 \pm \text{SE}0.02$ ,  $N = 1505$ ; Three-way ANOVA: Locality  $F_{1,3612} = 10.15$ ,  $P < 0.001$ ; Age  $F_{1,3612} = 18.58$ ,  $P < 0.001$ ; Sex  $F_{1,3612} = 82.29$ ,  $P < 0.001$ ; all interactions  $P > 0.14$ ), and a higher fat score (Vansa median: 1.0, max/min: 3/0,  $N = 2102$ , Bofia 0.5, max/min: 2/0,  $N = 1295$ ; Mann-Whitney test,  $Z = 2.76$ ,  $p < 0.01$ ). No differences in sexual rate nor age distribution was found between the two localities (Locality  $\times$  Age:  $\chi^2 = 1.36$ ,  $P = 0.24$ ; Locality  $\times$  Sex;  $\chi^2 = 0.00$ ,  $P = 1.00$ ; Locality  $\times$  Age  $\times$  Sex:  $\chi^2 = 0.03$ ,  $P = 0.86$ ).

#### 3.2 Preliminary analyses of survival and capture probability

Our analysis of citril finches captured as adults (Table 1) indicated evidence of area-specific but not sex-specific survival and capture probabilities. Survival was

TABLE 1. CJS models for adult citril finches recaptured in La Bofia and La Vansa, 1991-99

Model <sup>a</sup>	$\Delta \text{QAIC}_c^b$	$w_i$	$k$
$\phi(\text{area})p(\text{area}+t)$	0.00	0.60	11
$\phi(\cdot)p(t)$	2.82	0.15	9
$\phi(\cdot)p(\text{area}+t)$	4.12	0.08	10
$\phi(\text{area})p(t)$	4.41	0.07	10
$\phi(\text{sex})p(t)$	4.83	0.05	10
$\phi(\text{area}^*t)p(t)$	5.05	0.05	23
$\phi(\text{area}^*\text{sex})p(t)$	6.18	0.03	12
$\phi(\text{area})p(\text{area}^*t)$	7.23	0.02	18
$\phi(\text{area}+t)p(t)$	8.48	0.01	17
$\phi(\text{sex}^*t)p(t)$	8.86	0.01	23
$\phi(\text{area}^*\text{sex}^*t)p(t)$	26.11	0.00	39
$\phi(\text{area})p(\text{area}^*\text{sex}^*t)$	33.60	0.00	34
$\phi(\text{area}^*\text{sex}^*t)p(\text{sex}^*t)$	37.13	0.00	46
$\phi(\text{area}^*\text{sex}^*t)p(\text{area}^*\text{sex}^*t)$	49.36	0.00	60
$\phi(\text{area})p(\text{area}+t)$	52.81	0.00	4

<sup>a</sup>Variance adjustment factor  $\hat{c} = 1.06$ .

<sup>b</sup> $\Delta \text{QAIC}_c$  = difference in  $\text{QAIC}_c$  value from lowest valued model;  $w_i$  =  $\text{QAIC}_c$  weight for model  $i$ ;  $k$  = number of model parameters.

TABLE 2. Estimates of survival ( $\phi$ ) and capture ( $p$ ) based on weighted averaging of CJS models in Table 1 for adult citril finches recaptured in La Bofia and La Vansa, 1991-99

	Area	Year	$\hat{\theta}_a$	$SE(\hat{\theta}_a)$	Lower	Upper
$\phi$	La Bofia		0.3646	0.5456	-0.7039	1.4330
	La Vansa		0.4284	0.406	-0.3674	1.2243
$p$	La Bofia	1992	0.1192	0.0524	0.0164	0.2218
		1993	0.2822	0.0987	0.0885	0.4757
		1994	0.2650	0.0893	0.0897	0.4401
		1995	0.4024	0.1034	0.1996	0.6050
		1996	0.1355	0.0564	0.0248	0.2461
		1997	0.2515	0.0848	0.0851	0.4177
		1998	0.1051	0.0441	0.0185	0.1916
		1999	0.1037	0.4475	-0.7736	0.9809
	La Vansa	1992	0.0745	0.0338	0.0081	0.1408
		1993	0.1853	0.0472	0.0926	0.2778
		1994	0.1709	0.0387	0.0949	0.2467
		1995	0.2845	0.0666	0.1538	0.4151
		1996	0.0813	0.0203	0.0414	0.1210
		1997	0.1632	0.0385	0.0877	0.2387
		1998	0.0652	0.0256	0.0150	0.1154
		1999	0.0632	0.4275	-0.7747	0.9011

