Regulation of local bird populations: Deeper insights from integrated population models

Inauguraldissertation
der Philosophisch-naturwissenschaftlichen Fakultät
der Universität Bern

vorgelegt von

Fitsum Abadi Gebreselassie
aus Äthiopien

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Contents

1

Introduction

1.1 Introduction

Population size of many wildlife species has declined worldwide in recent years (Pimm and Raven 2000). Demographic models are one of the tools, which play an important role in identifying the cause of population declines and guide management decisions in the field of conservation biology (Caughley 1994, Williams et al. 2002, Norris 2004). This is because the demographic mechanisms (survival, reproduction, immigration, and emigration) causing population declines can be identified and further the relationship between these quantities and stochastic as well density dependent factors can be studied.

Three main approaches have for long been widely used to study population dynamics of wildlife species. The first approach focuses on the population growth rate, which is a key quantity for most ecological questions. Population growth rate is typically estimated using long-term time series data of population size (Coulson et al. 2000, Sibly and Hone 2002). Here the overall effect of both stochastic and density dependent factors on the population growth rate can easily be assessed. However, the main drawbacks are, first, that the demographic mechanism causing changes in population size remain unknown. This is because both stochastic and density dependent factors do not have a direct influence on the population growth rate, but rather on demographic parameters. Second, the time series data are rarely free of observation error and this is a problem in particular when the relationship between population growth rate and density is studied. If the error is large and not accounted for, it may show spurious density dependence at the population level (Shenk et al. 1998, Freckleton et al. 2006).

The second approach focuses on the estimation and modeling of demographic parameters. In many species, fecundity can easily be determined based on the counted number of offspring if the probability of breeding is high (Sandercock 2006). Estimation of survival probabilities relies widely on the analysis of capture-recapture data (i.e. data on individually marked animals) and ring-recovery data using the well known Cormack-Jolly-Seber (CJS) models (Lebreton et al. 1992, Catchpole et al. 1998). Great advancement and extension of statistical methods for the analysis of capture-recapture data have been made in recent years. Pradel (1996) and Link and Barker (2005) incorporated recruitment parameters in the Jolly Seber model. Despite these developments, methods to estimate other demographic parameters such as immigration and emigration rates are less developed (Nichols and Pollock 1990, Burnham 1993, Peery et al. 2006, Schaub et al. 2006, O'Hara et al. 2009, Reynolds et al. 2009). In most studies, immigration and emigration are assumed to be negligible. This assumption is fairly justified if the study is conducted at large spatial scales (Baillie and Schaub 2009). In case of capture-recapture studies, emigration is accounted for in the estimate of apparent survival probability (Lebreton et al. 1992). The problem remains how to estimate immigration, irrespective of the analytical framework. Generally, the difficulty of obtaining direct observational data makes estimation of these two parameters more difficult and challenging.

The third approach focuses on the combined analysis of time series (population count) and demographic data in an ad hoc fashion. First, the population growth rate is estimated from the population count data. Next, demographic parameters such as survival and fecundity are estimated from the available data and then used as an input in population projection (Leslie) matrices (Caswell 2001). Comparison is then made between the population growth rate derived from projection matrices and the one obtained from the time series data. Sensitivity and elasticity analyses of the population growth rate to changes in demographic parameters can also be performed. However, this approach has a number of drawbacks: (i) there is no formal way to account for the uncertainty in demographic parameters, (ii) unless information about all demographic parameters is included (e.g. immigration), population growth rates derived from Leslie matrices are underestimated, (iii) it is inefficient as it does not use or fully integrate information about demographic parameters.

Recently, a very promising and flexible approach that combines different sources of demographic data to modeling the population dynamics of wildlife species has been developed (Besbeas et al. 2002). This newly developed method called "integrated population models" involves the use of state-space models to describe the population count data. A state equation describes population changes as a consequence of the underlying demographic parameters, and an observation process accounts for the observation error in the population count (Besbeas et al. 2002, Brooks et al. 2004, Schaub et al. 2007). Next, under the assumption of independence, other demographic parameters can be combined with population count data and form the likelihood of integrated population models, which is the basis for inference.

Empirical studies have shown the benefits of integrated population models. The model allows the estimation of demographic parameters with improved precision. This increases the power to detect temporal variation between demographic parameters and environmental covariates. It allows estimation of demographic parameters that are unidentifiable from a single source (Besbeas et al. 2002). For instance, fecundity can be estimated by combining population counts and capture-recapture data otherwise non-identifiable from either of the data sets. The method is also very useful in estimating demographic parameters from limited data sets (Schaub et al. 2007, Veran and Lebreton 2008). Estimation and modeling of demographic parameters from various pieces of demographic data using integrated population models offers great potential in conservation/ecological studies as diagnosis and management actions are often based on incomplete and sparse data.

1.2 Aims of the thesis

Although the integrated population model is a very powerful and promising tool, its development has just begun. The focus of this thesis is therefore to assess the performance of integrated population models with respect to different statistical properties, and to develop further the model to address key ecological questions. The specific objectives are categorized into four parts. The first three parts focus on the methodological development, and the last part focuses on its application to get insight into the dynamics of two threatened species.

First, the performance of integrated population models is little known, especially with respect to a possible violation of the basic assumption of independence of the model. Further, the bias, and precision of parameter estimates obtained from this model were not thoroughly assessed so far. This PhD thesis is trying to fill this gap in knowledge. Thus, using extensive simulations, the bias, precision and accuracy of parameter estimates must be evaluated. The impact of the violation of the assumption of independence in the precision of parameter estimates should also be investigated. It is often the case that adequate sample size is lacking in wildlife studies and therefore the benefits from integrated population models in comparison to the existing methods under varying sample size have to be assessed as well.

Second, the model is often used to estimate apparent survival probability and fecundity (Besbeas et al. 2002). This study was conducted at large spatial scales and hence immigration and emigration were almost negligible. However, in small scale studies or geographically open populations, emigration and immigration need to be estimated in addition. While emigration is included in capture-recapture data (Lebreton et al. 1992), immigration is not. Thus, in the present thesis the integrated population model is extended to study the dynamics of geographically open populations and hence all demographic parameters (survival, fecundity, and immigration) as well as population growth rate can be estimated.

Third, another interesting problem that can be exploited using integrated population models is density-dependence. Density-dependence is an important ecological concept which has practical relevance in applied ecology. A problem that often arises in studying density-dependence is that the population counts are rarely exact. The effect of density is also often investigated at the population level or looked at via a single demographic parameter (e.g. either survival probability or fecundity). This makes our inference limited. Using integrated population models, the density-dependence will be assessed both at the population and demographic levels simultaneously while accounting for observation error. Consequently, the demographic mechanism causing density-dependence can be identified.

Fourth, the integrated population model is going to be applied to study the population dynamics of hoopoes and wrynecks, two threatened species in Switzerland. The findings will help refining current conservation guidelines.

1.3 Structure of the thesis

The structure of the thesis is as follows: Chapter 2 focuses on the assessment of the integrated population model with respect to statistical properties and violation of the basic assumption of independence of the model. In chapter 3, the model is further developed to estimate a key demographic parameter: immigration rate. Chapter 4 focuses on assessments of density-dependence both at the population and demographic level in a coherent fashion. In chapter 5, the integrated population model is applied to study the population dynamics of two endangered species, hoopoes and wrynecks, in Central Europe. Chapter 6 emphasizes the main contributions of this thesis and presents possible future directions of the development of integrated population models. Supporting information for each chapter are provided in Appendix A. I have also been involved in two other projects of habitat selection modeling, which were besides the mainstream of this PhD work. The corresponding manuscripts are provided in Appendix B.

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2

An assessment of integrated population models: bias, accuracy, and violation of the assumption of independence

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2.1 Abstract

Understanding population dynamics requires accurate estimates of demographic rates. Integrated population models combine demographic and survey data into a single, comprehensive analysis and provide more coherent estimates of vital rates. Integrated population models rely on the assumption that different data sets are independent, which is frequently violated in practice. Moreover, the precision that can be gained using integrated modeling compared to conventional modeling is only known from empirical studies. The present study used simulation methods to assess how the violation of the assumption of independence affects the statistical properties of the parameter estimators. Further, the gains in precision and accuracy from the model were explored under varying sample sizes. For capture-recapture, population survey and reproductive success, we generated independent and dependent data which were analyzed with integrated and conventional models. We found only a minimal impact of the violation of the assumption of independence on the parameters estimates. Furthermore, we observed an overall gain in precision and accuracy when all the three data sets were analyzed simultaneously. This was particularly pronounced when the sample size was small. These findings contribute to clearing the way for the application of integrated population models in practice.

Key words: Accuracy; Bayesian; capture-recapture; dependent; independent; individual-based model; Leslie matrix model; population survey data; reproductive success; state-space model

2.2 Introduction

The dynamics of populations are essentially driven by the variation in the number of surviving and newly recruited individuals. To understand the demographic mechanisms that drive population trajectories, it is thus essential to accurately estimate vital rates. This is indeed crucial for effective species management and conservation (Williams et al. 2002, Norris 2004). As the study of the dynamics of wildlife populations usually requires detailed demographic data, researchers often collect different kind of data such as capture-recapture, ring or tag recovery from dead animals, fecundity, and/or population survey data. Traditionally, these data sets are analyzed individually while studying demographic processes. However, separate analyses will lead to more uncertainty and bias in the estimated demographic rates, in particular if sample size is small (Doak et al. 2005).

A promising, recently developed tool to analyze different sources of data simultaneously is *integrated population modeling* (Besbeas et al. 2002, 2003, Buckland et al. 2004, Thomas et al. 2005). The core of this model is a projection matrix parameterized with demographic parameters, which maps population sizes of different age or stage classes from one year to the next. Typically, part of the demographic information comes from capture-recapture type of data, while the information about population size is drawn from population surveys. Integrated population models have successfully been used to jointly analyze ring-recovery and population survey data (Besbeas et al. 2002, Brooks et al. 2004), capture-recapture and population survey data (Gauthier et al. 2007), capture-recapture, population survey, and productivity data (Schaub et al. 2007) as well as estimates of abundance and data on incidental mortality in fisheries (Hoyle and Maunder 2004). Empirical studies have shown that integrated population models deliver demographic estimates with a higher precision than separate, conventional models (Besbeas et al. 2003). For estimating some parameters that are especially difficult to evaluate and cannot be retrieved from single analyses (e.g. fecundity from either capture-recapture or population survey data), they even constitute the only feasible solution (Besbeas et al. 2002, Schaub et al. 2007). This is due to the fact that the information about all demographic processes is included in the population survey data, and with the integrated model the entire information can be extracted. Eventually, it is the combination of different, independent information for a given parameter (e.g. survival probability determined through population survey and capture-recapture data) that leads to an increase in precision.

Although integrated population models are very appealing in principle and potentially very useful, a thorough assessment of their accuracy for parameter estimation has never been performed. Moreover, the model relies on the critical assumption that the different data sets that are jointly analyzed are independent from each other. This assumption must be met because the joint likelihood of the model is calculated as the product of the likelihoods of the different data sets. It is currently little known whether the model performs well if this assumption is violated. Besbeas et al. (2009) combined ring-recovery and census data to test this assumption and concluded that the effect of dependency is a serious issue. In practice, however, it is often easier to obtain capture-recapture than ring-recovery data. It would thus be worth assessing the violation of the assumption in integrated models combining capture-recapture with other sources of demographic information such as data on population surveys and reproductive success.

The aim of this paper is to make a thorough assessment of the performance of integrated population models using extensive simulations. To study parameter performance we considered the life history of a short-lived species and used three different classes of sample size for evaluating the behavior of this model to variation in sample size. Generally, we expect a greater benefit of the integrated population model at small than at large sample sizes. We addressed the following three main issues considering different sample sizes.

First, we assessed the magnitude of the improvement in the estimates of demographic rate in the integrated population model compared to conventional, separate analyses. Second, we evaluated the accuracy of the demographic parameters for which no empirical data are available and can thus solely be extracted from population survey data. Third, we assessed the extent to which the violation of the assumption of data sets inter-independency affects the accuracy of the estimated parameters. In the strict sense of the term, this assumption of independence requests that the different data sets have no individuals in common, which could be achieved either by sampling individuals from different populations or by sampling different individuals from the same population. The former further requires that the dynamics of the different populations under scrutiny is identical. The latter can be difficult to achieve in practice, especially when data stem from small populations as is often the case in conservation science; the likelihood of sampling the same individual several times would be high under these circumstances. Fulfilling these assumptions of data sets independency would thus be particularly challenging precisely when the benefits of integrated modeling would be expected to be greatest, i.e. in small and local populations for which a clear demographic diagnosis (e.g. population trend, viability analysis) is essential.

2.3 Methods

We examined the performance of the integrated population model with simulations. We first created populations using age-structured individual-based population models. We simulated each individual separately such that its complete life sequence was known. Second, we sampled from the population three different types of data (capture-recapture, productivity, population survey) under various degrees of independence and with different sample sizes. Third, we analyzed these data under two different kinds of integrated population models (all three types of data above versus using only capture-recapture and population survey data) and with separate analyses considering only capture-recapture data or only fecundity data. We repeated these steps 500 times. Next we describe each of the three steps in more detail.

2.3.1 Creation of the life-history in the population and the data sets

To create the populations from which data were then sampled we considered the life history of a short-lived bird species such as the hoopoe (*Upupa epops*). We assumed geographic closure (no immigration or emigration), constant survival probabilities and fecundity and a pre-breeding census. We further assumed two age classes (1 and 2+ years), with reproduction starting from age 1, and the simulation only included female animals. Fecundity (average number of females produced per female, f) was set at 2.6, juvenile survival (survival from birth until 1 year old, ϕ_{juv}) at 0.2 and adult survival (annual survival after 1 year of age, ϕ_{ad}) at 0.5. The expected number of individuals in the two age classes at time $t+1$ is given by the product of the population vector (containing the number of individuals) in year t and the projection matrix (Caswell 2001, Buckland et al. 2007) as

$$E(\boldsymbol{N}_{t+1}|\boldsymbol{N}_t) = \begin{pmatrix} f\phi_{juv} & f\phi_{juv} \\ \phi_{ad} & \phi_{ad} \end{pmatrix} \begin{pmatrix} N_{1,t} \\ N_{2+,t} \end{pmatrix} \tag{2.1}$$

where $N_{1,t}$ is the number of 1 year old individuals at time t and $N_{2+,t}$ is the number of individuals older than 1 year at time t.

Using this population matrix model and an initial population size of 300 individuals per age group, we carried out the following steps to create the life history of each individual in the population for 10 years:

1. Select an individual from the initial population or from the produced offspring (juvenile) at time t.
2. If the individual is at least one year old, generate the number of offspring produced at time t by drawing a random number from a Poisson distribution with parameter equal to the fecundity (f). If an individual is a juvenile, move to step 3.
3. Determine whether the individual survives from year t to $t+1$ by drawing a random number from a Bernoulli distribution with parameter equal to the age-specific survival probability (ϕ_{juv} or ϕ_{ad}).
4. If the individual survives, it moves to the next time $t+1$ and to the next age class

if it is not yet in the oldest age class. Repeat steps 2 to 3 until it dies or until the end of the study period.

5. If the individual does not survive, pick the next individual and repeat steps 2 to 5.

Thus, for each year we stored information about the state of an individual (dead or, if alive, in which of the considered age classes it is) and the number of newborn it has produced. The population reaches a stable age distribution very quickly, but we discarded the first five years to avoid transition effects of the initial conditions. Examples of the life histories of three individuals, along with the stored information, are provided in Figure A1.1 in Appendix A.

To obtain completely independent samples, we randomly selected individuals in such a way that none of them appeared in common in any of the three data types. To create highly dependent samples, we selected a random sample of individuals at the beginning and created samples for the three different data types using only these individuals. To create three levels of sample size the number of randomly selected individuals was varied (small: 200 individuals; medium: 1000 individuals; large: 2000 individuals). Sample size may differ between iterations, because not all individuals that were initially considered were marked or surveyed. We stored the sample size for each iteration and also the number of identical individuals that are selected in the three different data sets.

Capture-recapture data - We created individual capture-recapture histories using the individuals that were subject to capture-recapture sampling. For each year and when a specific individual was alive, we determined by a Bernoulli random number, with parameter equal to the capture probability, whether or not the individual was captured. The probability of initial capture was set at 0.76 for juveniles and 0.60 for adults, and the probability of recapture was set at 0.60.

Reproductive success data - We created reproductive success data using the individuals that were subject to sampling for this data type. For each year when an individual was reproducing, we generated a random number from a Bernoulli distribution with probability equal to 0.9 to determine whether its reproductive success was recorded.

Population survey data - We created population survey data using the individuals that were subject to sampling of this data type. For each breeder and year we generated a random number from a Bernoulli distribution with probability equal to 0.9 and determined whether it was included in the count. We then stored the number of detected breeders in each year.

2.3.2 Data analysis

We performed three different analyses for the sampled data. First, we analyzed all data types simultaneously using an integrated population model (IPM3); second, we analyzed only the capture-recapture and the population survey data simultaneously in another integrated population model (IPM2); and third, we analyzed the capture-recapture data and fecundity data separately with a Cormack-Jolly-Seber (CJS) model and a Poisson regression model, respectively. We first describe the likelihood of each single data set and then show how the integrated likelihoods are created.

Likelihood for the capture-recapture (CR) data - We summarized the capture-recapture data in matrix m_{t_1,t_2}, $t_1 = 1, 2, \ldots, T-1$, $t_2 = t_1+1, \ldots, T+1$, where m_{t_1,t_2} denotes the number of individuals released at time t_1 and subsequently recaptured for the first time at time t_2 for $t_2 \leq T$, $m_{t_1,T+1}$ denotes the number of individuals never recaptured after being released in year t_1, and T denotes the number of capture occasions (m-array; Burnham et al. 1987). Then, each row of the data matrix is of a multinomial form and the likelihood (L) can be calculated as

$$L_{CR}(\boldsymbol{m}|\phi_{juv}, \phi_{ad}, p) \propto \prod_{t_1=1}^{T-1} \prod_{t_2=t_1+1}^{T} \pi_{t_1,t_2}^{m_{t_1,t_2}} \prod_{t_1=1}^{T-1} \chi_{t_1}^{(R_{t_1} - \sum_{t_2=t_1+1}^{T} m_{t_1,t_2})} \tag{2.2}$$

where R_{t_1} denotes the number of animals released in year t_1 and $\chi_{t_1} = 1 - \sum_{t_2=t_1+1}^{T} \pi_{t_1,t_2}$; π_{t_1,t_2} denotes the cell probability of m_{t_1,t_2}, which is a function of survival and recapture probabilities. We defined π_{t_1,t_2} as follows:

$$\pi_{t_1,t_2} = \begin{cases} \phi_{juv} p (\phi_{ad}(1-p))^{(t_2-t_1-1)}, & \text{for individuals released as juveniles} \\ \phi_{ad} p (\phi_{ad}(1-p))^{(t_2-t_1-1)}, & \text{for individuals released as 1yr old or 2yr+} \end{cases} \tag{2.3}$$

where $t_1 = 1,2,\ldots,T-1$, $t_2 = t_1+1,\ldots,T$ and p is recapture probability. This is the well known Cormack-Jolly-Seber model (see Lebreton et al. 1992).

Likelihood for the population survey (PS) data - We used a state-space model to describe the population survey data (Besbeas et al. 2002, de Valpine and Hastings 2002, Buckland et al. 2004). The state process models the true, but unknown population trajectory under the population matrix model defined by eqn 2.1, and the observation process links the observed population counts to the true population sizes assuming an observation error.

We describe the population trajectory (state process) using Poisson(Po) and binomial(Bin) distributions as

$$N_{1,t+1} \sim Po((N_{1,t} + N_{2+,t}) f \phi_{juv}) \tag{2.4}$$

and

$$N_{2+,t+1} \sim Bin(N_{1,t} + N_{2+,t}, \phi_{ad}) \tag{2.5}$$

The likelihood of the state process is a product over Poisson and binomial densities and denoted by $L_{SY}(\mathbf{N}|\phi_{juv}, \phi_{ad}, f)$, where $\mathbf{N} = (\mathbf{N}_1, \mathbf{N}_{2+})'$ is a vector of the true population sizes.

The observation process expresses the population indices actually observed at time t (y_t) conditional on the state process. Here, the observation equation is given as $y_t = (1,1) \times (N_{1,t}, N_{2+,t})' + \eta_t$. The term η_t accounts for the observation error and we assume that $\eta_t \sim N(0, \sigma_y^2)$. The variance ($\sigma_y^2$) was small enough to ensure that negative values for the number of animals (y_t) were not sampled. Thus, the likelihood of the observation process, denoted by $L_{OB}(y|\mathbf{N}, \sigma_y^2)$, is a product over normal densities.

Then, the corresponding likelihood of the population survey data is given by

$$L_{PS}(y|\mathbf{N}, \phi_{juv}, \phi_{ad}, f, \sigma_y^2) = L_{OB}(y|\mathbf{N}, \sigma_y^2) \times L_{SY}(\mathbf{N}|\phi_{juv}, \phi_{ad}, f) \tag{2.6}$$

Likelihood for reproductive success (RS) data - We assumed that the number of newborn females in year t (J_t) follow a Poisson distribution with parameter written as function of the number of reproducing females (N_t) and the fecundity (f), hence, $J_t \sim$Po($N_t f$). Thus, the likelihood is a product over Poisson densities and denoted as $L_{RS}(J|f)$.

Likelihoods of the integrated models - Assuming the different data types are independent, the joint likelihood of the integrated models is constructed as a product of the single data likelihoods (Besbeas et al. 2002, 2003, Brooks et al. 2004). That is, for IMP3 it is

$$\begin{aligned} &L_{IPM3}(\boldsymbol{m}, \boldsymbol{y}, J | \phi_{juv}, \phi_{ad}, p, f, \boldsymbol{N}, \sigma_y^2) \\ &\qquad = L_{CR}(\boldsymbol{m} | \phi_{juv}, \phi_{ad}, p) \times L_{PS}(\boldsymbol{y} | \boldsymbol{N}, \phi_{juv}, \phi_{ad}, f, \sigma_y^2) \times L_{RS}(J | f) \end{aligned} \tag{2.7}$$

and for IPM2 it is

$$\begin{aligned} &L_{IPM2}(\boldsymbol{m}, \boldsymbol{y} | \phi_{juv}, \phi_{ad}, p, f, \boldsymbol{N}, \sigma_y^2) \\ &\qquad = L_{CR}(\boldsymbol{m} | \phi_{juv}, \phi_{ad}, p) \times L_{PS}(\boldsymbol{y} | \boldsymbol{N}, \phi_{juv}, \phi_{ad}, f, \sigma_y^2) \end{aligned} \tag{2.8}$$

All models were fitted within the Bayesian framework, specifying non-informative priors for all model parameters. Specifically, we used the beta distribution ($\beta(1,1)$) for the survival and recapture parameters, an inverse gamma with parameters 0.0001 and 0.0001 for the variance (σ_y^2), a normal distribution with mean 100 and variance 10^4 truncated to positive values for age-specific population sizes, and a uniform distribution between 0 and 10 for fecundity parameter. We first ran three Markov chain Monte Carlo (MCMC) chains (Gilks et al. 1996) in parallel for 10,000 iterations, discarding the first 3,000 iterations. The values of all parameters were less than 1.01, suggesting that convergence had been reached (Brooks and Gelman 1998). We then ran 100,000 iterations with the first 30,000 as burn-in and thinned so that every 70^{th} observation was retained.

We simulated 500 repetitions and calculated relative bias, precision (standard error), and accuracy (mean squared error) for all demographic parameters. The data were generated with R 2.6.1 (R Development Core Team 2005) and the analyses were performed in WinBUGS (Lunn et al. 2000) using the R2WinBUGS package (Sturtz et al. 2005). The R and WinBUGS codes used for simulating the data and fitting the models are available in `http://www.esapubs.org/archive/ecol/E091/001/`.

2.4 Results

The average sample sizes across the 500 simulations for the independent and the dependent data are provided in Table 2.1. Between 72% and 94% of all individuals occurred in two or three data sets in the dependent data, indicating strong data dependency.

Table 2.1: *The average number of unique individuals involved in data sampling, for different sample sizes and independence.*

		Independent			Dependent		
Size	Type of data	CR	RS	PS	CR	RS	PS
Small (200 ind.)	CR	23	-	-	23	22	22
	RS	-	30	-	-	30	29
	PS	-	-	31	-	-	30
Medium (1000 ind.)	CR	156	-	-	155	147	147
	RS	-	202	-	-	204	192
	PS	-	-	203	-	-	204
Large (2000 ind.)	CR	310	-	-	309	293	293
	RS	-	407	-	-	406	382
	PS	-	-	407	-	-	405

Notes: The three data types are: CR, capture-recapture; RS, reproductive success; PS, population survey. The number in the diagonal shows the sample size of the corresponding data type; the off-diagonals contain the numbers of adults included in two data types.

Integrated versus independent analyses

Generally, integrated population models provided slightly more precise, less biased and more accurate parameter estimates compared to the separate analyses (Figure 2.1, Table A1.1 in Appendix A). As expected, the increase in precision and accuracy was more pronounced at small sample size. With medium or large sample sizes, the difference became minute. The increase in precision and accuracy, and the decrease in bias differed among demographic parameters. The benefit of the integrated analysis was slightly higher for juvenile survival than for adult survival, while for fecundity the precision and accuracy of the integrated analysis, which used the three data sets, was virtually similar to that of the separate analysis.

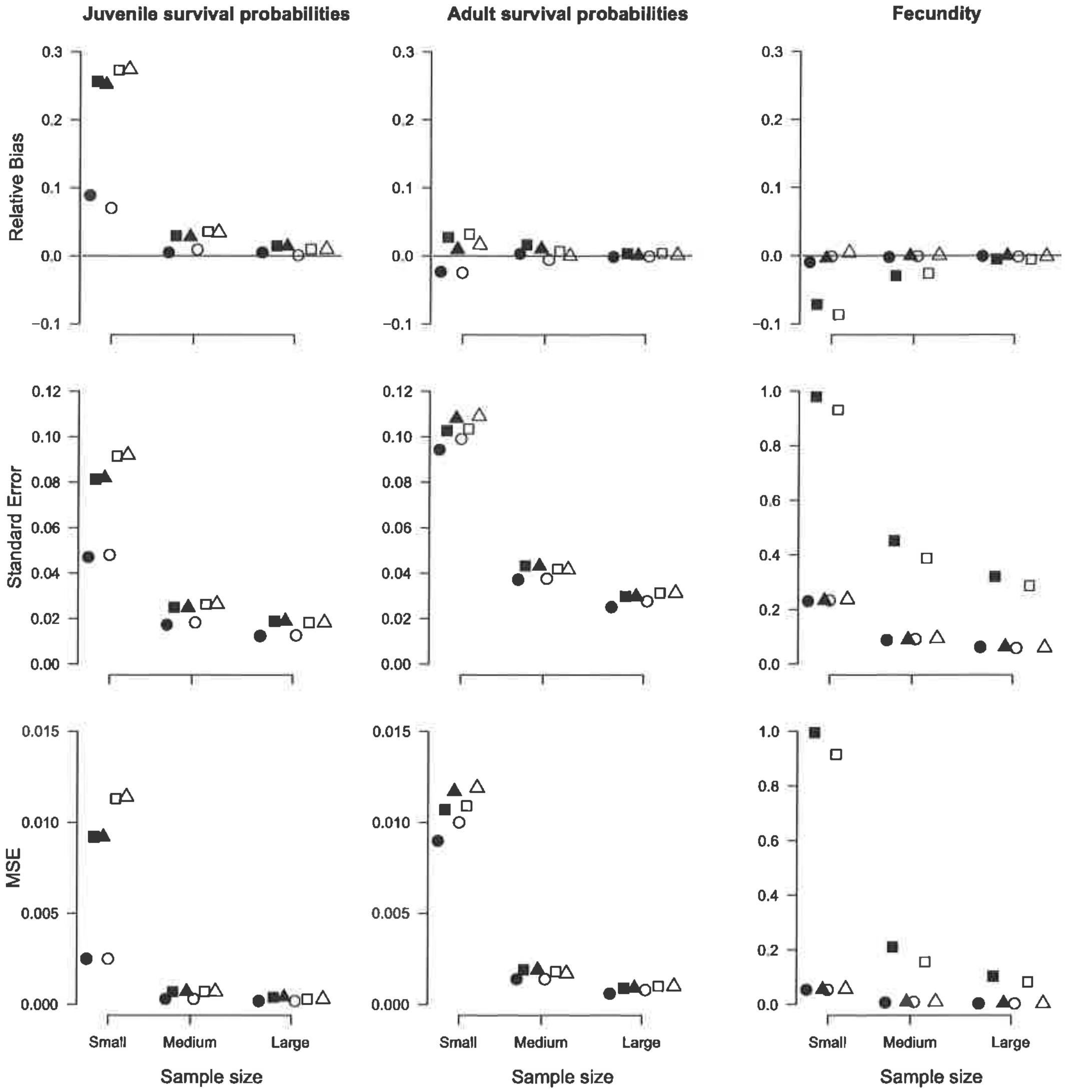

Figure 2.1: *Relative bias, standard error (precision) and mean squared error (MSE, accuracy) of juvenile and adult survival probabilities, and of fecundity, all as a function of sample size, estimated with different analyses. Estimates obtained with the integrated analyses are shown as circles (three data sets) and as squares (two data sets); estimates obtained with separate analyses are shown with triangles. Closed symbols represent independent data; open symbols represent dependent data.*

Differences between integrated analyses

The performance of the two integrated population models differed only slightly for the estimated survival probabilities for which explicit data were available (Figure 2.1, Table A1.1 in Appendix A). Still, the integrated population model that used all three types of data (IPM3) provided slightly less biased, more precise and accurate survival estimates than the model which only used two types of data (IPM2). The difference was slightly larger when sample size was small compared to when sample size was large. For fecundity, the difference between the two integrated population models was much more important: fecundity estimated with the integrated population model that used no explicit data for fecundity (IPM2) were clearly more biased, less precise and accurate compared to the estimates coming from the integrated population model that used explicit data on fecundity. As for the other parameters this strongly depended on sample size. If sample size was medium or large, then the performances of the two models were not very different.

Assumption of independence

Bias, precision, and accuracy of the parameter estimates originating from the independent and the dependent data were nearly the same, regardless of sample size (Figure 2.1, Table A1.1 in Appendix A). Accuracy for the independent data tended to be slightly higher than for the dependent data in case of small sample and almost the same with large sample size, indicating that the violation of the assumption of independence does not have a strong impact on the performance of the estimators.

2.5 Discussion

Using extensive simulations, we show that integrated population models performed better than separate analyses as the parameter estimates were more accurate and because integrated population models allow estimating parameters for which no explicit data were collected (Besbeas et al. 2005). Moreover, the violation of the assumption of independence had only minor consequences on the precision and accuracy of the parameter estimates. These are very encouraging results for the practical application of integrated population models(IPMs).

Empirical studies have stressed that the main advantages of integrated compared to separate analyses are that parameter precision is increased and provides estimates for parameters that cannot be estimated when using each data set in isolation. Our simulation study shows that integrated analyses provide more precise parameter estimates, but that the difference compared to separate analyses is slight only, even if sample size is low. These results are in agreement with the empirical findings of Besbeas et al. (2002) and Brooks et al. (2004). In their work, estimated precision of survival were slightly increased when coming from an integrated analysis (ring-recovery and census data) compared to when coming from a separate ring-recovery model. The reason for this only slight increase of precision is that most information about survival and fecundity comes from the capture-recapture and reproductive success data, respectively. Borysiewicz et al. (2009) demonstrated that the improvement in precision is much more pronounced for multi-site compared to single-site integrated population models. This suggests that the integration of additional information has an effect on parameter accuracy, when the content of information in the original data source is low. We expect therefore that the benefit is largest when complicated models with many parameters, as needed in ecological studies, are used. Increased precision of parameter estimates can be of importance if temporal patterns in the parameter estimates will be evaluated, because the power to detect patterns is enhanced. However, given the small increase in precision restricted basically to small data sets, it appeared that the gain of precision was an advantage of practical relevance only when data sets are small. Still, it is exactly in such small data sets, for instance stemming from localized and small populations of conservation concern, that we would be most likely to want to apply an integrated analysis.

By contrast, the possibility to be able to estimate additional demographic parameters is an important advantage of integrated compared to separate analyses (e.g. Besbeas et al. 2003, Schaub et al. 2007). Using an integrated analysis, our simulations showed that fecundity could be accurately estimated even if only capture-recapture data and population survey data are available. Accuracy very strongly increased with sample size. If the sample size was medium, the accuracy of the fecundity estimate was almost similar to that from separate analyses, regardless of whether data on fecundity were available. For demographic monitoring with limited financial resources our result suggests that sampling data on fecundity is not necessary provided that sample size of the other data is large enough. Using the simulations as performed in this paper allows one to identify the necessary sample size of different sources of data to find the most efficient monitoring strategy for the desired precision of parameter estimates.

It is currently not known whether other combinations of available information still allow estimating all relevant demographic parameters. For example, one might envision constructing an integrated population model when only population survey data and data on fecundity are available. However, because in that case no explicit data are available for two parameters (juvenile and adult survival), there may be more problems to get accurate estimates. Future studies might investigate the minimal data required to estimate demographic processes.

The violation of the assumption of independence does not appear to have strong effects on the parameter estimates. This was true despite the fact that the degree of dependence in our data was strong, with the majority of individuals appearing in all three or two data sets, and even if the sample size was low. This result is very important for the practical application of integrated population models, since in most cases individuals appear in several data sets. This means that samples from the same population can be used and hence it is less important to sample from different populations and to assume that their dynamics is the same. In this study, we specified high detection probabilities and this led to a strong dependency in the data. Had we specified lower detection probabilities, the degree of dependency would have been lower and hence less subject to the violation of the assumption of independence. A likely reason why the violation of the independence assumption did not had a strong impact on parameter accuracy is that most of the information about survival and fecundity originates from capture-recapture and fecundity data, respectively, and only little information about these parameter is taken from the survey data (Besbeas et al. 2009). Besbeas et al. (2009) showed that the accuracy of the parameter estimates decreased when there was a dependency between ring-recovery and census data. Unlike capture-recapture data, ring-recovery data do not dominate survey data to provide information about common parameters, and in this case the violation of the independence assumption has a stronger impact on parameter accuracy. It is possible to envision another, more extreme level of dependence. In our study we assumed that the different data sets were obtained independently from each other, but that individuals could be present in different data sets. One might consider that exactly the same data are exploited two or several times. For example, instead of conducting a separate population survey, the number of captured individuals derived from the capture-recapture data might be used as an index of population size. Although we have not studied this kind of dependence, we expect that in this case the consequences in terms of parameter performance would be serious.

We used a relatively simple model in our simulations, since one of the main goals was the assessment of the violation of the independence assumption and not the performance of differently complicated models. Moreover, the life history that we used and the type of data that we simulated reflect a frequent situation, at least in ornithological studies. However, since integrated population modeling is a very general and flexible framework, many more different scenarios could be envisioned (e.g. life history with delayed maturity, inclusion of density-dependence) and simulated, and we discuss few possible extensions. A frequent situation is time dependence in demographic parameters. We have conducted few simulations in this regard, and our preliminary findings indicate that the violation of the assumption of independence was not a serious concern in estimating time-dependent demographic parameters. In our study all individuals are assumed to have the same vital rates, but in reality vital rates differ individually. If individual variation is strong and not accounted for in the integrated analysis, we expect a greater effect of data dependence on the precision of the parameter estimates. Finally, capture-recapture data could be used to estimate population size (Schwarz and Seber 1999). It would thus be possible to use information about population size not only from the population surveys, but also from the capture-recapture data. In that case we would expect a greater effect of data dependence on the parameter estimates, because more common information stemming from two data sets are treated as independent.

To sum up, the findings of this study provide support for the use of integrated population model even if the assumption of independence is violated. Integrated population models give slightly more precise parameter estimates and allow estimating demographic parameters for which no specific data have been sampled. These properties are indeed important in assessing the status of wildlife populations and in identifying factors that affect their demography. We therefore expect that integrated population models will become frequently used in future.

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3

Estimation of immigration rate using integrated population models

Abadi, F., Gimenez, O., Ullrich, B., Arlettaz, R., and Schaub, M. (2010). *Journal of Applied Ecology*, **47**, 393-400.

3.1 Summary

1. The dynamics of many populations is strongly affected by immigrants. However, estimating and modeling immigration is a real challenge. In the past, several methods have been developed to estimate immigration rate but they either require either strong assumptions or combine in a piecewise manner the results from separate analyses. In most methods the effects of covariates cannot be modeled formally.

2. We developed a Bayesian integrated population model which combines capture-recapture data, population counts and information on reproductive success into a single model that estimates and models immigration rate, while directly assessing the impact of environmental covariates.

3. We assessed parameter identifiability by comparing posterior distributions of immigration rates under varying priors, and illustrated the application of the model with long term demographic data of a little owl *Athene noctua* population from

Southern Germany. We further assessed the impact of environmental covariates on immigration.

4. The resulting posterior distributions were insensitive to different prior distributions and dominated by the observed data, indicating that the immigration rate was identifiable. Average yearly immigration into the little owl population was 0.293 (95% credible interval 0.183 - 0.418), which means that ca 0.3 female per resident female entered the population every year. Immigration rate tended to increase with increasing abundance of voles, the main prey of little owls.

5. *Synthesis and applications*. The means to estimate and model immigration is an important step towards a better understanding of the dynamics of geographically open populations. The demographic estimates obtained from the developed integrated population model facilitate population diagnoses and can be used to assess population viability. The structure flexibility of the model should constitute a useful tool for wildlife managers and conservation ecologists.

Key-words: *Athene noctua;* Bayesian; capture-recapture; identifiability; population counts; reproductive success; survival; state-space model

3.2 Introduction

Immigration and emigration are important demographic processes which can have a strong impact on population dynamics (Ward 2005, Lampila et al. 2006, Schaub et al. 2006, Grøtan et al. 2009). In an attempt to fully understand the dynamics of a population, it is therefore important to be able to estimate and include these parameters into a population dynamical model. Knowledge of immigration and emigration is also essential for identifying whether a local population is a source or a sink (Pulliam 1988, Peery et al. 2006) which may be of interest in conservation and other management applications.