TABLE 3. CJS models for adult and juvenile citril finches (sexes combined) recaptured in La Bofia and La Vansa, 1991-99

Model <sup>a</sup>	$\Delta\text{QAIC}_c^b$	$w_i$	$k$
$\phi(\text{age} + t) p(\text{area} + t)$	0.00	0.40	18
$\phi(\text{area} + \text{age} + t) p(\text{area} + t)$	0.77	0.27	19
$\phi(\text{area} * \text{age} + t) p(\text{area} + t)$	2.65	0.11	20
$\phi(\text{area} + \text{age}) p(\text{area} + t)$	3.42	0.07	12
$\phi(t) p(\text{area} + t)$	4.24	0.05	16
$\phi(\text{area} + t) p(\text{area} + t)$	4.53	0.04	17
$\phi(\text{area} + \text{age} + t) p(\text{area} * t)$	5.69	0.02	25
$\phi(\text{age} + t) p(\text{area} * t)$	5.74	0.02	24
$\phi(\text{area} * \text{age} + t) p(\text{area} * t)$	7.49	0.01	26
$\phi(\text{area} * \text{age} * t) p(t)$	28.60	0.00	39
$\phi(\text{area} * \text{age} * t) p(\text{area} * t)$	32.29	0.00	46

<sup>a</sup>Variance adjustment factor  $\hat{c} = 1.48$ .

<sup>b</sup> $\Delta\text{QAIC}_c$  = difference in  $\text{QAIC}_c$  value from lowest valued model;

$w_i$  = AIC weight for model  $i$ ;  $k$  = number of model parameters.

higher for adults in La Vansa than in La Bofia; however, standard errors for these estimates were large, resulting in very large confidence intervals (Table 2). Nonetheless, the results provided justification for proceeding with the age-specific (sexes pooled) CJS analysis (Tables 3 and 4). Again, model comparisons (Table 3) indicated area as well as age specificity in survival, with both factors included in two of the top-ranked three models. Model-averaged estimates (Table 4) confirmed

TABLE 4. Estimates of survival ( $\phi$ ) and capture ( $p$ ) based on weighted averaging of CJS models in Table 3 for adult and juvenile citril finches recaptured in La Bofia and La Vansa, 1991-99

	Area	Age	Year	$\hat{\theta}_a$	SE( $\hat{\theta}_a$ )	Lower	Upper
$\phi$	La Bofia	Adult	1991	0.228	0.090	0.051	0.405
			1992	0.604	0.123	0.363	0.845
			1993	0.300	0.068	0.166	0.433
			1994	0.249	0.058	0.134	0.363
			1995	0.637	0.142	0.359	0.915
			1996	0.396	0.143	0.116	0.676
			1997	0.326	0.145	0.042	0.610
			1998	0.323	0.598	-0.849	1.495
		Juvenile	1991	0.153	0.079	0.002	0.309
			1992	0.477	0.144	0.195	0.758
			1993	0.205	0.057	0.093	0.317
			1994	0.168	0.061	0.049	0.287
			1995	0.513	0.148	0.222	0.803
			1996	0.285	0.140	0.010	0.560
			1997	0.228	0.126	-0.020	0.475
			1998	0.256	0.523	-0.769	1.282
	La Vansa	Adult	1991	0.247	0.095	0.061	0.434
			1992	0.629	0.120	0.394	0.863
			1993	0.322	0.071	0.183	0.462
			1994	0.269	0.061	0.149	0.389
			1995	0.661	0.135	0.397	0.925
			1996	0.422	0.145	0.138	0.707
			1997	0.350	0.150	0.057	0.643
			1998	0.342	0.606	-0.846	1.531
		Juvenile	1991	0.169	0.085	0.003	0.335
			1992	0.507	0.143	0.227	0.787
			1993	0.225	0.061	0.106	0.344
			1994	0.185	0.064	0.059	0.311
$p$	La Bofia		1992	0.145	0.081	-0.013	0.303
			1993	0.135	0.045	0.047	0.223
			1994	0.238	0.062	0.117	0.360
			1995	0.518	0.118	0.286	0.749
			1996	0.111	0.037	0.039	0.183
			1997	0.205	0.073	0.062	0.349
			1998	0.115	0.054	0.009	0.221
			1999	0.293	0.448	-0.586	1.172
	La Vansa		1992	0.102	0.059	-0.015	0.218
			1993	0.095	0.030	0.036	0.154
			1994	0.165	0.043	0.080	0.250
			1995	0.418	0.108	0.206	0.629
			1996	0.076	0.021	0.034	0.118
			1997	0.142	0.049	0.046	0.238
			1998	0.079	0.037	0.006	0.153
			1999	0.205	0.362	-0.505	0.914