Existing methods can be used to estimate emigration rate by combining capture-recapture and dead recovery data (Burnham 1993, Reynolds et al. 2009). In most population studies where emigration cannot be directly estimated, it is accounted for in the estimate of apparent survival (function of mortality and permanent emigration), which is obtained from capture-recapture data (Lebreton et al. 1992). Unlike emigration, the rate of immigration is notoriously difficult to estimate. Consequently, relatively little is known about its role in population dynamics and about factors affecting its variability across space and time. The problem of estimating immigration stems from the difficulty of making direct observations: immigrants can only be distinguished from established individuals if all members of one of these groups are marked. Only in very intense studies, in which all individuals in the population are marked each year, can immigration be readily inferred from the number of unmarked individuals. However, such an intensive capture effort is very rarely applied because in natural conditions complete capture is usually not possible (Møller 2002, Grøtan et al. 2009). To date, several approaches have been used to deal with this problem. Key to all of them is the availability of capture-recapture data. However, some methods require additional demographic data which then need to be combined with capture-recapture data to estimate immigration rate.

Initially, immigration was inferred from direct observations of the movement of marked individuals between populations using multistate capture-recapture models (Spendelow et al. 1995). These methods solve the problem that not all individuals in the population are captured each year. However, immigrants can originate from very different populations that may be far away, and in practice it is almost impossible to mark individuals at all potential source populations. Therefore, this method usually results in an underestimation of the immigration rate.

Secondly, if all locally born individuals are marked each year and if a fraction of adults is captured each year, immigration can be estimated (O'Hara et al. 2009). Under this sampling protocol, it is clear that any unmarked individual in the population must be an immigrant, but owing to the imperfect capture of adults, it is not clear when they have immigrated. This latter problem can be solved by the application of the Jolly-Seber model (O'Hara et al. 2009). The critical requirement is that all young born in the population must be marked every year. This can only be achieved in rare situations.

Thirdly, immigration can be estimated if capture-recapture data are sampled under the robust design (Nichols and Pollock 1990). Here the population is sampled at least twice within short time each year, allowing the estimation of population sizes of young and adult individuals as well as their survival probabilities. By rearranging these quantities, the total number of immigrants can be estimated. The disadvantage of this approach is that this special sampling design is rarely applied due to the high sampling effort it requires.

Fourthly, immigration can be estimated if ordinary capture-recapture data of young and adults and data on the reproductive success are available (Cooch et al. 2001, Peery et al. 2006, Schaub et al. 2006). Pradel's (1996) temporal symmetry model applied to the capture-recapture data of the adults allows estimating population growth rate (λ) or total recruitment (f, immigration plus local recruitment). From the capture-recapture data, apparent juvenile (ϕ_{ju}) and adult (ϕ_{ad}) survival probabilities are estimated (Lebreton et al. 1992). Apparent survival probability is the joint probability to survive and to remain in the study population (i.e. a function of both mortality and permanent emigration). For species that start to reproduce in their first year of life, immigration rate (imm) can then be estimated either as $imm = f - b\phi_{ju}$ (Peery et al. 2006) or as $imm = \lambda - b\phi_{ju} - \phi_{ad}$ (Schaub et al. 2006), where b is the reproductive output. Similar calculations are possible for species with delayed start of reproduction (Cooch et al. 2001). Standard errors of the estimates are obtained using the delta method or by bootstrapping. Disadvantages of this method are that covariances between the parameters stemming from different data sets remain unknown and immigration rate is not treated as a model parameter but is derived. Therefore, this method is not flexible to test whether immigration is changing as a function of environmental covariates. Other drawbacks relate to the assumptions of the temporal symmetry model. If immediate trap response or transients occur, or if the initial capture probability is different than the recapture probability (typical in studies using color bands), the estimated λ and f are strongly biased (Hines and Nichols 2002), and consequently immigration would be as well. Trap response and transients are frequent in capture-recapture studies (Perret et al. 2003, Schmidt et al. 2005, Schaub et al. 2009).

Fifthly, Grøtan et al. (2009) recently modeled the immigration process using a beta-binomial model based on population count data (i.e. the number of breeding birds). To estimate immigration they assumed that the number of available nest boxes in the study area is equal to the maximum number of immigrants. However, this assumption is only reasonable if very few birds breed in natural cavities. Further, they assumed that all adults unmarked or marked outside the study area are immigrants, which may not always be true.

From this overview, it is evident that a coherent method to estimate immigration is needed, which is applicable to the typical data that are sampled in geographically open populations. In this paper, we propose a new method to estimate immigration using integrated population models (Besbeas et al. 2002) that does not suffer from these problems. Integrated population models need population counts or indices of population size which are combined with other sources of data (typically capture-recapture data, data on fecundity) in one coherent model, with the advantage that otherwise non-estimable parameters can become estimable (Besbeas et al. 2002). This is possible because the population size contains information about all demographic processes in the population, and this information is extracted. The rationale behind our novel approach is similar. We show how to estimate immigration, and how to model immigration as a function of covariates. We illustrate the method with a case study on little owls *Athene noctua* Scopoli. Immigration in this population was previously estimated using the combination of capture-recapture and fecundity data (Schaub et al. 2006). Keeping the best structure for survival and recapture probabilities, as well as fecundity from the previous analysis, we tested whether immigration showed trends across time and whether immigration is affected by the density of voles *Microtus arvalis* Pallas, the main prey of the little owl.

3.3 Materials and Methods

3.3.1 The integrated population model

The core of the integrated population model is a population projection model describing the development of the population sizes of each age class from one year to another. The projection matrix is parameterized with the demographic rates. Owing to the life history of little owl, we used a simple age-structured model (Caswell 2001) with two age classes (1 and 2 years or older) and a pre-breeding census. Let $N_{1,t}$ be the number of 1 year old females at time t, $N_{2+,t}$ be the number of females older than 1 year at time

t, $\phi_{ju,t}$ and $\phi_{ad,t}$ are the juvenile and adult (1 year or more) apparent survival probabilities of a female between time t and $t+1$ respectively, b_t is fecundity at time t, and imm_t is the immigration rate, defined as the number of female immigrants in year $t+1$ per female in the population in year t. Following Buckland et al. (2007), the expected number of females present in year $t+1$ are given by

$$E(N_{t+1}|N_t) = E\begin{pmatrix} N_{1,t+1}|N_{1,t} \\ N_{2+,t+1}|N_{2+,t} \end{pmatrix} = \begin{pmatrix} \phi_{ju}b/2 & \phi_{ju}b/2 \\ \phi_{ad}+imm & \phi_{ad}+imm \end{pmatrix}_t \begin{pmatrix} N_{1,t}|N_{1,t-1} \\ N_{2+,t}|N_{2+,t-1} \end{pmatrix} \tag{3.1}$$

The model is female based, but fecundity (b) refers to the complete reproductive output. We assumed an even sex ratio of the fledglings and thus divide b by 2. Further, we assumed that immigrants add to the individuals that are at least 2 years old. However, results would be identical if immigrants were assumed to add to the 1-year-old individuals.

The capture-recapture data contribute to the estimation of survival, the data on reproductive success to the estimation of fecundity and the population count data to the estimation of the population sizes and all demographic rates. For each data set, a likelihood can be formulated and finally the complete integrated model is the joint likelihood of these different parts. In the following we describe briefly the different likelihoods (for details see Brooks et al. 2004, Schaub et al. 2007, Abadi et al. 2010).

We used the Cormack-Jolly-Seber (CJS) model to analyze the capture-recapture data (Lebreton et al. 1992). The frequency of individual encounter histories ($\boldsymbol{m}$) follows a multinomial distribution with cell probabilities that are function of age-specific apparent survival ($\boldsymbol{\phi}$) and recapture probabilities ($\boldsymbol{p}$). The formulation of the likelihood of this model ($L_{cr}(\boldsymbol{m}|\boldsymbol{\phi},\boldsymbol{p})$) is straightforward and described in many papers (e.g. Lebreton et al. 1992).

We estimated fecundity ($\boldsymbol{b}$) from the number of recorded reproducing females ($\boldsymbol{R}$) and total number of offspring ($\boldsymbol{J}$) produced by them in year t. We assumed that J_t follows a Poisson distribution with parameter written as a product of R_t and b_t, hence, $J_t \sim \text{Po}(R_t b_t)$. The likelihood of this model is denoted as $L_{rp}(\boldsymbol{J},\boldsymbol{R}|\boldsymbol{b})$.

The population count data were analyzed with a state-space model (Besbeas et al. 2002, de Valpine and Hastings 2002, Buckland et al. 2004). The state-space model is defined by two processes: a state process that describes the evolution of the true population sizes across time and an observation process which describes the observation of the true process. The state process is already defined by our population model (eqn 3.1), but here we introduce demographic stochasticity using Poisson (Po) and binomial (Bin) distributions as

$$N_{1,t+1} \sim Po((N_{1,t} + N_{2+,t})(b_t/2)\phi_{ju,t}) \tag{3.2}$$

and

$$N_{2+,t+1} \sim (Bin((N_{1,t} + N_{2+,t}), \phi_{ad,t}) + Po((N_{1,t} + N_{2+,t})imm_t)) \tag{3.3}$$

The observation process is conditional on the state process. Here, only breeding females are counted, and we assume the counts to follow a Poisson distribution. That is, $y_t \sim \mathrm{Po}(N_{1,t} + N_{2+,t})$, where y_t is the number of observed breeding females in year t. The likelihood of the state process is $L_{sy}(\boldsymbol{N}|\boldsymbol{\phi}, \boldsymbol{b}, \boldsymbol{imm})$, the likelihood of the observation process is $L_{ob}(\boldsymbol{y}|\boldsymbol{N})$ and the likelihood of the state-space model is the product of the two likelihoods.

Likelihood of the integrated model

The likelihoods of the three data sets have some parameters in common, as displayed graphically by the directed acyclic graph (Figure 3.1). Thus, by combining these data sources into a single analysis using an integrated population model, more information can be used to estimate demographic parameters. Under the assumption of independence between the three data sources, the joint likelihood for the combined data, which is a basis for inference, is obtained as the product of the likelihoods of the three data sources (Besbeas et al. 2002, 2003, Brooks et al. 2004, Abadi et al. 2010), thus

$$\begin{aligned} L_{joint}(\boldsymbol{m}, \boldsymbol{J}, \boldsymbol{R}, \boldsymbol{y}|\boldsymbol{N}, \boldsymbol{\phi}, \boldsymbol{b}, \boldsymbol{imm}, \boldsymbol{p}) = {} & L_{cr}(\boldsymbol{m}|\boldsymbol{\phi}, \boldsymbol{p}) \times L_{rp}(\boldsymbol{J}, \boldsymbol{R}|\boldsymbol{b}) \\ & \times L_{ob}(\boldsymbol{y}|\boldsymbol{N}) \times L_{sy}(\boldsymbol{N}|\boldsymbol{\phi}, \boldsymbol{b}, \boldsymbol{imm}) \end{aligned} \tag{3.4}$$

The calculation of the joint likelihood (eqn 3.4) relies on the assumption that the data are independent which is frequently violated in practice. However, a simulation study, which combined capture-recapture, population count and reproductive success data, showed that the violation of this assumption has only minimal impact on the accuracy

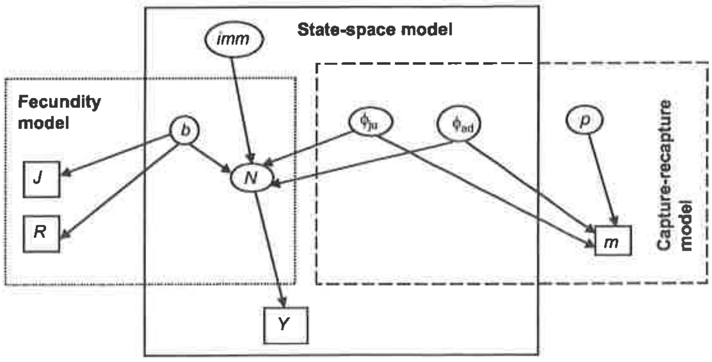

Figure 3.1: *Structure of the integrated population model: Directed acyclic graph of the integrated population model for the little owl population Göppingen, showing that some demographic parameters are common to different sources of information. Estimated parameters are represented by circles and the data are represented by rectangles. Arrows represent dependences between nodes. Node notations:* m*, capture-recapture data;* y*, population count data;* J*, number of newborns;* R*, number of recorded reproducing females;* b*, fecundity;* ϕ_{ju}*, juvenile survival probability;* ϕ_{ad}*, adult survival probability; imm, immigration rate;* p*, recapture probability;* N*, population size.*

of parameter estimates (Abadi et al. 2010). Since our model to estimate immigration uses the same kind of data as the simulation study by Abadi et al. (2010), the potential violation of the independence assumption is likely to have little impact on the estimators.

3.3.2 Case study

We used demographic data on little owls to illustrate the estimation and modeling of immigration rate using the integrated population model. The little owl is a small-sized owl preying mostly on voles in Central Europe and inhabiting semi-open landscapes. It is a cavity breeder and readily accepts nest boxes (Cramp 1985). We collected the demographic data near Göppingen (Southern Germany; 48 °40′ N, 9 °38′ E), where nest boxes were installed and the population was monitored from 1978 to 2003. Each year we checked all nest boxes several times, recorded reproductive success ($n = 353$ breeding attempts), marked nestlings with rings ($n = 659$) and captured and marked adults that were in the nest boxes at the time of the checks ($n = 73$). Thus, capture-recapture data, data on reproductive success and on population size (number of occupied nest boxes) were available. Further, we recorded a two-level index of vole abundance (high, low) each spring based on the number of vole hills and holes. For further details see Schaub et al. (2006).

3.3.3 Parameter estimation and sensitivity analysis

The joint likelihood of the model (eqn 3.4) is constructed based on data of females only. However, we had also capture-recapture data of males. These data were also included and modeled, but they contributed to the joint likelihood only, if at least one parameter was identical (e.g. if survival was not sex-specific), improving the precision of the estimates common in both sexes.

We performed a Bayesian analysis of the integrated population models, which gives us more flexibility regarding model assumptions to form the likelihood of the population count data (Brooks et al. 2004, Schaub et al. 2007, King et al. 2008). To estimate demographic rates, we mimic as closely as possible the Schaub et al. (2006) analysis. We used constant immigration and those structures of the other demographic rates that turned out to be best in Schaub et al. (2006). We assessed whether the integrated analysis provides an identifiable estimate of immigration by comparing the prior and posterior distributions for immigration rate. In the Bayesian context, a parameter is considered to be identifiable if the posterior distribution differs from the prior distribution (Garrett and Zeger 2000, Gimenez et al. 2009). If this is so the data do contain information about the parameter under scrutiny. We specified four prior distributions for immigration (three with uniform distributions between 0 and 5 ($U(0,5)$), 0 and 2 ($U(0,2)$), and 0 and 1 ($U(0,1)$); one with a normal distribution with mean 0 and variance 0.25 truncated to the values between 0 and 2 ($N(0,0.25)I(0,2)$). The first three prior distributions assumed that immigration is equally likely within the given ranges, whereas the normal prior assumed that low immigration is much more likely than high immigration. We regard the $U(0,5)$ prior as non-informative and the normal prior as the most informative. If immigration is identifiable, we expect the choice of the prior to have only limited impact on the posterior distribution. Thirdly, we estimated the demographic rates while using only capture-recapture and population count data, but not the data on fecundity. This allows us to check whether estimation is still possible in the case where explicit data for two different parameter types (immigration and fecundity) are lacking.

In all cases we specified the following prior distributions for the other model parameters than immigration. Since survival and recapture probabilities are modeled as linear functions of time and sex on a logit scale, we assigned a $N(0, 10^4)$ prior to the regression coefficients. Further we used a $U(0,5)$ prior for fecundity and a $N(0, 10^4)$ truncated to positive values on the age-specific population sizes.

Unfortunately, no measure of goodness-of-fit (GOF) is available yet for integrated population models. Therefore, the best thing to do is to assess the GOF of single data sets. Schaub et al. (2006) assessed the GOF of the CJS model and found no lack of fit.

3.3.4 Modeling immigration as a function of covariates

In this section, we show how the integrated model can be used to model immigration rate as a function of environmental covariates and to make inference. In fact, the inclusion of a covariate is easy and straightforward. We modeled the log of immigration rate as a linear function of covariates using the linear relationship

$$log(imm_t) = \beta_0 + \sum_{j=1}^{v} \beta_j X_{jt} \tag{3.5}$$

where X_{jt} is the value of the j^{th} covariate at the t^{th} sampling occasion, the β's are regression coefficients. We used a $N(0, 10^4)$ prior for the unknown regression parameters (β's).

Either classical hypothesis tests (i.e. evaluating whether β is different from 0) or model selection (e.g. using the deviance information criterion DIC (Spiegelhalter et al. 2002, van der Linde 2005) or performing reversible jump MCMC (Green 1995)) can be used to make inference about immigration in relation to covariates. Here, we compared several models based on the DIC. We used the DIC as a preliminary tool for comparing different models. The models that we compared had all different structures for immigration, but the same structure for all other model parameters.

An extensive model selection by Schaub et al. (2006) revealed that survival was best estimated using the same linear time trend for both age classes with an additional sex effect, that recapture probability was best modeled time-specific with an additive sex effect and that reproductive success was different in each year (model denoted as $\phi_{age2+T+sex}, p_{t+sex}, b_t$). We defined six different models for immigration. The first model considers that immigration is time-dependent (imm_t). Secondly, we assumed that immigration had systematically changed with time, either linearly (imm_T) or following a quadratic function (imm_{T+T^2}). The fourth model assumes the immigration to depend on the abundance of voles (imm_v). We expect high vole abundance to have a positive impact on immigration. The next model assumes that immigration is constant across time ($imm_.$). Finally, to test whether immigration was important at all, we considered a model where we assumed no immigration (imm_0).

3.3.5 Model implementation

All analyses were carried out using WinBUGS (Lunn et al. 2000) called from R 2.7.1 (R Development Core Team 2008) with the R2WinBUGS package (Sturtz et al. 2005). WinBUGS performs Markov chain Monte Carlo (MCMC) techniques to sample from the posterior distribution of each parameter. We used the Brooks and Gelman diagnostic ($\hat{R}$) to assess the convergence of the MCMC simulations (Brooks and Gelman 1998). Initial trials with three independent chains showed that convergence ($\hat{R} < 1.01$) was obtained after 20,000 iterations with a burn-in period of 10,000 iterations. For all analyses we therefore ran single chains of 200,000 iterations, of which the first 100,000 were removed as a burn-in period and thinned such that every 100^{th} observation was retained. The R and WinBUGS codes used for fitting the model which included a covariate are available in `http://www3.interscience.wiley.com/journal/123303675/suppinfo/`.