the pattern of higher survival for both adults and juveniles in La Vansa than in La Bofia, and higher adult than juvenile survival in both areas.

### 3.3 Multistate model

The deviance-based goodness of fit statistic for the global age-, and time-specific multistate model was large ( $\hat{c} = 6.3$ ) suggesting lack of fit. Again, however, as with the CJS models, we have little confidence in this as a measure of goodness of fit, because of the small sample sizes involved. Unfortunately, at present there exist no alternatives, because a bootstrap procedure has not yet been developed for the multistate models in MARK. Therefore, we used the variance adjustment factor computed for the age-specific CJS model in lieu of an estimate based on the multistate model. Our rationale for this was that the multistate model essentially incorporates the separate, site-specific models as components. Under an assumption of no intersite movement, the multistate estimates should be equivalent to separate CJS estimates for each site. We assume, therefore, that the degree of lack of fit in the multistate model is at least that of the age- and site-stratified CJS model, but of course it may be worse. In lieu of a good alternative, therefore, we retained the CJS variance factor for use in model comparisons and calculation of standard errors and confidence intervals. It is to be hoped that future versions of MARK or other estimation software will allow testing for fit via bootstrapping or other methods, thus rendering our approach obsolete.

Based on this approach, we compared the multistate models using QAIC<sub>c</sub> adjusted as above (Table 5). None of the best models ( $\Delta\text{QAIC}_c < 5$ ,  $w_i > 0.05$ ) included time effects for either survival or movement rates, but all included an interactive effect between time and age for capture rates. Area and age were included in at least some of these models for both survival and movements. Based on these results, we developed model-averaged estimates of survival, movement, and capture rates, ignoring time effects for the first two, and area effects for the last (Table 6). As with the CJS models, estimated adult survival was higher than juvenile survival for both sites, and survival higher for both age classes at La Vansa than at La Bofia (Table 6, Fig. 2). Movement rates were clearly asymmetric

TABLE 5. Evaluation of multistratum models for citril finches recaptured 1991–99 in La Bofia and La Vansa<sup>a</sup>

Model <sup>a</sup>	$\Delta\text{QAIC}_c^b$	$w_i$	$k$
$\phi(\text{area} + \text{age}) p(\text{area}^*t) \psi(\text{area} + \text{age})$	0.00	0.52	22
$\phi(\text{age}) p(\text{area}^*t) \psi(\text{area} + \text{age})$	1.42	0.25	21
$\phi(\text{area}) p(\text{area}^*t) \psi(\text{area} + \text{age})$	2.71	0.13	21
$\phi(.) p(\text{area}^*t) \psi(\text{area} + \text{age})$	4.77	0.05	20
$\phi(\text{area} + \text{age}) p(\text{area}^*t) \psi(\text{area})$	5.08	0.04	21
$\phi(\text{area} + \text{age}) p(\text{area} + t) \psi(\text{area} + \text{age})$	10.02	0.00	15
$\phi(\text{area} + \text{age}) p(\text{area}^*t) \psi(\text{age})$	10.53	0.00	21
$\phi(.) p(\text{area}^*t) \psi(.)$	15.15	0.00	18
$\phi(\text{area}^*\text{age}^*t)p(\text{area}^*t)$	59.38	0.00	77

<sup>a</sup>Variance adjustment factor  $\hat{c} = 1.48$ .

<sup>b</sup> $\Delta\text{QAIC}_c$  = difference in QAIC<sub>c</sub> value from lowest valued model;  $w_i$  = AIC weight for model  $i$ ;  $k$  = number of model parameters.

TABLE 6. Weighted average estimates of multistate models for citril finches recaptured in La Bofia and La Vansa, 1991-99

Parameter	Area	Age	Year	$\hat{\theta}_a$	$SE(\hat{\theta}_a)$	95% Confidence interval	
						Lower	Upper
$\phi$	LaBofia	Adult		0.3525	0.0444	0.2652	0.4396
		Juvenile		0.2797	0.0499	0.1817	0.3776
	La Vansa	Adult		0.4151	0.0358	0.3448	0.4853
		Juvenile		0.3362	0.0546	0.2290	0.4433
$p$	La Bofia		1992	0.1229	0.0631	-0.0008	0.2467
			1993	0.1602	0.0588	0.0448	0.2756
			1994	0.4064	0.1187	0.1735	0.6391
			1995	0.2929	0.0939	0.1086	0.4771
			1996	0.1262	0.0515	0.0251	0.2272
			1997	0.3660	0.1255	0.1199	0.6120
			1998	0.0770	0.0415	-0.0044	0.1583
		1999	0.2393	0.0931	0.0567	0.4218	
	LaVansa		1992	0.0434	0.0305	-0.0164	0.1032
			1993	0.1578	0.0407	0.0778	0.2377
			1994	0.0873	0.0236	0.0409	0.1337
			1995	0.2885	0.0587	0.1733	0.4035
			1996	0.1164	0.0235	0.0701	0.1626
			1997	0.1664	0.0384	0.0911	0.2417
		1998	0.0908	0.0279	0.0360	0.1456	
	1999	0.0729	0.0268	0.0202	0.1255		
$\psi$	BV	Adult		0.1770	0.0576	0.0639	0.2900
		Juvenile		0.3754	0.0978	0.1836	0.5672
	VB	Adult		0.0343	0.0133	0.0081	0.0604
		Juvenile		0.0907	0.0347	0.0225	0.1588

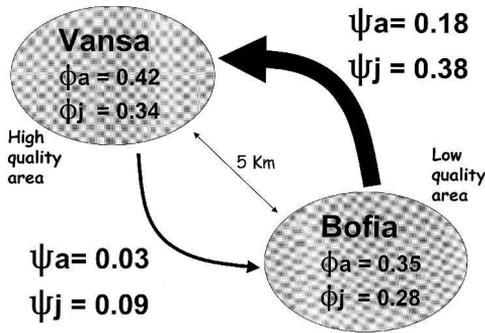


FIG. 2. Schematic representation of metapopulation survival and movement parameters for citril finches at La Bofia and La Vansa localities. ‘a’ refers to adult birds and ‘j’ to juveniles.

between sites, with overall higher movement between La Bofia and La Vansa than in the reverse direction; the highest rates of movement were for juveniles from La Bofia to La Vansa ( $0.38 \pm 0.10$ ) and the lowest for adults moving from La Vansa to La Bofia ( $0.03 \pm 0.01$ ) (Table 6, Fig. 2).

TABLE 7. Evaluation of multistratum models incorporating time-specific covariates for citril finches recaptured 1991–99 in La Bofia and La Vansa<sup>a,b,c</sup>