3.4 Results

Parameter estimation and sensitivity analysis

The estimated immigration rate from our simplest constant model was 0.293 with 95% credible interval (CRI) 0.183 - 0.418 (under prior $U(0,2)$). This means that for every breeding female in year t, about 0.3 female had immigrated in year $t+1$. As can be seen in Figure 3.2, the prior distributions had little effect on the posterior distribution of immigration rate, indicating that the posterior distribution was highly dominated by the observed data. The posterior means and 95% CRIs for the immigration rate were almost the same under different priors [posterior mean (95% CRI): under $U(0,5)$: 0.290 (0.173 - 0.417); under $U(0,1)$: 0.292 (0.183 - 0.415); under ($N(0,0.25)I(0,2)$): 0.296 (0.175 - 0.425)]. Consequently, immigration is identifiable using the integrated population model.

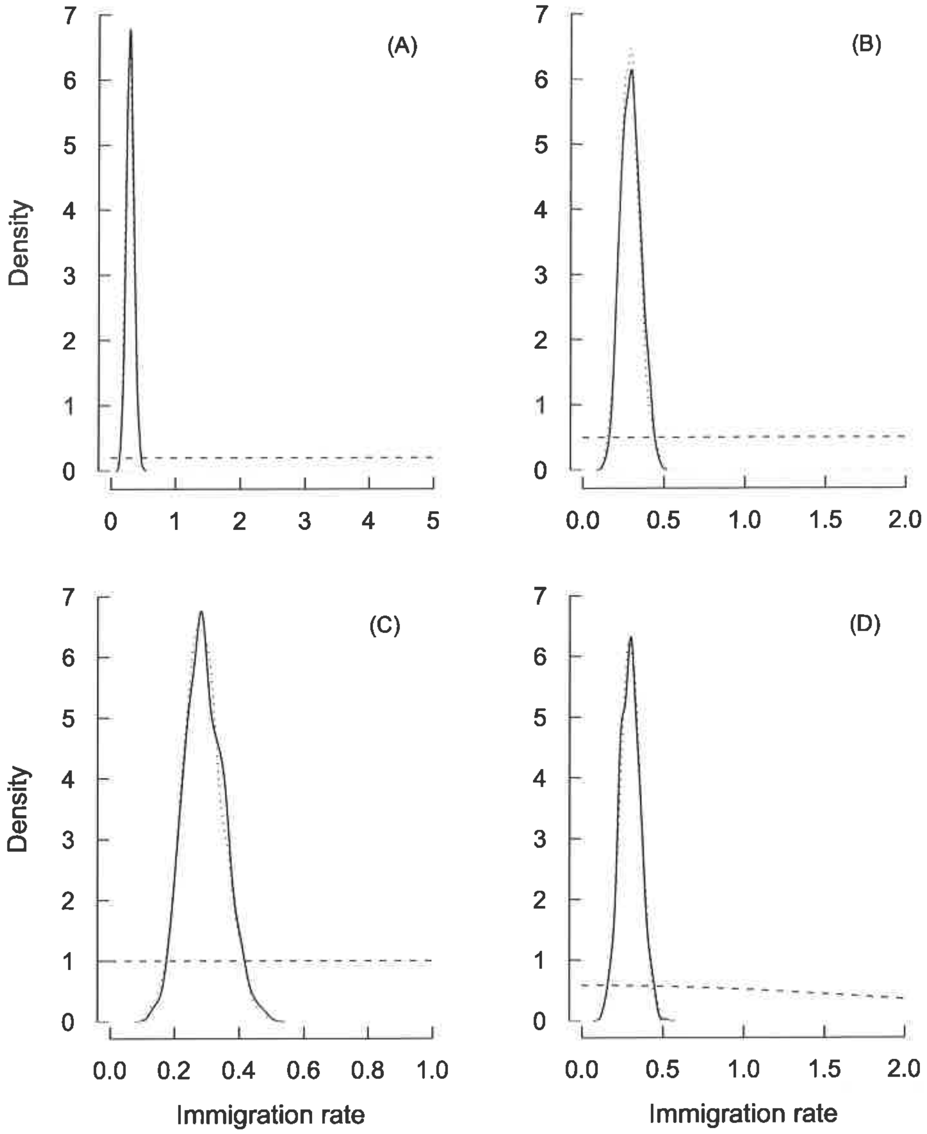

Figure 3.2: *Parameter identifiability: Prior (dashed line) and posterior (solid and dotted lines for model with and without fecundity data, respectively) distributions of the immigration rate, estimated using the integrated population model, where immigration rate was constrained to be constant over time (model denoted as* $\phi_{age2+T+sex}$, p_{t+sex}, b_t, *imm.*, *Table 3.1). A* $U(0,5)$ *(Panel A), a* $U(0,2)$ *(Panel B), a* $U(0,1)$ *(Panel C) and a* $N(0,0.25)I(0,2)$ *(Panel D) prior are used. Note that the posterior for the model without fecundity is hardly visible, because it matches almost completely the posterior of the model including fecundity.*

The estimated immigration rate obtained from the analysis without fecundity data was 0.288 with 95% credible interval 0.170- 0.425, which was virtually identical to the one obtained from the analysis which did include fecundity data. Also in this case was the posterior distribution of immigration insensitive to the prior distributions, indicating again that immigration was identifiable (Figure 3.2). However, the wide credible intervals indicated uncertainty in the estimates of immigration in all cases.

The annual point estimates of all demographic rates were very similar regardless of whether they stem from the integrated population models or from the "two steps" approach (Schaub et al. 2006, see Table A2.1–A2.3 in Appendix A).

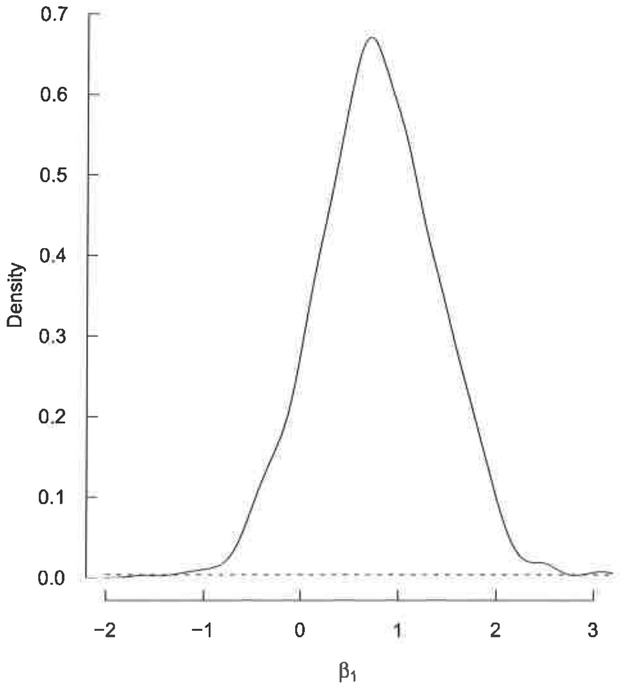

Figure 3.3: *Resource-dependence of immigration rate: Prior (dashed) and posterior (solid line) density of the vole abundance effect* (β_1) *on immigration rate. A* $N(0, 10000)$ *prior for* β_1 *was used. The probability that* β_1 *was positive is 0.900.*

Modeling immigration with covariates and model selection

Model selection of immigration rate showed that the model where immigration was a function of vole abundance was favored by DIC (Table 3.1). However, the difference in DIC to the next best model with constant immigration rate was small. Thus, there is uncertainty whether immigration really depended on vole abundance. This is also reflected in the posterior distribution of the vole abundance effect which includes zero (Figure 3.3). The models where immigration changes deterministically across time and where immigration rate was different in each year were clearly lower ranked. In particular, the model where no immigration occurred was ranked as the worst, indicating that immigration was important in this little owl population. The estimates of all demographic rates with associated 95% credible intervals based on the best model are shown in Figure 3.4.

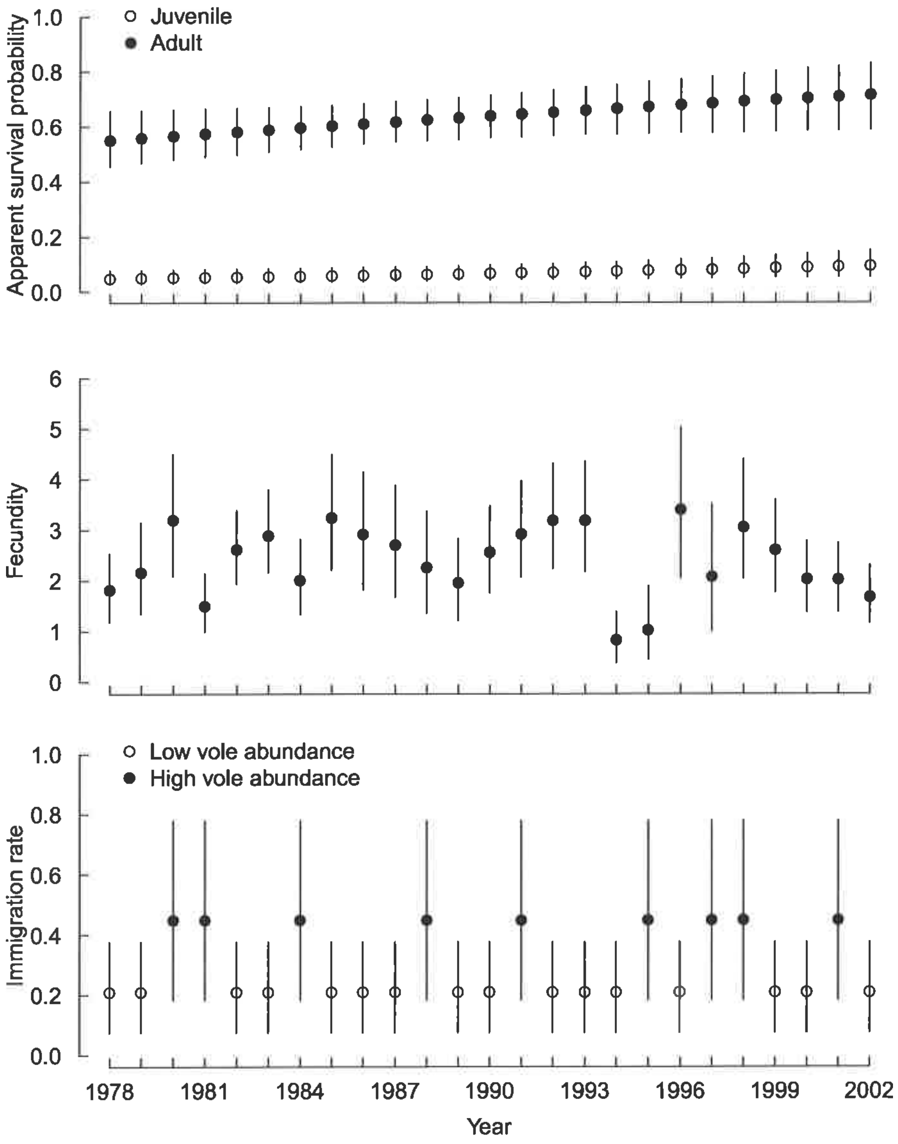

Figure 3.4: *Parameter estimates: Annual apparent survival probabilities, fecundity, and immigration rates of little owls females based on the best integrated population model (model* $\phi_{age2+T+sex}$, p_{t+sex}, b_t, imm_v, *Table 3.1). Points are the posterior means, vertical lines indicate the 95% credible intervals.*

Table 3.1: *Model selection results for different patterns of immigration rate (imm) of little owls using integrated population models. The model deviance, the effective number of parameters (pD), and the DIC difference (ΔDIC) between the current model and the best model are provided. The model subscript t stands for year-specific rates, T and T^2 denote a linear and quadratic trend over time, respectively, 0 denotes no immigration, '.' denotes constancy over time, and v denotes a vole abundance effect. For survival ($\phi_{age2+T+sex}$), recapture (p_{t+sex}) and fecundity (b_t) the same structure was used for all models.*

Immigration model	Deviance	pD	ΔDIC
imm_v	583.44	63.95	0
$imm_.$	573.99	73.7	0.31
imm_t	579.71	72.34	4.66
imm_T	584.51	67.86	4.98
imm_{T+T^2}	584.65	66.77	5.03
imm_0	588.18	76.82	17.61

3.5 Discussion

Immigration to geographically open population is often an important demographic component to population growth (Lampila et al. 2006, Peery et al. 2006, Schaub et al. 2006, Grøtan et al. 2009, Reichlin et al. invited revision), but immigration rate is one of the most difficult demographic rates to estimate. Here we propose an extension of an integrated population model to estimate immigration rate using population count, capture-recapture and fecundity data. We show that immigration is estimable and can furthermore be modeled as a function of environmental covariates. This is a step forward to model the dynamics of geographically open populations.

A key advantage of integrated population models in general is that they allow estimating demographic parameters for which no explicit data are sampled (Besbeas et al. 2002, Abadi et al. 2010). This is possible because the population count data contain information about all demographic processes in the population and because this information is extracted with the inclusion of independent data about some of these processes. Previously developed integrated population models showed that fecundity can be estimated if count data are combined either with ring-recovery data (Besbeas et al. 2002, Brooks et al. 2004) or with capture-recapture data (Abadi et al. 2010). Here, we show that immigration can be estimated, if count data are combined with capture-recapture data. The inclusion of data on fecundity contributes little to the estimation of immigration rate. This might be different in a situation where survival from birth to recruitment as breeder is high. However, it is very encouraging that the integrated population model has the power to estimate two demographic parameters (i.e., immigration rate and fecundity) for which no explicit data are available.

Our analyses revealed that the posterior distributions of immigration were not very sensitive to different priors. Because the posterior distribution generally becomes independent of the prior distribution when the data are highly informative, our result indicated that the immigration rate could be estimated based on the information from the observed data.

Other approaches to estimate immigration have been proposed and we reviewed them briefly in the introduction. The integrated population model has several advantages over the existing methods. The first advantage is that the model allows immigration to be modeled as a function of covariates. Often, the interest is not just in a point estimate, but on testing biological hypotheses about immigration. This is only possible if covariates can be included. Secondly, our approach does not rely on strong assumptions, as other approaches do. In particular there is no requirement for all unmarked individuals that are born in the population to be marked, that the population is counted without error or that all unmarked individuals are assumed to be immigrants. In our view, relaxing these assumptions provides much more realism to the data than has been possible previously. Yet, the integrated population model is also based on some assumptions. The different data must be independent from each other. A simulation study in a slightly different context has shown that the violation of this assumption has limited impact only on parameter accuracy (Abadi et al. 2010). Furthermore, the assumptions of the capture-recapture model (Lebreton et al. 1992) like identity of estimates of survival and recapture among individuals must hold. However, some frequent reasons for the violation of these assumptions such as occurrence of transients (Pradel 1996), trap-dependence (Pradel 1993) or non-random temporary emigration (Schaub et al. 2004) can be relaxed by specifying a different capture-recapture model. This can be included into the integrated population model. In contrast, for methods that rely on the reverse-time modeling of capture-recapture data (Peery et al. 2006, Schaub et al. 2006) this is not possible.

The integrated population model yielded less precise estimates of the immigration rate in comparison to the "two steps" approach (Schaub et al. 2006, see Table A2.1–A2.3 in Appendix A). However, the precision from the "two steps" approach is based on the assumption that the covariances between all parameter estimates to be zero. Presumably, this was violated resulting in an overly optimistic precision. In contrast, the integrated model provides a more realistic picture of the uncertainty in all the estimates. In integrated population models, the precision of fecundity when no explicit fecundity data were included was much lower, than when data on fecundity were included (Abadi et al. 2010, see Table A2.1–A2.3 in Appendix A). This is likely to be generally true. Thus, as there are no explicit data on immigration included, the low precision of the estimates could be expected. To increase precision, explicit data on immigration must be included. This could be achieved if capture-recapture data are sampled using the robust design, allowing estimates of immigration rates to be obtained (Nichols and Pollock 1990). The robust design model can then be included into the integrated population model. In the Bayesian context, one could also introduce more informative prior information that could be obtained from another population or from a closely related species to improve the precision of the estimates of immigration rate.

We foresee several areas for further developing the novel analytical framework presented here. First, the model could be modified to include random effects. This is of importance when the temporal variance of demographic rates and the temporal covariances between them must be estimated. Such estimates are crucial for assessing the contribution of demographic rates to the variation of the population growth rate (Horvitz et al. 1997, Burnham and White 2002, Loison et al. 2002). Moreover, a hierarchical formulation is useful to model the effect of covariates on demographic rates, relaxing the assumption that the complete variation in the demographic rates over time is determined by the covariates alone. Also, a random-effects formulation for year-specific parameters is more parsimonious than explicitly estimating one independent effect for every year. Secondly, the state-space model could be extended to account for over-dispersion by specifying beta-binomial or negative binomial distributions for the state process (King et al. 2008). Thirdly, the model could be adapted to different life histories, such as a life history with delayed maturity or with explicit inclusion of both sexes. It may then possible to estimate age and/or sex specific immigration rates.

In conclusion, our newly extended integrated population model will be a useful tool to estimate immigration rate in a geographically open population permitting a deeper understanding of the dynamics of such populations and to help conservation biologists conducting population diagnoses (e.g. population viability analysis) and proposing efficient management actions.

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4

Estimating the strength of density-dependence in the presence of observation errors using integrated population models

Abadi, F., Gimenez, O., Arlettaz, R., and Schaub, M. (in prep.).

4.1 Abstract

The estimation of the strength of density-dependence is crucial to understand population dynamics, but its estimation is difficult. Because population size and demographic parameters usually include errors due to imperfect detection, estimates of the strength of density-dependence are biased if obtained with conventional methods which in addition lack statistical power to detect density-dependence. We propose a Bayesian integrated population model that combines different sources of demographic information into a single model to study density-dependence. The model allows assessing the effect of density both on the population growth rate and on the demographic parameters while accounting for imperfect detection. We studied the performance of this model by simulation and illustrate its use with a case study on hoopoes *Upupa epops*. Our simulation results show that the strength of density-dependence is identifiable and estimated with good precision. The strength of density-dependence is also estimated with more precision with the integrated population model compared to a conventional regression model, which ignores the observation error. The results showed that a conventional regression model, which ignores the observation error tended to estimate a stronger density-dependence at the population than at the demographic level. The analysis of hoopoes data revealed a negative density-dependence at the population scale, most likely caused by density-dependent fecundity. This work highlights the potential of integrated population models in assessing density-dependence and its practical application in conservation studies.

Key words: Bayesian; demographic parameters; density-dependence; integrated population model; observation error; population growth rate; population size; simulation; *Upupa epops*

4.2 Introduction

Factors that regulate population size are broadly classified into density-independent (stochastic) and density-dependent (deterministic) factors (Williams et al. 2002). Density-independent factors (e.g. weather) affect the same proportion of individuals in a population regardless of population density. In contrast, the effects of density-dependent factors intensify as the population density increases. Depending on their effect and cause, they can be differentiated as negative and positive density-dependent processes. The negative effects of density-dependence occur if a demographic rate decreases as density increases, whereas positive effects occur when both increase (Williams et al. 2002). Competitions for resources (e.g. food, nest site) and predation are the main mechanisms of negative density-dependence (Newton 1998, Gunnarsson et al. 2006), while a low chance to find mates is one of the known mechanisms resulting in positive density-dependence (the Allee effect)(Sæther et al. 1996, Morris 2002).

In order to better understand how populations are regulated, the effect of density should be quantified. Knowledge of density-dependence is also crucial in practical applications such as conservation or harvest regulations (Hanski et al. 1996, Sinclair and Pech 1996, Drake 2005). Many studies used long-term time series data to estimate the strength of density-dependence processes (Dennis and Taper 1994, Lande et al. 2003).

The main principle is to study whether there is a negative relationship between population growth rate and population size. An important limitation of this approach is that it needs the assumption that population counts are perfect, i.e. without observation error. If the observation error is large and not accounted for, it inflates the type I error and misleadingly indicate the presence of density-dependence (Shenk et al. 1998, Freckleton et al. 2006, Knape 2008, Lebreton 2009). More recently, state-space models have been used to reduce or remove bias in parameters or functional forms of density relationships resulting from observation error (de Valpine and Hastings 2002, Jamieson and Brooks 2004, Dennis et al. 2006). However, estimates are unbiased only if the observation error is relatively small (Knape 2008). A further limitation is that the analysis of population counts only reveals the effect of density at the population level and consequently, the demographic mechanism causing density-dependence remains unknown.

Few studies have used long-term data to assess the impact of density at the demographic level by regressing estimates of demographic parameters on population counts (Coulson et al. 2000, Sæther et al. 2000, Paradis et al. 2002, Barbraud and Weimerskrich 2003, Tavecchia et al. 2007). To get unbiased estimates of the strength of density-dependence this approach requires parameters of demographic rates and population sizes estimates that are not subject to observation errors. If there are observation errors (either on the demographic rates and/or on the population size), the test for density-dependence will suffer from a lack of statistical power (Lebreton 2009). Recently, Schofield et al. (2009) applied the Jolly Seber model on mark-recapture data to estimate the strength of density-dependence on survival. Using this model, estimates of survival and of population sizes are obtained while accounting for imperfect detection, and thus the power to detect density-dependence is maximized.

Despite the development of different methods for studying density-dependence, there are currently no approaches to assess the effect of density on all demographic parameters simultaneously while accounting for observation error. This is a drawback, because the demographic mechanism of density-dependence cannot rigorously be studied.

In this article, we propose the use of a Bayesian integrated population model to study density-dependence in a coherent fashion. Integrated population models combine different sources of demographic data into a single model and provide estimates of all demographic parameters and population size with improved precision and that are free of observation error (Besbeas et al. 2002, Brooks et al. 2004, Schaub et al. 2007, Abadi et al. 2010*a*). Parameters that are unidentifiable from a single source can be estimated with these models (e.g. fecundity (Besbeas et al. 2002), immigration rate (Abadi et al. 2010*b*)). The models also are very appealing and powerful when the sample size is small (Abadi et al. 2010*a*). So far, these models have been successfully used to estimate key demographic parameters (Brooks et al. 2004, Schaub et al. 2007, King et al. 2008, Veran and Lebreton 2008, Reynolds et al. 2009, Abadi et al. 2010*b*) and their performances have been investigated using simulations (Besbeas et al. 2009, Abadi et al. 2010*a*).

The model we propose for studying density-dependence potentially has several advantages. Firstly, because integrated population models involve the use of state-space models, we are able to assess density-dependence based on the true population sizes rather than the population counts including errors, which avoid the confounding effect of observation error. Secondly, because all demographic parameters are estimated, it allows test of density-dependence for all of them and thus the demographic mechanism of density-dependence can be identified. It also allows assessing density-dependence at the population level using the derived population growth rate. Thirdly, combined analysis of demographic data results in improved estimates of precision, which likely increases the statistical power to detect density-dependence.

Since integrated population models have never been investigated for assessing density-dependence, we conduct simulations to examine its performance in estimating the strength of density-dependence under different degrees of observation error. We illustrate the method using a data set on hoopoes *Upupa epops*.

4.3 Methods

We describe first the simulation setup and the procedure to generate the data sets, then the integrated population model to estimate the strength of density-dependence and how it is analyzed in the Bayesian framework. Finally, we describe the case study.

4.3.1 Simulation study

Using simulations we evaluated the identifiability and the precision of estimates of density-dependence at varying levels of observation error under the integrated population model. We also evaluated the effect of ignoring the observation error on the estimates of density-dependence obtained by regressing demographic rates on observed population sizes.

A. Simulation of the data

The conducted simulations are analogous and very similar to the one described in Abadi et al. (2010*a*). It consists of creating a population by simulating fates of individuals (individual based), sampling demographic data from this population, and analyzing these data with an integrated population model. These steps are repeated several times and point estimates stored, serving the base to evaluate the performance of the model.

To create the population, we mimic a short-lived bird species, and we differentiated between 2 age classes (yearling: 1 year old; adults: older than 1 year). Newborn individuals have survival probability of ϕju to become yearling, while yearlings and adults have an annual survival probability of ϕad. Fecundity (i.e. number of new born per adult females) of both yearlings and adults is f. We assume an even sex ratio, a geographically closed population, and a female based model. Following Buckland et al. (2007), the expected number of individuals at year $t+1$ conditional on numbers at year t are given by

$$E\begin{pmatrix} N_{1,t+1} \\ N_{2+,t+1} \end{pmatrix} = \begin{pmatrix} \phi ju_{t,N} f_{t,N}/2 & \phi ju_{t,N} f_{t,N}/2 \\ \phi ad_{t,N} & \phi ad_{t,N} \end{pmatrix} \begin{pmatrix} N_{1,t} \\ N_{2+,t} \end{pmatrix} \tag{4.1}$$

To induce density-dependence, all demographic parameters are assumed to depend on the actual population size and to vary over time. We specified the demographic parameters in year t as

$$logit(\phi ju_{t,N}) = 0 - 0.005N_t + \varepsilon_{\phi ju_{t,N}} \qquad \varepsilon_{\phi ju_{t,N}} \sim N(0,(0.15)^2) \tag{4.2}$$

$$logit(\phi ad_{t,N}) = 0.619 - 0.001N_t + \varepsilon_{\phi ad_{t,N}} \qquad \varepsilon_{\phi ad_{t,N}} \sim N(0,(0.20)^2) \tag{4.3}$$

$$log(f_{t,N}) = 0.993 - 0.003N_t + \varepsilon_{f_{t,N}} \qquad \varepsilon_{f_{t,N}} \sim N(0,(0.10)^2) \tag{4.4}$$

where $N_t = N_{1,t} + N_{2+,t}$ is the population size at year t, and the ε are the random terms. Parameter values were chosen to have weak density-dependence on the demographic parameters.

Next, we created the life history of individuals in the population for 20 years. To start the creation of the population, we set the initial population size at 100 individuals. We then specified the actual probabilities of survival and fecundity applying eqns 4.2–4.4 under consideration of the actual population size. For each individual alive in the population it was then simulated whether it survived until the next year, how many juveniles it produced, and how many of the juveniles survived until the next year. The sum of the number of yearlings and surviving adults gives then the new population size, and we specified the demographic rates for the following year. This was repeated for 20 years. Information about the state of an individual (dead, alive, in which age group it is given alive) and the number of offspring it has produced were stored. To avoid the transition effects we only used the last 10 years of simulating data sets.

Once we created the population, the next step was to sample individuals for the different studies. Here we independently sampled 2,000 individuals from the population for capture-recapture and reproductive success studies. To create the capture-recapture histories and reproductive success data based on individuals subject to each study, we set the initial capture probability at 0.90 and 0.50 for juveniles and adults (1 year and older), respectively, and the recapture probability at 0.50. The probability to detect and record reproductive success was set at 0.90. All these capture/recapture and detection probabilities were assumed to be constant across time. To create the population counts in each year, we used a binomial distribution with parameters the actual population size in the given year (N_t) and probability to detect them (P_s). This probability is also assumed to be constant over time. We considered two scenarios, one with detection probabilities of female breeders of 0.50, and one with 0.90. Low detection probability corresponds to large observation error in the population counts and vice versa. This is because the variation of binomial sampling (i.e. $NP_s(1\text{-}P_s)$) is largest with P_s=0.50. Here it is important to note that our sampling procedures was not completely independent as some individuals that involved in either capture-recapture or reproductive success studies had a chance to be included in the population counts. We repeated the sampling procedures and simulated 100 capture-recapture, population counts, and reproductive success data sets.

B. Integrated population model with density-dependence

Integrated population models first require the formulation of the likelihood for all available data sets. Detailed discussion of the likelihood formulation is provided in Brooks et al. (2004), King et al. (2008), Abadi et al. (2010*a*). In brief, we used the standard Cormack-Jolly-Seber (CJS) model (Lebreton et al. 1992) for the capture-recapture data. We assumed the number of individual encounter histories summarized in the m-array ($\boldsymbol{m}$) follows a multinomial distribution with parameters a function of age-specific apparent survival ($\boldsymbol{\phi ju}$, $\boldsymbol{\phi ad}$) and recapture probabilities ($\boldsymbol{p}$). We denoted the likelihood of this model by $L_{cr}(\boldsymbol{m}|\boldsymbol{\phi ju}, \boldsymbol{\phi ad}, \boldsymbol{p})$. For reproductive success data, we assumed that the number of offspring produced per female ($\boldsymbol{J}$) is Poisson distributed with parameter the product of fecundity ($\boldsymbol{f}$) and number of recorded producing female ($\boldsymbol{R}$). The likelihood is denoted by $L_{rp}(\boldsymbol{J}, \boldsymbol{R}|\boldsymbol{f})$.

We use a state-space model which consists of a process and an observation model to describe the population counts (Besbeas et al. 2002). The process model describes the evolution of the true underlying population sizes over time thus it determines the link between the demographic rates and population size. This link is basically described by the projection matrix model (eqn 4.1), yet we now consider in addition demographic stochasticity. Thus, we assume that the number of 1 year old (N_1) and at least 2 years individuals (N_{2+}) are Poisson (Po) and binomially (Bin) distributed as

$$N_{1,t+1} \sim Po(N_t(f_{t,N}/2)\phi ju_{t,N}) \tag{4.5}$$

$$N_{2+,t+1} \sim Bin(N_t, \phi ad_{t,N}) \tag{4.6}$$

The observation model links the population counts (i.e the number of detected and counted female breeders, denoted by y_t) to the true latent population sizes (N_t). We then assume

$$y_t \sim N(N_t, \sigma_y^2) \tag{4.7}$$

The likelihood of the state-space model then is given by the product of the likelihood of the process and observation models, $L_{sy}(\boldsymbol{N}|\phi ju, \phi ad, f) \times L_{ob}(y|\boldsymbol{N})$. The likelihood of complete integrated population models is obtained as the product of the likelihoods of all three data sources under the assumption of independence.

$$\begin{aligned} &L_{joint}(\boldsymbol{m}, \boldsymbol{J}, \boldsymbol{R}, \boldsymbol{y}|\phi ju, \phi ad, f, \boldsymbol{p}, \boldsymbol{N}, \sigma_y^2) \\ &\quad = L_{cr}(\boldsymbol{m}|\phi ju, \phi ad, \boldsymbol{p}) \times L_{rp}(\boldsymbol{J}, \boldsymbol{R}|f) \times L_{ob}(\boldsymbol{y}|\boldsymbol{N}, \sigma_y^2) \times L_{sy}(\boldsymbol{N}|\phi ju, \phi ad, f) \end{aligned} \quad (4.8)$$

A simulation study by Abadi et al. (2010*a*) that combined and analyzed completely dependent data of capture-recapture, population counts, and reproductive success showed that the violation of this assumption did not affect much the precision of parameter estimates. We assume that this is true in the present study too as the sampling procedure was partially independent.

C. Modeling density-dependence in the integrated population model

All the demographic parameters and population size appear in the likelihood of the integrated models as shown in eqn 4.8. This allows us regressing demographic parameters on population size in a single model. We assume a logistic and logarithmic relationship for survival probability and fecundity, respectively and specify

$$logit(\phi ju_{t,N}) = \beta_0 + \beta_1 s(N_t) + \varepsilon_{\phi ju_{t,N}} \qquad \varepsilon_{\phi ju_{t,N}} \sim N(0, \sigma^2_{\phi ju}) \quad (4.9)$$

$$logit(\phi ad_{t,N}) = \beta_2 + \beta_3 s(N_t) + \varepsilon_{\phi ad_{t,N}} \qquad \varepsilon_{\phi ad_{t,N}} \sim N(0, \sigma^2_{\phi ad}) \quad (4.10)$$

$$log(f_{t,N}) = \beta_4 + \beta_5 s(N_t) + \varepsilon_{f_{t,N}} \qquad \varepsilon_{f_{t,N}} \sim N(0, \sigma_f^2) \quad (4.11)$$

where $s(N_t)$ is the standardized population size. The goal here is to estimate the regression parameters and the temporal variability (β, σ^2). The slope parameters with population size (β_1, β_3, β_5) estimate the strength of density-dependence on juvenile survival, adult survival and fecundity, respectively. We modeled the recapture probability ($\boldsymbol{p}$) with a random year parameter.

After the estimation of the demographic parameters and population size, we also estimate the strength of density-dependence on population growth rate (i.e. at the level of the population). This was done by first calculating the population growth rate ($\lambda_t = N_{t+1}/N_t$), and then regressing the growth rate on population size

$$log(\lambda_{t,N}) = \beta_6 + \beta_7 s(N_t) + \varepsilon_{\lambda_{t,N}} \qquad \varepsilon_{\lambda_{t,N}} \sim N(0, \sigma^2_\lambda) \tag{4.12}$$

We calculated this regression outside the integrated population model, because we did not want to induce any constraints on the density-dependence at the population level, since density-dependence at the population level is always the result of density-dependent variation of demographic rates.

We also estimated the strength of density-dependence, ignoring the observation error, by regressing demographic rates estimated with single data analysis (i.e survival probabilities from capture-recapture data estimated with the CJS model; fecundity estimated from data on reproductive success with a Poisson regression model) on observed population sizes. The model specifications were similar with eqns 4.9–4.12, but here the population size is given by $s(y_t)$ rather than $s(N_t)$. Further, the population growth rate is derived as $\lambda_t = y_{t+1}/y_t$.

D. Bayesian analysis of the model

For the Bayesian analysis of the model we specified non-informative priors in order to reflect little knowledge about the parameters. Specifically, we assigned a $N(0,100)$ prior on the regression coefficients (β's). A $N(100,100)$ truncated to positive values was assigned for age specific initial population sizes, and a $U(0,5)$ for the temporal standard deviations of demographic parameters. To assess the convergence of Markov chain Monte Carlo (MCMC) algorithm to the stationary distribution, we ran three chains, each with different initial values, of 7,000 iterations with a burn-in of 5,000 iterations. The $\hat{R}$ (Brooks and Gelman 1998) values were less than 1.1 for all parameters, suggested convergence. We then ran a single chain of 15,000 MCMC iterations with a burn-in of 10,000 thinning every 5^{th} observation in order to compute the posterior summary statistics. We used the R software version 2.9.1 (R Development Core Team 2008) to simulate the data and the analyses were done using the WinBUGS software calling it from R through the package R2WinBUGS (Sturtz et al. 2005). The R and WinBUGS codes used for fitting the models are available on request.

4.3.2 Case study

We use 8 years (2002-2009) demographic data of hoopoe *Upupa epops* to illustrate the method. The hoopoe is a medium-sized bird of semi-open farmlands that has experienced a decline in Central Europe over the last decades and is red-listed in Switzerland (Tucker and Heath 1994, Reichlin et al. invited revision). The data sets (capture-recapture, population counts, and data on reproductive success) on this species were collected in the upper valley (Valais, Switzerland). Detailed information about the study species, study site, and data collection is available in Reichlin et al. (invited revision). After the installation of many nest boxes the local hoopoes population increased strongly and remained stable in recent years. The goal is here to estimate the strength of density-dependence at the population level and of the demographic rates to assess through which demographic mechanisms density-dependence operates in this population.

Because the studied hoopoe population is geographically open, we had to include immigration (Abadi et al. 2010*b*). Therefore, we modified the state-space model (eqns 4.5–4.7) as follows: the number of 1 year old individuals (N_1) follows a Poisson process with

$$N_{1,t+1} \sim Po(N_t(f_{t,N}/2)\phi ju_{t,N}) \tag{4.13}$$

The number of immigrants ($N_{im,t+1}$) is modeled with Poisson distribution as

$$N_{im,t+1} \sim Po(N_t imm_t) \tag{4.14}$$

where the immigration rate (imm_t) is defined as the number of immigrants of at least 1 years old in year $t+1$ per breeding females in the previous year (N_t). The number of at least 2 years old surviving individuals follows a binomial process with

$$N_{ad,t+1} \sim Bin(N_t, \phi ad_{t,N}) \tag{4.15}$$

Here the total number of individuals in year t is given by N_t=$N_{1,t}$+$N_{ad,t}$+$N_{im,t}$.

For the observation equation, we assume a Poisson distribution. Thus, the annual number of counted breeding females in year t (y_t) is $y_t \sim Po(N_t)$. The Poisson observation process appears to be more reasonable as the observation error increases with population size.

To estimate the strength of density-dependence of the demographic parameters, we fitted the models specified in eqns 4.9–4.12. We modeled immigration rate with a random year parameter, but did not impose density-dependence. We also fitted a model that all demographic parameters are only time dependent and not constraint by density-dependence. i.e., both the annual survival probabilities and fecundity are the realization of a random process that can be described by a mean and a variance. Here the recapture probability (p) was modeled as constant through time.This model is important to check whether population size explained much of the variation in the demographic parameters.

Convergence was achieved after 20,000 iterations with a burn-in of 10,000. We then ran a single chain of length 1,000,000, discarding the first 100,000 as burn-in, thinning every 100^{th} observation and thus the posterior summary statistics were computed based on 10,000 samples.

4.4 Results

Simulation study

Our simulation study clearly showed that the strength of density-dependence on the demographic rates as well as on the population growth rate was identifiable with the integrated population model regardless of the degree of observation error, indicated by smooth posterior densities with a clear peak (Figure 4.1 and 4.2). If the parameters were not identifiable, we would have expected a posterior density that is similar to the specified prior distribution (Gimenez et al. 2009). The widths of the posterior distributions resulting from the integrated population model were narrower when the observation error was small compared to when it was large. This indicated that the precision of the density-dependence estimator declines with increasing observation error of the count data. Further, the strength of density-dependence was estimated with more precision at the population level than at the demographic level, indicated by a narrow width of the posterior distributions (Figure 4.1 and 4.2).