Model	$\Delta\text{QAIC}_c$	$w_i$	$k$
$\phi(\text{area} + \text{age} + \text{bp})p(\text{area}^*t)\psi(\text{area} + \text{age})$	0.00	0.318	24
$\phi(\text{area} + \text{age} + \text{temp} + \text{ppt})p(\text{area}^*t)\psi(\text{area} + \text{age})$	0.67	0.227	24
$\phi(\text{area} + \text{age} + \text{bp} + \text{mp})p(\text{area}^*t)\psi(\text{area} + \text{age})$	1.39	0.158	24
$\phi(\text{area} + \text{age} + \text{temp} + \text{ppt} + \text{bp})p(\text{area}^*t)\psi(\text{area} + \text{age})$	2.36	0.098	25
$\phi(\text{area} + \text{age} + \text{temp} + \text{ppt} + \text{mp} + \text{bp})p(\text{area}^*t)\psi(\text{area} + \text{age})$	3.04	0.070	26
$\phi(\text{area} + \text{age} + \text{bp} + \text{mp})p(\text{area}^*t)\psi(\text{area} + \text{age} + \text{bp} + \text{mp})$	3.39	0.058	26
$\phi(\text{area} + \text{age} + \text{temp} + \text{ppt})p(\text{area}^*t)\psi(\text{area} + \text{age} + \text{temp} + \text{ppt})$	3.86	0.046	26
$\phi(\text{area} + \text{age} + \text{bp} + \text{mp})p(\text{area}^*t)\psi(\text{area} + \text{age} + \text{temp} + \text{ppt} + \text{bp} + \text{mp})$	6.27	0.014	28
$\phi(\text{area} + \text{age} + \text{temp} + \text{ppt} + \text{bp} + \text{mp})p(\text{area}^*t)\psi(\text{area} + \text{age} + \text{temp} + \text{ppt} + \text{bp} + \text{mp})$	7.85	0.006	30
$\phi(\text{area} + \text{age})p(\text{area}^*t)\psi(\text{area} + \text{age})$	8.78	0.004	22
$\phi(\text{area} + \text{age})p(\text{area}^*t)\psi(\text{area} + \text{age} + \text{temp} + \text{ppt})$	11.63	0.001	24

<sup>a</sup>Model parameters are annual survival ( $\phi$ ), capture ( $p$ ), and interstratum movement rates ( $\psi$ ). Predictors are area (La Bofia or La Vansa), age (adult or juvenile), black (bp) or mountain pine (mp) productivity, precipitation (ppt), and temperature (temp).

<sup>b</sup>Variance adjustment factor  $\hat{c} = 1.48$ .

<sup>c</sup> $k$  = number of model parameters;  $\Delta\text{QAIC}_c$  = difference above lowest corrected QAIC value;  $w_i$  = model weight based on  $\Delta\text{QAIC}_c$ .

TABLE 8. Model-averaged estimates of covariate effects for survival of citril finches recaptured 1991–99 in La Bofia and La Vansa

	$\hat{\beta}_a$	$SE(\hat{\beta}_a)$	95% Confidence interval	
			Lower	Upper
Intercept	−1.360	0.524	−2.386	−0.334
Age	0.549	0.197	0.163	0.935
Area	−0.344	0.207	−0.749	0.062
black pine	0.481	0.244	0.003	0.959
mountain pine	−0.314	0.371	−1.041	0.413
Precipitation	0.623	0.348	−0.060	1.306
Temperature	0.114	0.291	−0.456	0.685

Although there was a lack of strong indication in a time effect for either citril finch survival or movement, we did include environmental variables in analyses, in an effort to see whether these factors improved model fit over the constant parameter models. Our comparison of covariate models to model  $\phi(\text{area} + \text{age})p(\text{area}^*t)\psi(\text{area} + \text{age})$  revealed several covariate models as strong competitors, notably those including pine productivity, temperature, and precipitation as predictors of survival (Table 7). The relationship for pine productivity was weak and somewhat contradictory, with black pine positively and mountain pine negatively associated with survival. Of the environmental predictors, both precipitation and temperature appears positively related to survival, although the confidence intervals are wide in all cases (Table 8). These results, although suggestive of an effect of these factors, are thus inconclusive.

#### 4 Discussion

Spatial heterogeneity in ecological and genetic processes is widely recognized in recent years (Blondel & Lebreton, 1996). Our data on the citril finch demonstrate

an apparent relationship between environmental heterogeneity and survival rates, with birds at La Vansa locality, characterized by a moister and a higher abundance of the mountain pine, a protein enriched food supply (Pulliainen, 1974), and dandelion, with highly energetic seeds (Kendeigh & West, 1965), showing a better body condition and a higher survival rate than birds at La Bofia. The fact that the two localities are just 5 km away from each other emphasizes the small scale at which spatial heterogeneity, and hence metapopulations, may operate.