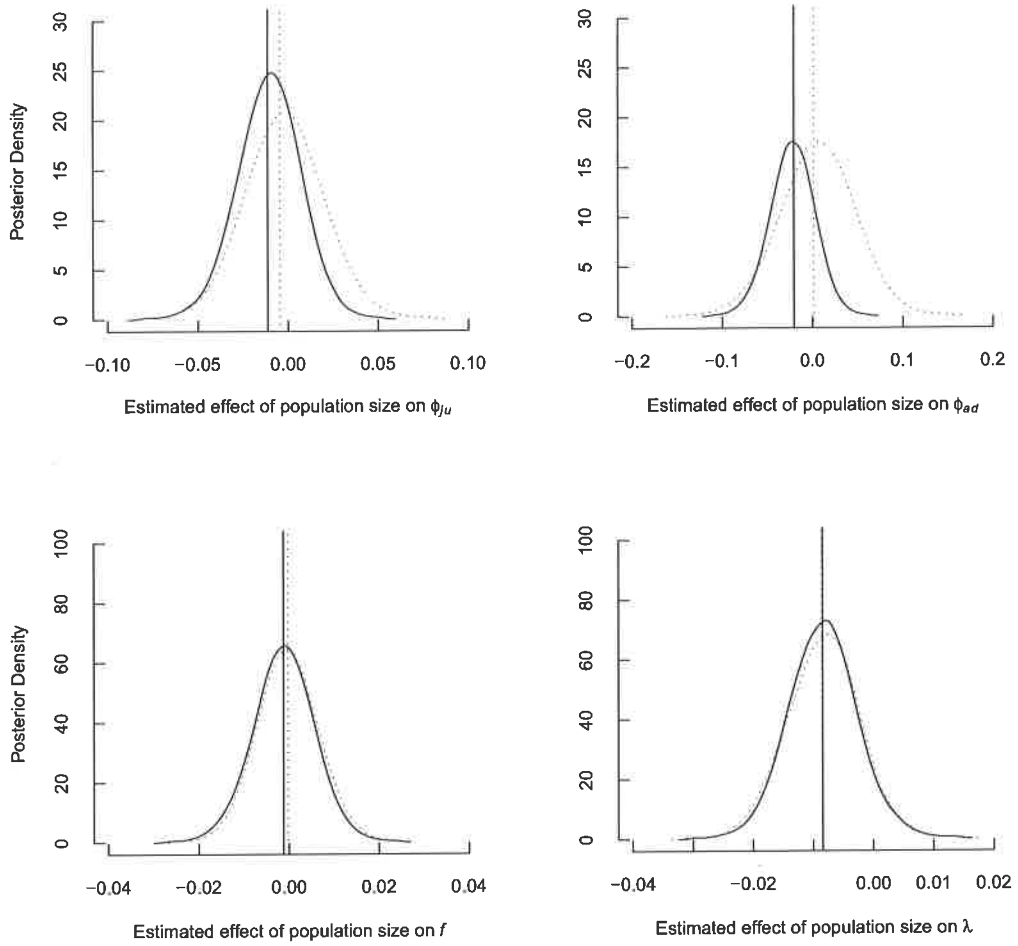

Figure 4.1: *Density plots of the 100 estimated posterior means of strength of density-dependence on juvenile survival (ϕ_{ju}), adult survival (ϕ_{ad}), fecundity (f) and population growth rate (λ) obtained from integrated population models (solid line), and from single data analysis ignoring observation error (dotted line) when the observation error for population count data was large (probability to detect female breeders = 0.50). Vertical lines are the means of the estimated posterior means of the strength of density-dependence over 100 simulations.*

As expected, the estimates of strength of density-dependence on demographic parameters were shifted towards zero when the observation error was large and not accounted for (Figure 4.1 and 4.2). This effect was most pronounced on adult survival and least on fecundity. At the population level, ignoring the observation error tended to show little impact, as the estimates of the strength of density-dependence was nearly the same than that of the integrated population models, yet slightly less precise (Figure 4.1 and 4.2).

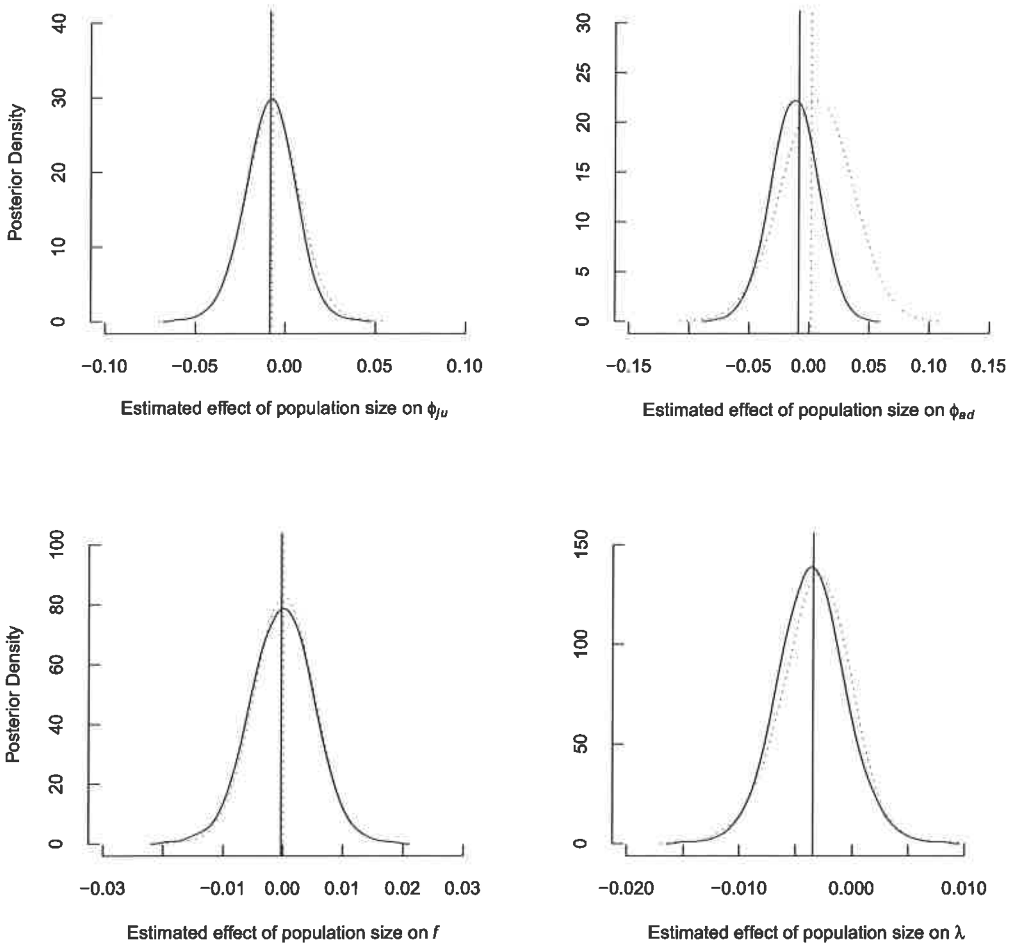

Figure 4.2: *Density plots of the 100 estimated posterior means of strength of density-dependence on juvenile survival (ϕ_{ju}), adult survival (ϕ_{ad}), fecundity (f) and population growth rate (λ) obtained from integrated population model (solid line), and from single data analysis ignoring observation error (dotted line) when the observation error for population count data was small (probability to detect female breeders = 0.90). Vertical lines are the means of the estimated posterior means of the strength of density-dependence over 100 simulations.*

Case study

The annual estimates of age-specific survival, fecundity and population growth rate declined with increasing population size in hoopoes (Figure 4.3), suggesting density-dependence in these demographic parameters and at the population level. We then explicitly estimated the strength of density-dependence on the demographic parameters and on the population growth rate using the integrated population model. The estimated linear relationships between demographic rates as well as population growth rate (on the transformed scale) and population size are shown in Figure 4.3.

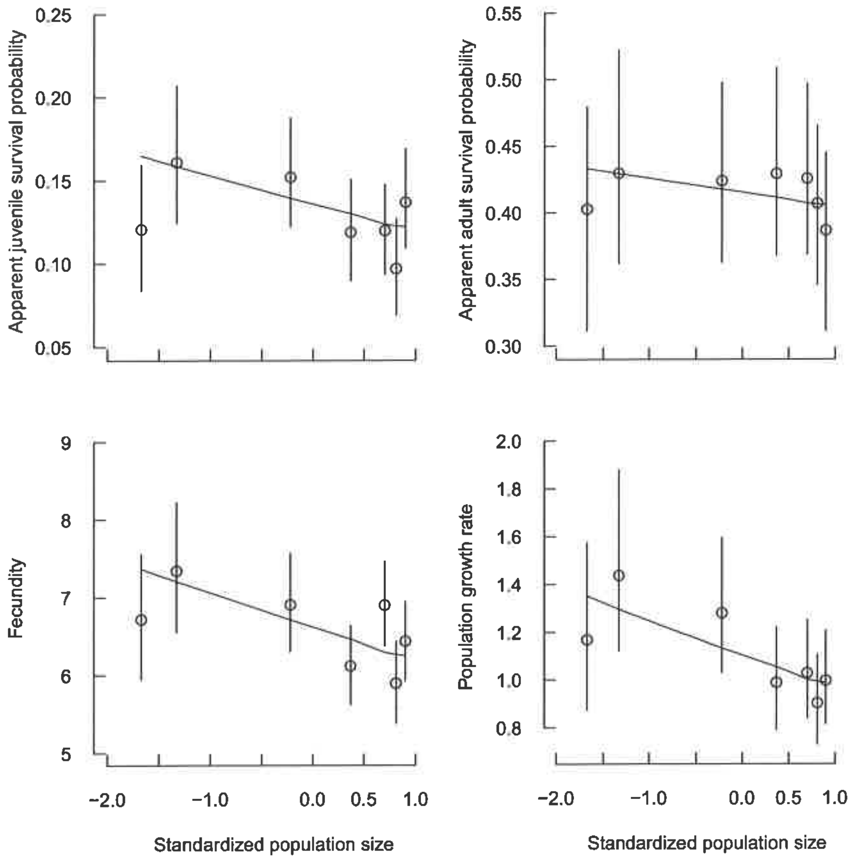

Figure 4.3: *Annual variation in demographic rates and population growth rate against standardized population size in the hoopoe population from the Valais. Posterior means (open circles) with 95% credible intervals (vertical line) obtained from a model without density-dependence, along with the estimated linear relationship between demographic parameters as well as population growth rate and standardized population size to the hoopoes data.*

As expected, the estimates of density-dependence were negative in all parameters: juvenile survival: -0.0070 (95% CRI: (-0.0210, 0.0073)); adult survival: -0.0021 (95% CRI: (-0.0162, 0.0127)); fecunidty: -0.0034 (95% CRI:(-0.0084, 0.0017)); population growth rate: -0.0066 (95% CRI: (-0.0085, 0.0006)). However, the credible intervals for all parameters included zero, thus there was uncertainty about the significance of density-dependence. The most narrow credible intervals had the density-dependence estimates of fecundity and population growth rate (Figure 4.4).

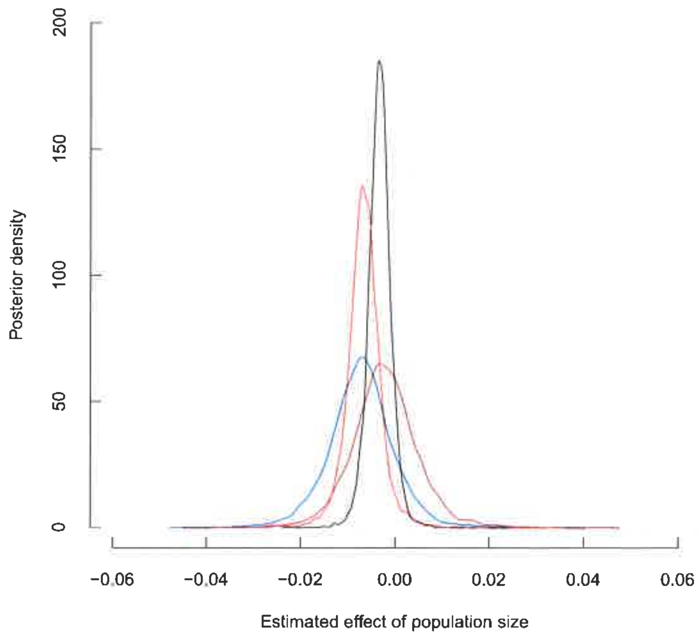

Figure 4.4: *Posterior distributions of the estimated strength of density-dependence on juvenile survival (blue), adult survival (brown), fecundity (black), and population growth rate (red) in hoopoes from the Valais.*

4.5 Discussion

Density-dependence is an important ecological concept, and understanding how it operates is crucial in conservation and harvesting (Sinclair and Pech 1996) or for accurate predictions. In this paper we provide a framework for studying density-dependence using a Bayesian integrated population model. A key advantage of this unifying framework is that it allows estimating strength of density-dependence both at the demographic and population level while accounting for observation error and consequently, the mechanism causing density-dependence can be identified. In contrast, most techniques for testing density-dependence relying on time series data and do not account for observation error or focus either on the effect of density on population growth rate or they consider only a single demographic parameter.

Using simulations, we showed that integrated population models provide estimates of the effect of population size on demographic parameters as well as population growth rate with good precision. The parameters estimating the strength of density-dependence were identifiable regardless of the degree of measurement error in our model. As expected, the estimates were slightly more precise when the observation error was small than large. Our results also highlight that ignoring observation error had different impact on the estimators of the strength of density-dependence at the population and at the demographic level. The results showed that a conventional regression model, which ignores the observation error tended to estimate a stronger density-dependence at the population than at the demographic level. These results are in agreement with previous findings by other authors (e.g. Shenk et al. 1998, Freckleton et al. 2006, Lebreton 2009).

We also illustrated the application of the method using demographic data from a geographically open hoopoe population. We found little support for density-dependence on the demographic parameters with the exception of fecundity and population growth rate. In this study we had only 8 years of observation and the chance to detect strong density-dependence was relatively low (Brook and Bradshaw 2006). However, our integrated population models provide some encouraging results even with this short data set. Our results suggest that the studied hoopoe population is regulated (at least partially) by density, and the underlying demographic mechanism is most likely fecundity.

In our simulation as well as in the case study we expressed density in terms of population size. Since the study area associated with the hoopoes population remained the same over time, the use of population size as a measure of density was justified. However, it is important to note that the influence of density on biological processes can be overlooked due to an inappropriate measure of density (Williams et al. 2002, Barker et al. 2002). Moreover, the main driving force for density-dependence is often competition for resources and not space. Ideally, one would therefore model the strength of density-dependence not with population size, but with available resources per individual. Our model could easily be extended in this way if an estimate of resource availability is at disposition.

The scopes of our simulation were mainly on assessing the identifiability of the estimates of strength of density-dependence and on the evaluation of the effect of observation error. We specified relatively weak density-dependence and a short study period (i.e 10 years), thus conditions where the detection of density-dependence were hard. Yet, the model was able to detect density-dependence in this set-up. However, we could further examine the performance of the model in different directions. For instance, we could set up a simulation varying the strength of density-dependence and also the length of study period. The ability to detect density-dependence is often increases with long time series data (Brook and Bradshaw 2006). We could also assess whether density-dependence could be estimated for parameters for which no explicit data are available. For instance, it would be interesting to assess density-dependence on fecundity based on an integrated analysis that considers only capture-recapture and population count data. In the present study, we looked at the direct effect of density but it is possible that density-dependence can affect demographic parameters and population growth rate with time lag (Paradis et al. 2002). Our model could be extended to study delayed density-dependence. In this study, we used the density-dependence model of the Ricker type for population growth rate (Dennis and Taper 1994). However, our model would be flexible in specifying other density-dependence models which are discussed in the literature (e.g. Dennis and Taper 1994, Jamieson and Brooks 2004). Moreover, some studies have shown the effect can be non-linear (Paradis et al. 2002, Sæther and Engen 2002, Tavecchia et al. 2007). We think that the integrated model could also be extended to assess non-linear density-dependence, for instance by using penalized splines (Gimenez et al. 2006).

Overall, this model provides an improved statistical tool over current methods for estimating density-dependence and offers great potential in conservation/ecological studies.

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5

Immigration is crucial for the local population dynamics and persistence of two rare migratory birds

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5.1 Summary

1. The exchange of individuals between populations can have strong implications for the dynamics and persistence of open, local populations. Yet, the estimation of immigration remains one of the greatest challenges for demographers. Little empirical knowledge exists about the impact of immigration on population dynamics. This situation hampers effective conservation action.

2. Newly integrated population models using a Bayesian framework enable simultaneous estimation of survival, fecundity and immigration, and provide information about the temporal variation of these demographic rates. Retrospective perturbation analysis allows the variation of the population growth rate to be decomposed into relative contributions of the different demographic rates.

3. We applied this novel integrated analytical framework to scrutinize the demography of two populations of long-distance cavity-nesting migratory birds, the hoopoe *Upupa epops* and the wryneck *Jynx torquilla*, which breed sympatrically in south-western Switzerland.

4. The hoopoe population increased annually by 9%, while the wryneck population remained stable (mean annual increase 0.7%). Apparent survival probability (both juvenile and adult) and fecundity differed only slightly between the two species, but immigration was about one third higher in the hoopoe than in the wryneck. In both species, the temporal variation of immigration contributed most to the changes in population growth rate, with a more pronounced relative contribution in the wryneck. The second most important contribution to growth rate was juvenile survival in hoopoes and adult survival in wrynecks.

5. This study provides the first assessment of demographic rates for the hoopoe and the wryneck, two rare and threatened species of Central Europe. The finding that immigration is in both species the factor impacting most on population growth rate shows that demographic regulation takes place beyond the local population, which calls for wide-scale conservation action.

Key-words: Bayesian integrated modeling; demography; *Jynx torquilla*; life table response experiment; *Upupa epops*

5.2 Introduction

The focus of conservation is often a specific population with negative demographic symptoms (Norris 2004) which is geographically open, i.e. characterized by complex patterns of immigration-emigration events. In species exhibiting a high dispersal capacity such as birds (Paradis et al. 1998), there is increasing evidence that the exchange of individuals between populations has a strong impact on local population dynamics and persistence (Newton and Marquiss 1986, Ward 2005, Lampila et al. 2006, Schaub et al. 2006). Of course, other demographic rates such as juvenile and adult survival (Robinson et al. 2004, Schaub et al. 2006) or fecundity (Seamans et al. 2002) may also play a crucial role.

The establishment of the spatial scale at which populations are regulated is important for defining reasonable conservation management units and implementing appropriate action (Baillie et al. 2000, Zannèse et al. 2006, Sirami et al. 2008). The identification of the main demographic process involved in local population dynamics can help to establish such scales. If the variation of reproduction strongly impacts local population dynamics, the spatial scale of regulation and thus conservation action will also be local. If local population dynamics mostly results from variation in survival, the scale depends on the migratory behavior of the species: appropriate mitigation of the main mortality causes must be undertaken at the right place. In resident species, the scale of regulation will be local by definition. In migratory species regulation may operate either on the breeding grounds (hereafter defined as the local scale), or the scale may be extended to include stopover and/or wintering sites. A wider scale for regulation and conservation management must also be accounted for if it is the variation in immigration which is crucial for local population dynamics.