Both natal and breeding dispersal in citril finches between these two localities were asymmetric, with birds moving from the low-quality habitat (La Bofia) to the high-quality one (La Vansa), rather than the reverse. This is clearly the reverse of source-sink models (Pulliam, 1988; Dias, 1996), in which animals disperse from the high- to the low-quality habitats. Citril finch dispersal conforms more closely to an Ideal Free Distribution (Fretwell & Lucas, 1970), in which animals distribute themselves among the different patches according to their current quality. However, the fact that dispersal probability did not vary between years, that the good-quality locality consistently maintained a higher survival than the low-quality one, and the presence of a higher morphological variation and genetic pool in the good locality (Senar *et al.*, personal observations) suggests that the citril finch does not clearly conform to Ideal Free Distributions as outlined in models of Balanced (Doncaster *et al.*, 1997) or Neutral dispersal (Payne, 1991). Hence we propose a new model of dispersal, of 'sources & pools', in which animals consistently disperse from low to high quality localities, the high quality localities acting as pools of genetic variability. These dynamics may be maintained because of the high abundance and stability of productivity of the mountain pine (Génard & Lescourret, 1987), one of their main food sources, and which allows the birds at the high-quality habitat not to reach carrying capacity, and also because of the fact that the species is not territorial (Newton, 1972).

We additionally show, as generally recognized (Greenwood & Harvey, 1982), that dispersal is mainly an issue for juvenile birds, with adults showing high levels of site faithfulness. No sex bias in dispersal was detected, which is consistent with the opportunistic breeding habits of citril finches (Borras & Senar, 1991), for which neither sex is expected to benefit more from site-familiarity than the other; other species that breed opportunistically also show no sex-bias in dispersal (e.g. zebra finch *Taeniophygia guttata*, Zann & Runciman, 1994; greater flamingo *Phoenicopterus ruber*, Nager *et al.*, 1996).

### Acknowledgements

We are most grateful to Toni and Josep Cabrera, Xavier Colomer and other members of the Bages ringing group (GBA) for their help in the field, and Enrique Hernández and Joan Perramon for allowing us to trap birds in their properties. 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 grant BOS 2000-0141 to JCS. 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

- BACCETTI, N. & MÄRKI, H. (1997) Citril finch. In: W. J. M. HAGEMEIJER & M. J. BLAIR (Eds), *The EBCC Atlas of European Breeding Birds*, pp. 711 (London, T. & A. D. Poyser).
- BLONDEL, J. & LEBRETON, J. D. (1996) The biology of spatially structured populations: concluding remarks, *Acta Oecologica*, 17, pp. 687-693.
- BORRAS, A. & CABRERA, T. (1996) Crossbills *Loxia curvirostra* feeding on cypress seeds, *Butlletí Grup Català d'Anellament*, 13, pp. 53-55.
- BORRAS, A. & JUNYENT, F. (1993) *Vertebrats de la Catalunya Central*, pp. 1-319 (Manresa [Barcelona], Regió 7).
- BORRAS, A. & SENAR, J. C. (1991) Opportunistic breeding of the citril finch *Serinus citrinella*, *Journal für Ornithologie*, 132, pp. 285-289.
- BRANDL, E. & BEZEL, R. (1988) Body condition, sex ratio and breeding success in the citril finch, *Zoologischer Anzeiger*, 221, pp. 411-417.
- BROWNE, C., HINES, J. E., NICHOLS, J. D., POLLOCK, K. H. & HESTBECK, J. B. (1993) Capture-recapture studies for multiple strata including non-Markovian transitions, *Biometrics*, 49, pp. 1173-1187.
- BURNHAM, K. P. & ANDERSON, D. R. (1998) *Model Selection and Inference* (New York, Springer).
- CEBALLOS, P., MOLINA, J., FRANCO, A. & PALACIOS, B. (1984) *Manual del anillador*, pp. 1-129 (Madrid, Instituto Nacional para la Conservación de la Naturaleza—ICONA).
- CRAMP, S. & PERRINS, C. M. (1994) *The Birds of the Western Palearctic*, Vol. VIII (Oxford, Oxford University Press).
- DIAS, P. C. (1996) Sources and sinks in population biology, *Trends in Ecology and Evolution*, 11, pp. 326-330.
- DONCASTER, C. P., CLOBERT, J., DOLIGEZ, B., GUSTAFSSON, L. & DANCHIN, E. (1997) Balanced dispersal between spatially varying local populations: an alternative to the source-sink model, *The American Naturalist*, 150, pp. 425-445.
- FRETWELL, S. D. & LUCAS, H. L. (1970) On territorial behavior and other factors influencing habitat distribution in birds, *Acta Biotheoretica*, 19, pp. 16-36.
- GÉNARD, M. & LESCOURRET, F. (1987) The Common Crossbill *Loxia curvirostra* in the Pyrenees: some observations on its habitats and on its relations with conifer seeds, *Bird Study*, 34, pp. 52-63.
- GREENWOOD, P. J. & HARVEY, P. H. (1982) The natal and breeding dispersal of birds, *Annual Review of Ecology and Systematics*, 13, pp. 1-21.
- GUTIERREZ, E. (1991) Climate tree-growth relationships for *Pinus uncinata* Ram. in the Spanish pre-Pyrenees, *Acta Oecologica*, 12, pp. 213-225.
- HANSKI, I. (1999) *Metapopulation ecology* (Oxford, Oxford University Press).
- KENDEIGH, S. C. & WEST, G. C. (1965) Caloric values of plant seeds eaten by birds, *Ecology*, 46, pp. 553-555.
- MCCLURE, E. (1984) *Bird Banding* (Pacific Grove, CA, Box Wood Press).
- MCPEEK, M. A. & HOLT, R. D. (1992) The evolution of dispersal in spatially and temporally varying environments, *American Naturalist*, 140, pp. 1010-1027.
- NAGER, R. G., JOHNSON, A. R., BOY, V., RENDON-MARTOS, M., CALDERON, J. & CEZILLY, F. (1996) Temporal and spatial variation in dispersal in the greater flamingo (*Phoenicopterus ruber roseus*), *Oecologia*, 107, pp. 204-211.
- NEWTON, I. (1972) *Finches* (London, Collins).
- PAYNE, R. B. (1991) Natal dispersal and population structure in a migratory songbird, the indigo bunting, *Evolution*, 45, pp. 49-62.
- PINILLA, J. (Ed) (2000) *Manual para el anillamiento científico de aves* (Madrid, SEO/Bird Life & Oficina Anillamiento).
- PRADEL, R. (1996) Animal dispersal within subdivided populations: an approach based on monitoring individuals, *Acta Oecologica*, 17, pp. 475-483.
- PULLIAINEN, E. (1974) Winter nutrition of the common crossbill (*Loxia curvirostra*) and the pine grosbeak (*Pinicola enucleator*) in northeastern Lapland in 1973, *Annales Zoolgiste Fennici*, 11, pp. 204-206.
- PULLIAM, H. R. (1988) Sources, sinks, and population regulation, *The American Naturalist*, 132, pp. 652-661.
- SCHWARZ, C. J. & ARNASON, A. N. (1990) Use of tag-recovery information in migration and movement studies, *American Fisheries Society Symposium*, 7, pp. 588-603.
- SCHWARZ, C. J., SCHWEIGERT, J. F. & ARNASON, A. N. (1993) Estimating migration rates using tag-recovery data, *Biometrics*, 49, pp. 177-193.

- SLATKIN, M. (1985) Gene flow in natural populations, *Annual Review of Ecology and Systematics*, 19, pp. 393-430.
- SVENSSON, L. (1992) *Identification guide to European Passerines* (Stockholm, L. Svensson).
- WHITE, G. C. & BURNHAM, K. P. (1999) Program MARK—survival estimation from populations of marked animals, *Bird Study*, 46 (Suppl.), pp. 120-139.
- ZANN, R. & RUNCIMAN, D. (1994) Survivorship, dispersal, and sex-ratios of zebra finches, *Taeniopygia guttata*, in Southeast Australia, *Ibis*, 136, pp. 136-146.