A main obstacle in demographic analyses of open populations is the estimation of immigration rates. From capture-recapture data and data on fecundity, it is straightforward to estimate local recruitment based on apparent juvenile survival, as well as the probability to survive and remain in the population. Thus, all local losses (death plus emigration) can be specified, but only a part of the gains (i.e. local recruitment) is known, which does not allow a complete assessment of the population dynamics. This difficulty is often overcome by assuming that emigration equals immigration (e.g. Reid et al. 2004), which renders it impossible to quantify the relative contributions of the two processes to population dynamics. Other approaches have considered that all newly identified individuals in the population can be considered as recent immigrants (Møller 2002) or that all locally born individuals were marked (O'Hara et al. 2009). However, due to imperfect detectability, the former assumption is in most situations wrong: newly detected individuals might have immigrated into the study population at variable times prior to detection. It is also unlikely that all locally-born young were marked because usually not all breeding sites can be found. With reverse-time capture-recapture modeling it is possible to estimate total recruitment into populations (i.e. local recruitment plus immigration), but this requires the intensive Robust design sampling protocol for separating the two components (Nichols et al. 2000). A recently developed integrated population model (Abadi et al. 2010*b*) allows estimating immigration without relying on strong assumptions and/or cumbersome sampling protocols. This novel framework thus enables studying in detail all demographic components impacting population growth, which represents a major advancement for demographic analyses, especially in the field of conservation biology where one usually has to deal with small sample sizes.

The present study compares the local population dynamics of two long-distance migratory birds, the hoopoe *Upupa epops L.* and the wryneck *Jynx torquilla L.*, both of which have experienced major population declines over the last decades in Central Europe (Tucker and Heath 1994). These two species share several life history characteristics: they are insectivorous birds which search for prey on the ground in sparse vegetation (wryneck: ants, Freitag 1996; hoopoe: molecrickets, Fournier and Arlettaz 2001); both are secondary cavity breeders; they overwinter in the savannahs of the Sahelian belt in Africa (Glutz von Blotzheim and Bauer 1980, Reichlin et al. 2009); finally, they are relatively productive and start to reproduce at the age of one year. Knowledge about their demography is restricted to crude estimates of their life spans (4-6 years, Glutz von Blotzheim and Bauer 1980) and to the finding that adverse weather affects reproductive success (Geiser et al. 2008, Arlettaz et al. in review*a*).

We studied the population dynamics of hoopoes and wrynecks in the Upper Rhône valley (Valais, SW Switzerland) in the Central Alps. The hoopoe population is isolated and has dramatically increased recently (Arlettaz et al. in review*b*), while the wryneck population is part of a continuously distributed large population that seemed to have remained more or less stable. Our goals were (i) to estimate the demographic rates for each species. Then, (ii) we identified which demographic rates have contributed most to the local population growth rate, and finally (iii) which interspecific differences in demography were responsible for the divergent, species-specific demographic trends. We discuss our results in the light of the potential spatial scale of population regulation with respect to their respective geographic structure (isolated, continuous). We used integrated population models fitted in the Bayesian framework to estimate simultaneously all relevant demographic parameters (apparent survival, fecundity, immigration) from our two local, open populations. In order to obtain estimates of the temporal variation of the demographic rates, we extended this model hierarchically, assuming that the annual demographic rates are the realization of a random process with a mean and a variance that were estimated based on the data at hand. Using these estimates we then partitioned the variance of the population growth rate to contributions of the different demographic rates (life table response experiment sensu Horvitz et al. 1997, Caswell 2000, Oli and Armitage 2004). This approach enables a fine-grained recognition of the components of population demography, leading to better appreciation of the necessary underlying species-specific conservation requirements.

5.3 Materials and Methods

5.3.1 Study species and study site

The hoopoe and the wryneck are two small (approx. 75 g and 35 g, respectively) birds of semi-open farmland that are red-listed in Switzerland (Keller et al. 2001). Breeding starts in April and is usually completed in August. Many hoopoes have two regular broods in a breeding season, while this is less frequent in wrynecks. The study area (62 km^2) is situated on the plain of the Rhône valley in the canton of Valais (SW Switzerland, 46 °14′ N, 7 °22′ E; ca 500 m a.s.l.). The area is dominated by intensive agriculture, with numerous fruit tree plantations and vineyards. More than 700 nest boxes were sequentially installed in small agricultural shacks between 1998 and 2001 in an attempt to restore a relictual hoopoe population (Arlettaz et al. 2000). Although the nest boxes have a large cavity size to suit hoopoes' needs, they were also occupied by breeding wrynecks. Local hoopoes are exclusively dependent on these nest boxes as there are virtually no other cavities of suitable size available in the study area. This is different for the wryneck that also uses smaller cavities beyond our control in the study area (e.g. tree cavities or crevices under the roof of agricultural shacks, in piles of wood and poles).

5.3.2 Demographic data

From 2002-2009 we collected three types of demographic data: capture- recapture data (CMR), data on fecundity and population survey data. To obtain capture-recapture data, we ringed all nestlings from nest boxes (ringed nestlings: n_H = 3600, n_W = 1770; hereafter n_H and n_W are for sample sizes of hoopoe and wryneck, respectively) and all adults that we managed to catch using mistnets, traps, or that were taken directly from nest boxes after hatching (n_H = 426, n_W = 603). Because wrynecks react strongly to the song of conspecifics and in order to increase sample size, the wryneck sample additionally contained individuals that were mist-netted with the help of tape-luring during the pre-breeding phase (April). Adult hoopoes were sexed in the field based on the conspicuous uropygial gland, which is filled with a dark liquid in breeding females only (Martín-Vivaldi et al. 2009)(n_{male} = 198, n_{female} = 228). Adult wrynecks captured between 2002 and 2008 (n_{male} = 214, n_{female} = 221) and a subsample of nestlings of both species from the years 2002-2008 (n_H = 207; n_W = 155) were sexed genetically based on blood samples. The sex ratio of nestlings was balanced for both species (hoopoe: 53% females, $\chi^2_1 = 0.82$, $P = 0.37$; wryneck: 48% females, $\chi^2_1 = 0.16$, $P = 0.69$). Thus, we assigned unsexed nestlings to either sex, keeping the overall annual sex-ratio 1:1 (Nichols et al. 2004). A total of 168 adult wrynecks were not sexed.

To obtain data on fecundity, we tightly monitored all broods in nest boxes. Because both species regularly conduct two broods in a season, we calculated for each female the total number of fledglings she produced in a given year (fledged nestlings of known females: hoopoe: $n_{nestlings}$ = 3296 emerging from 725 broods; wryneck: $n_{nestlings}$ = 1474 emerging from 267 broods). For the wryneck we included also broods when the sex of the captured parent(s) was unknown (47 broods). This is justified by the fact that partners in this species usually stay together when performing a second brood (from 14 second broods in which both mates could be captured, none had changed mates relative to the first brood). The focus on the total number of fledglings produced in a season circumvents the difficulty to estimate the frequency of second broods (Cornulier et al. 2009). Thus, the estimated fecundity is an estimate of the total number of fledglings a female is producing in a season, not the number of fledglings per brood.

As a measure of population size, we relied on indices obtained from population surveys. For the hoopoes we used the maximal number of simultaneous broods taking place in the nest boxes in a year. For the wrynecks, nest box occupancy would not have given a reliable index of the population size because of frequent breeding outside our nest boxes. The observed apparent decrease in number of broods during the course of the study (2002: 72, 2009: 44) could have been caused by a progressive abandonment of the nest boxes by wrynecks due to a suboptimal cavity design (Zingg et al. 2010). Therefore, we considered haphazard observations by ornithologists and data collected through the breeding bird survey of the Swiss Ornithological Institute (SOI) in the whole Canton of Valais. From 2002 to 2009 wrynecks had been observed on 210 1 km^2-quadrants. For each quadrant and year, we checked for actual visits by ornithologists, irrespective of the bird species (wryneck or another bird species). We constructed a data matrix where the columns refer to years and the rows to sites, with entry 1 if a wryneck was detected, 0 when no wryneck was detected despite the visit, and a missing value (NA) if the site was not visited. We assumed that wrynecks would have been detected if the site was visited. As this approach aimed at estimating the number of occupied sites in a year, we had to estimate how many of the NA were in fact occupied. This was done by a Bayesian dynamic occupancy model with detection probability set to 1 (Royle and Dorazio 2008). We then used the estimated number of occupied sites as a population index for the integrated model of the wryneck.

5.3.3 Integrated population model

We used integrated population modeling in order to estimate demographic parameters. This model combines the different sources of demographic information into a single model, resulting in an improvement of the precision of parameter estimates, and the ability to estimate demographic parameters for which no explicit data have been sampled (Besbeas et al. 2002, Brooks et al. 2004, Schaub et al. 2007, Abadi et al. 2010*a*). Recently, this model was extended to estimate immigration rate, which renders the model particularly useful for our purpose (Abadi et al. 2010*b*).

The implementation of the integrated population model requires the formulation of the likelihoods of the different data sources (capture-recapture, population survey, and fecundity data). In brief, the likelihood of the capture-recapture data was constructed by assuming that each cohort of released individuals follows a multinomial distribution. This is the well-known Cormack-Jolly-Seber (CJS) model (Lebreton et al. 1992). Fecundity was estimated using a Poisson likelihood, in which the number of fledglings followed a Poisson distribution with the product of fecundity and the number of breeding females as the Poisson parameter.

The likelihood of population survey data is constructed using a state-space model (Besbeas et al. 2002, de Valpine and Hastings 2002), which consists of both a state and an observation process. The state process is described by a female-based, pre-breeding matrix projection model (Caswell 2001) with two age classes. We assumed that reproduction started at one year of age, and that the sex ratio was even. Following Abadi et al. (2010*b*), we used Poisson (Po) and binomial (Bin) models to describe the dynamics of the true population size over time, which directly account for demographic stochasticity. Thus, the number of females that are one year old ($N_{1,t+1}$) in year $t+1$ is given by

$$N_{1,t+1} \sim Po((N_{1,t} + N_{2+,t})(f_t/2)\phi_{ju,t}) + Po((N_{1,t} + N_{2+,t})i_t)$$

and the number of individuals older than 1 year ($N_{2+,t+1}$) is given by

$$N_{2+,t+1} \sim Bin((N_{1,t} + N_{2+,t}), \phi_{ad,t})$$

where $\phi_{ju,t}$ and $\phi_{ad,t}$ are the juvenile and adult apparent survival probabilities of a female at time t (probability that a female survives and does not emigrate permanently between year t and $t+1$), f_t is fecundity at time t, i_t is the immigration rate, defined as the number of female immigrants in year $t+1$ per breeding pair in the population in year t. Immigration was restricted to the class of one year old individuals, thus we assumed that natal dispersal occurred, but no breeding dispersal. This can be justified because natal dispersal is much stronger than breeding dispersal in most bird species (Paradis et al. 1998).

The observation process links the observed population counts (hoopoe) or the estimated number of occupied sites (wryneck) (y_t) in year t to the true population trend using a Poisson distribution, i.e. $y_t \sim Po(N_{1,t} + N_{2+,t})$. The Poisson distribution was used, because counts typically follow a Poisson distribution and because the variance (i.e. the observation error) increases with the mean, which seems appropriate.

To get estimates of the temporal variability of the demographic rates that are not inflated by sampling variability, we used a hierarchical formulation of the integrated model (also called random effect model, Burnham and White 2002). In this formulation, the annual estimates are thought to originate from a random process with a common mean and a temporal variance. For the logit of apparent survival probabilities, we used

$$logit(\phi_t) = \beta_0 + \varepsilon_t \qquad \varepsilon_t \sim N(0, \sigma^2_{logit(\phi)})$$

where β_0 is the mean and $\sigma^2_{logit(\phi)}$ the temporal variance of the logit of apparent survival. We used the log scale to model fecundity and immigration, thus

$$log(f_t) = \alpha_0 + \varepsilon_t \qquad \varepsilon_t \sim N(0, \sigma^2_{log(F)})$$

$$log(i_t) = \gamma_0 + \varepsilon_t \qquad \varepsilon_t \sim N(0, \sigma^2_{log(I)})$$

Again, α_0 and γ_0 are the means and $\sigma^2_{log(F)}$ and $\sigma^2_{log(I)}$ the temporal variances of the log of fecundity and immigration, respectively.

Assuming independence between the different data sources, the joint likelihood of the integrated model is obtained by multiplying the likelihoods of the different data sources (Besbeas et al. 2002, Brooks et al. 2004). A concern in implementing the integrated population model is the violation of the assumption of independence since individuals of the local population are often involved in two or more data sets. However, a recent simulation study using the same types of data as used here has shown that this violation exerts only a minimal impact on the accuracy of the parameter estimates (Abadi et al. 2010*a*). The likelihood of the capture-recapture data of the males were constructed in the same way as that for the females, but was not part of the joint likelihood, unless the sexes were constrained to be identical (see below).

We used the Bayesian approach via a Markov chain Monte Carlo (MCMC) simulation technique for model selection and parameter estimation (Gilks et al. 1996). This approach required defining prior distributions for all model parameters. We specified non-informative priors: normal ($N(0, 10^4)$) priors for the means (β_0,α_0,γ_0), $N(100, 10^4)$ priors truncated to positive values for age-specific population sizes, and uniform ($U(0, 10)$) priors for the temporal standard deviations ($\sigma_{logit(\phi)}$, $\sigma_{log(F)}$, $\sigma_{log(I)}$). We assessed the convergence of the MCMC simulations to the posterior distribution using the convergence diagnostic ($\hat{R}$) (Brooks and Gelman 1998). The $\hat{R}$ values were < 1.02 for all parameters after running three parallel chains of length 30,000, discarding the first 20,000 as burn-in. These results suggested the convergence of the MCMC algorithms. We finally ran a single chain for 1,100,000 iterations, discarding the first 100,000, and thinned such that every 100^{th} observation was retained for parameter estimation. We used the deviance information criterion (DIC, Spiegelhalter et al. 2002, van der Linde 2005), which is a Bayesian equivalent of Akaike information criterion (AIC) for model selection. The model with lowest DIC was considered to be the best among the candidate models. The analyses were performed in WinBUGS (Lunn et al. 2000) and facilitated by using the R2WinBUGS package (Sturtz et al. 2005) in R 2.9.1 (R Development Core Team 2009). The R and WinBUGS codes used for fitting the best model are available on request.

Our goal was to make inference from a simple model. We considered in the models temporal variation of all demographic parameters, because this variability was a crucial component for our inferences. However, we were not sure whether apparent survival also differed between sexes and whether recapture differed between sexes and was time-dependent or constant. We thus compared 16 different models that included or excluded sex effects in apparent survival as well as sex and time effects in recapture probabilities. We treated possible time-dependence of the recapture probability as fixed effects to simplify the models. Because the sex of wrynecks was unknown for all individuals captured in 2009, we evaluated the sex effect using the data until 2008 (see Table A3.1 in Appendix A). For the complete data set (2002-2009), we only fitted models without sex effects.

5.3.4 Life table response experiment

We used a random effects life table response experiment (LTRE) to assess the contribution of the variation of demographic rates to the variation in the population growth rate (λ) (Horvitz et al. 1997, Caswell 2000). The contribution of the variance of the demographic parameter θ is given by the sensitivity of λ to changes in θ ($\frac{\partial\lambda}{\partial\theta}$) and its temporal variability (σ^2_θ) as $\sigma^2_\theta(\frac{\partial\lambda}{\partial\theta})^2$. We assumed that there was no covariance among the demographic rates, because covariances are very difficult to estimate in short term studies and because they are not always important (Altwegg et al. 2007). Since the estimates of the temporal variability of the demographic rates are obtained on the logit or log scale, they were back-transformed to the original scale (survival: $\sigma_\theta^2 \approxeq \sigma_{logit(\theta)}^2 \theta^2 (1-\theta)^2$; fecundity and immigration: $\sigma_\theta^2 \approxeq \sigma_{log(\theta)}^2 \theta^2$.

5.4 Results

Temporal patterns in demographic rates and testing for sex effects

The model selection procedure in hoopoes revealed that the best model included no effect of sex on estimates of apparent survival probabilities, while recapture probability was constant (model 9; Table 5.1). There was no evidence for sex-specific differences in apparent survival probability for wrynecks either (Table A3.1 in Appendix A). Using the complete data set for wrynecks, the best model had a constant recapture probability, while the other demographic parameters were kept time-dependent (model 9; Table 5.1). Overall, the mean demographic rates of the two species were rather similar, but hoopoes produced slightly more fledglings than wrynecks (Table 5.2). The most striking difference between the demographic rates of the two species was in immigration, which was much higher in hoopoes compared to wrynecks. The average population growth rate of hoopoes was clearly larger than 1 (9% increase per year on average), while that of the wryneck was very close to 1 (0.7% increase per year). However, the population growth rates varied strongly over the study period (Figure 5.1). While the hoopoe population strongly increased from 2002-2004 ($\lambda > 1$) and remained fairly stable thereafter ($\lambda \sim 1$), the wryneck population declined from 2002-2004 ($\lambda < 1$) and then increased. The temporal pattern of demographic rates showed a decline in hoopoe fecundity during the course of the study, but no obvious trend in the other rates (Figure 5.1). The apparent survival probabilities of both species and age classes were little variable across time (Table 5.2).

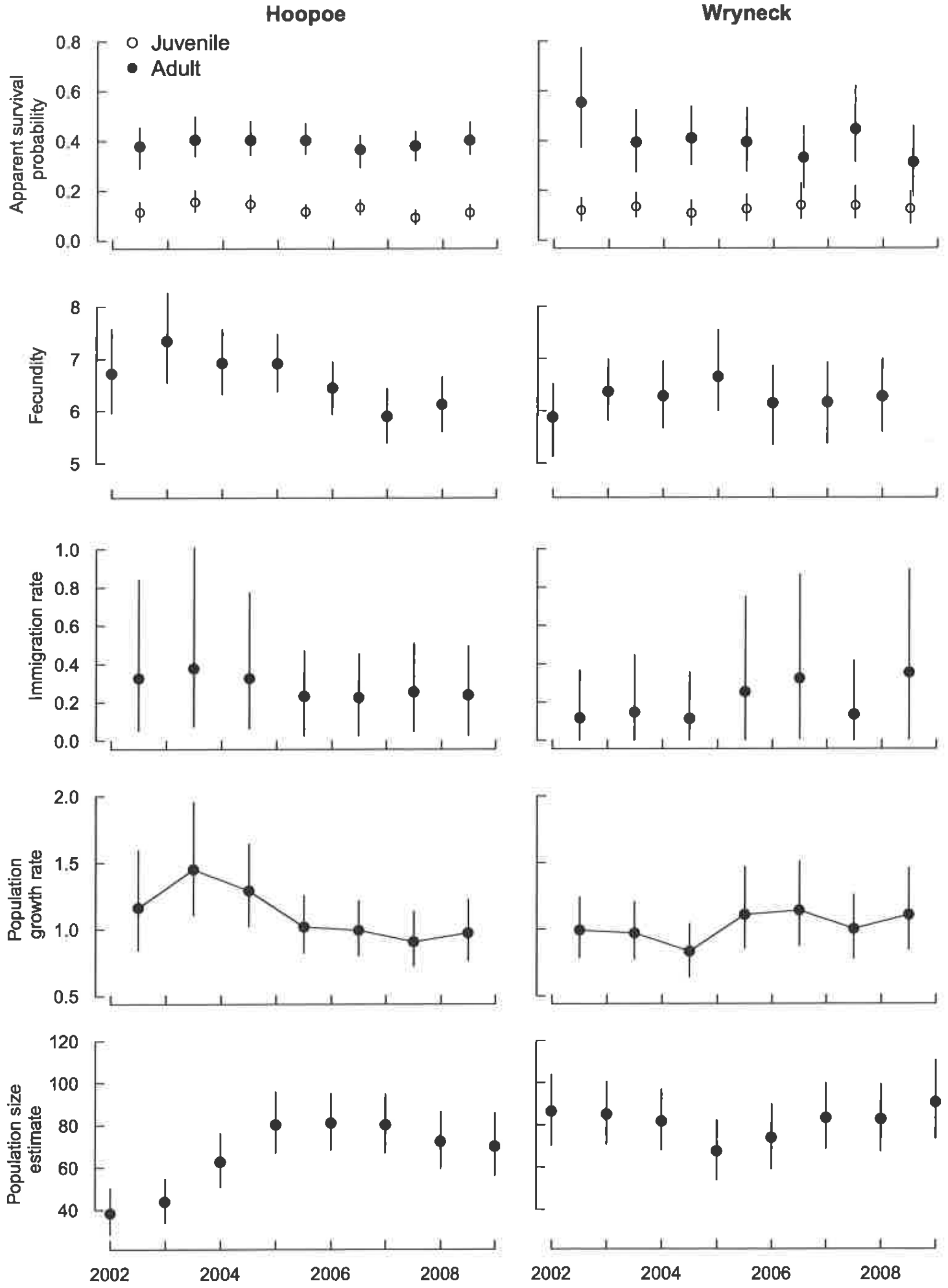

Figure 5.1: *Estimates of annual demographic parameters, population growth rates and population sizes obtained from the best model (Table 5.1) along with 95% credible intervals for hoopoe (left panel) and wryneck (right panel).*

Table 5.1: *Model selection results for the best pattern of demographic rates of hoopoe and wryneck from the Valais (2002-2009) based on the deviance information criterion (DIC). The model deviance, the effective number of parameters (pD), and the difference between the DIC of the current model and the best model (ΔDIC) are provided.* ϕ_{ju} *and* ϕ_{ad} *are juvenile and adult apparent survival probabilities, respectively, p is the recapture probability, f is fecundity, i is the immigration rate, (t) stands for year-specific rates - treated as random factor for survival, fecundity and immigration rates but as fixed factor for recapture rates; (.) stands for constant, and (s) for the sex effect.*

Model number	Model notation	Hoopoe			Wryneck		
		Deviance	pD	ΔDIC	Deviance	pD	ΔDIC
1	$\phi_{ju}(t), \phi_{ad}(t), p(t), f(t), i(t)$	292.40	30.45	32.80	317.80	24.30	20.40
2	$\phi_{ju}(t), \phi_{ad}(t), p(t+s), f(t), i(t)$	294.75	30.72	35.41	-	-	-
3	$\phi_{ju}(t), \phi_{ad}(t+s), p(t), f(t), i(t)$	297.79	30.58	38.32	-	-	-
4	$\phi_{ju}(t), \phi_{ad}(t+s), p(t+s), f(t), i(t)$	300.10	32.19	42.23	-	-	-
5	$\phi_{ju}(t+s), \phi_{ad}(t), p(t), f(t), i(t)$	297.68	31.15	38.77	-	-	-
6	$\phi_{ju}(t+s), \phi_{ad}(t), p(t+s), f(t), i(t)$	300.87	31.91	42.73	-	-	-
7	$\phi_{ju}(t+s),\phi_{ad}(t+s), p(t), f(t), i(t)$	303.09	31.96	44.99	-	-	-
8	$\phi_{ju}(t+s), \phi_{ad}(t+s), p(t+s), f(t), i(t)$	306.11	32.77	48.83	-	-	-
9	$\phi_{ju}(t), \phi_{ad}(t), p(.), f(t), i(t)$	264.78	25.28	0.00	291.77	30.00	0.00
10	$\phi_{ju}(t), \phi_{ad}(t+s), p(.), f(t), i(t)$	270.61	26.47	7.02	-	-	-
11	$\phi_{ju}(t+s), \phi_{ad}(t), p(.),f(t), i(t)$	270.21	26.15	6.30	-	-	-
12	$\phi_{ju}(t+s), \phi_{ad}(t+s), p(.),f(t), i(t)$	275.78	27.70	13.42	-	-	-
13	$\phi_{ju}(t), \phi_{ad}(t), p(s), f(t), i(t)$	269.09	26.71	5.75	-	-	-
14	$\phi_{ju}(t), \phi_{ad}(t+s), p(s), f(t), i(t)$	274.11	27.96	12.02	-	-	-
15	$\phi_{ju}(t+s), \phi_{ad}(t), p(s), f(t), i(t)$	269.48	26.30	5.73	-	-	-
16	$\phi_{ju}(t+s), \phi_{ad}(t+s), p(s), f(t), i(t)$	280.30	28.60	18.85	-	-	-

Table 5.2: *Estimates of posterior mean with 95% credible intervals (CRI) and temporal variance ($\hat{\sigma}^2$) of demographic rates obtained from the best model (Model 9, Table 5.1) for hoopoe and wryneck from Valais (2002-2009).*

Demographic rates	Hoopoe		Wryneck	
	Mean (95% CRI)	$\hat{\sigma}^2$	Mean (95% CRI)	$\hat{\sigma}^2$
Juvenile survival	0.1219 (0.0913, 0.1579)	0.001	0.1263 (0.0849, 0.1750)	0.0008
Adult survival	0.3907 (0.3418, 0.4423)	0.002	0.4038 (0.2800, 0.5526)	0.0180
Fecundity	6.6056 (5.9540, 7.3241)	0.559	6.2423 (5.6670, 6.8000)	0.2150
Immigration	0.2597 (0.0672, 0.4713)	0.031	0.1704 (0.0010, 0.4654)	0.0720
Population growth rate	1.0910 (1.0360, 1.1490)	-	1.0068 (0.9678, 1.0470)	-

Contribution of demographic rates to the variation in growth rate

The LTRE analyses revealed that the variation of immigration rate contributed most and the variation of fecundity least to the observed variation in population growth rate in both species (Figure 5.2). For hoopoes, variation of apparent juvenile survival contributed second most to the observed changes in population growth rate, while for wryneck the variation of apparent adult survival contributed second most.

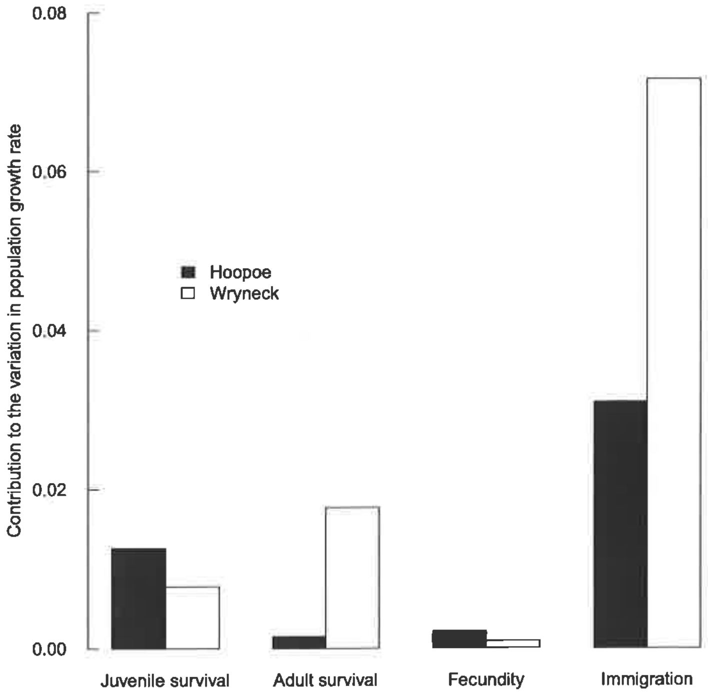

Figure 5.2: *The contributions of each of the demographic rates to the variation in the population growth rate for hoopoe (black) and wryneck (white).*

5.5 Discussion

Our study revealed that the temporal variation of the immigration rate had a strong impact on the dynamics of two local populations of hoopoe and wryneck, while the temporal variation of fecundity had virtually no effect at the local population level. The impact of apparent survival was intermediate and differed between the two species according to age class: variation in apparent adult survival contributed much to variation in growth rate in the wryneck, whereas variability in apparent juvenile survival was a major component of the variation of population growth in the hoopoe. The striking difference in population development of the two species (hoopoes increased dramatically whilst wrynecks remained more or less stable) was mostly due to differential immigration, since the other demographic parameters were nearly identical in both species.

In the study of population dynamics, integrated models can provide detailed information, especially as regards immigration, which was so far in most cases assessed based on untested assumptions such as perfect capture probability (Møller 2002): the price to be paid is the relatively low precision in the estimation of immigration, which may hamper inference. An apparent weakness of our model is the assumption that all immigrants are one-year old birds. However, since apparent survival and fecundity of one-year old birds and older birds did not differ, the immigration rate would be the same had we assumed that all immigrants were older than one year. Thus, the assumption appears to have an impact on the inference, but not on the estimate itself. The reliance on a hierarchical formulation further enabled us to estimate the temporal variance of the demographic rates, which was crucial for the decomposition of the variance components with respect to population growth. Contrastingly, in fixed effects models, the observed fluctuation of the demographic rates from year to year is assumed to be determined entirely by mechanistic differences among years, without considering that these rates were also subject to sampling variation (variation stemming from the fact that only a subset of the population is sampled). In that case, only approximations have been used to separate temporal from sampling variation (Gould and Nichols 1998, Burnham and White 2002). However, even with our applied hierarchical models, there remains the problem of the relatively short time series (8 years), which weakens the precision of the demographic rate estimates.

Immigrants are individuals breeding in the study population but that were born outside it. Depending on the distribution of other populations with respect to the study population, immigrants may originate from far or from nearby. The studied hoopoe population is very much isolated; the next hoopoe populations of comparable sizes are 250 to 350 km away (Trento, Italy; Kaiserstuhl, Germany). In between, there are only scattered breeding pairs (Canton of Vaud, Switzerland; Valle d'Aosta, Italy). We furthermore have a good control of the Valais breeding population because hoopoes occupy almost exclusively nest boxes, which are systematically controlled since years. Thus, in the case of the hoopoe, immigrants are most probably individuals that were born in populations several dozens of kilometers away from our study population. The origin of these immigrants remains unknown, as analyses of stable isotopes in feathers have found no distinctive signature in isotopic values of local birds vs. possible immigrants (Reichlin et al. in prep.). The situation is different for wrynecks because they also breed in cavities other than our nest boxes and because our study population is part of a larger population. For this species, immigrants are therefore not only individuals imported from another population, but may include individuals born within the same local population. Consequently, the interpretation of the immigration rate of the wrynecks must be considered with caution.

The main outcome regarding the crucial role of immigration can be explained by a high sensitivity of the two bird population growth rates to changes in immigration and/or by the large temporal variation of the immigration rate. Immigration was not only the main demographic mechanism for the boost of the hoopoe population during the colonization phase, but also remained an important component in the stabilizing phase (Figure 5.1). The population growth rates of both species would be similar if no immigration had occurred (hoopoe: 0.83; wryneck: 0.84). These values well below 1 suggest that both populations would not be self-sustainable without immigration. Yet, true juvenile survival is probably higher than estimated here (hoopoe: 0.092 - 0.154; wryneck: 0.108 - 0.140), i.e. closer to what is observed in birds of similar body size ($\sim$0.2, Siriwardena et al. 1998). This indeed suggests that a large fraction of the juveniles emigrate from the local populations. The proportion of emigrants can roughly be estimated under a simplistic scenario where i) no adult would settle outside our local populations (Greenwood and Harvey 1982), i.e. the observed apparent adult survival were the true survival (0.39 and 0.40, for hoopoes and wrynecks, respectively); and ii) immigration would be absent. Under these assumptions, population growth rate would be a mere function of adult survival plus fecundity multiplied by juvenile survival. The latter is the only unknown parameter in the equation and is calculable. Under this fictive scenario, juvenile survival must be 0.21 and 0.19 for local hoopoes and wrynecks, respectively, to obtain the actual, observed population growth rates (Table 5.2). This would result in an emigration probability of juveniles of 0.43 in hoopoes (1-0.12/0.21) and 0.32 in wrynecks (1-0.13/0.19). Although true emigration rates cannot be assessed definitely, the hoopoe and wryneck populations appear thus to be part of an open-recruitment system, in which an important part of the recruited breeding birds were not produced locally, while the local populations export a lot of young individuals. For hoopoes this system extends over a large area, while for the wryneck the spatial extent is uncertain, but likely much smaller than in hoopoes. Open-recruitment systems seem to be frequent in spatially structured bird populations (Newton and Marquiss 1986, Stacey and Taper 1992, Lambrechts et al. 1999, Baillie et al. 2000, Murphy 2001, Franklin et al. 2004, Schaub et al. 2006). Assessing whether the systems have the characteristics of sink-source dynamics (Dias 1996) or of balanced dispersal (McPeek and Holt 1992) would require detailed knowledge of the demographic performance of several single local populations, which remains a logistic research challenge (Doncaster et al. 1997).

Besides immigration, variation of apparent survival also contributed to variation of population growth. The importance of recruitment to population dynamics is usually distinctive for short-lived species (Sæther and Bakke 2000). In the hoopoe, juvenile apparent survival - i.e. a component of local recruitment (local recruitment = fecundity × apparent juvenile survival) - was important, but not adult survival. In contrast, in the wryneck, it is the variation of adult survival which contributed more to population growth. From a conservation viewpoint, it would be essential to identify the factors impacting on species- and age-specific survival. However, in order to obtain more precise estimates and to identify causes of their temporal variability, longer time series than 8 years are needed.

Although both species were very productive and fecundity fluctuated markedly over time, the variation in the total number of fledglings produced did only weakly contribute to the variation of the population growth rates. Most probably, this is because many of the fledged individuals emigrated from the populations. This does not mean, however, that local reproduction is unimportant. The locally produced young that emigrate from the local population are the immigrants to other populations, which may be a very central component for the latter population. Thus, local reproduction is important to stabilize the system of spatially structured populations, but not so much for the local population under scope (Baillie et al. 2000, Schaub et al. 2006).

The dynamics of many bird populations are synchronized across large spatial scales (e.g. Sæther et al. 2007, Jones et al. 2007), implying that population regulation operates beyond the local scale. Theoretical models suggest spatial correlation of the environment and dispersal to be the main reasons for population synchrony (Lande et al. 1999), and much empirical evidence is in favor of the former mechanism (Schaub et al. 2005, Sæther et al. 2007). Our demographic analysis showed that immigration was the main driver of local population dynamics, thus there is the potential of larger scale population synchrony due to dispersal. Indeed, population trends of both species are known to be synchronized across different countries (Glutz von Blotzheim and Bauer 1980). Because the regulation of both studied populations probably operates beyond the study area, conservation management must be planned on a wider spatial scale. For the hoopoe, the scale of management extends over several dozens of kilometers. The situation of the wryneck is less clear and requires further studies.

This study establishes that the population dynamics of two endangered sympatric species exhibiting similar life histories was strongly dependent on immigration, which was much higher in hoopoes than in wrynecks. The hoopoe population, which was on the brink of extinction before the start of our study, has been rapidly recovering after the installation of hundreds of nest boxes since 1999, which increased the number of breeding sites that were the most limiting factor locally (Fournier and Arlettaz 2001). The fast population increase was facilitated by high immigration from pre-existing population reservoirs. In contrast, the wryneck population seems to have remained relatively stable, with an immigration rate possibly typical of saturated populations. Effective conservation of such geographically structured populations thus necessitates maintaining and/or restoring of habitat of suitable quality within and beyond the focal population.

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6

Summary and future directions

6.1 Summary

The main aims of this thesis have been to assess the performance of basic integrated population models, to further extend them to geographically open populations, and to use them to estimate the strength of density-dependence. In Chapter 2, we demonstrated that combining different sources of information into a single model leads to improved precision of the estimates of demographic parameters, particularly when the sample size is small. This finding mitigates the problem of low sample size, which is often a serious problem in conservation/ecological studies. The performance of population models that integrate capture-recapture data, population survey, and data on reproductive success was good, even if the basic assumption of independence was violated. In Chapter 3, we developed a Bayesian integrated population model to estimate immigration to a geographically open population. We showed that this parameter can be estimated without having explicit data to it and that it is possible to model the effect of environmental covariates. In Chapter 4, we extended the integrated population model to estimate the strength of density-dependence. A simulation study demonstrated how inference about density-dependence can be obtained simultaneously both at the population and demographic level while accounting for observation errors. This allowed to infer which demographic mechanism has caused density-dependence. In

Chapter 5, we applied an integrated population model in open populations of two endangered bird species. The results showed that the local hoopoe population increased, while the wryneck population remained stable. In both species, immigration contributed most to the changes in the population growth rate.

6.2 Future directions

The development of integrated population models is still in progress; a number of possible areas of future research could be envisioned. In the integrated population model we considered, capture-recapture data were used to extract information about survival probability only. However, capture-recapture data would also contain information about population size, recruitment, and population growth rate (Schwarz and Seber 1999, Pradel 1996). Theoretically, it would thus be possible to use this information in the integrated population model. However, it is not clear whether this would result in biased estimates of uncertainty, because the assumption of independence is heavily violated in this case. This issue could be explored by simulations. At the same time it could be evaluated whether the extraction of other demographic information than survival from the capture-recapture data significantly improves the precision of the parameter estimates and what additional insights can be gained.

We have shown that the estimation of immigration rate without having explicit data on it is possible using an integrated population model. However, there are still some open questions for future research. For instance, it is not clear how the observation error associated with the population counts affects the estimate of immigration rate. This could be explored by a further simulation study.

The integrated population model could also be extended to estimate all demographic parameters (survival, birth, immigration, and emigration) of geographically open populations. This could be achieved, for instance, by combining capture-recapture, ring-recovery, population counts, and data on reproductive success into a single model. This work could be seen as an extension of the model proposed by Burnham (1993) where capture-recapture and dead-recovery data were analyzed simultaneously to obtain separate estimates of true survival and permanent emigration. This kind of model would be useful to assess whether a local population is a source or a sink in a more coherent fashion.

In wildlife studies, demographic and time series data could be arising from several study sites (locations). Extending the standard integrated population models to modeling the spatial variation would be a useful future research topic as it would give more realism to the type of data we have in most ecological studies. In this case, a spatial effect could be incorporated within a hierarchical formulation into the existing integrated population models. Moreover, this could allow to scale up, i.e. to study whether the same demographic mechanisms are responsible for population regulation at the local and at larger spatial scales.

In this thesis, the strength of density-dependence was explored assuming a linear relationship between demographic parameters/population growth rate (on the transformed scale) and density. Many studies have shown that the effect of density can be non-linear (e.g. Sæther and Engen 2002). Thus, an integrated population model could be developed in such a way to address this issue. One way to achieve this is using penalized splines (Ruppert et al. 2003, Gimenez et al. 2006). In this case the shape of the relationship is determined by the data rather than specified *a priori*.

Although the use of integrated population model in wildlife studies becomes increasing, still no goodness-of-fit (GOF) test is available for this model. The development of GOF approach is very crucial for establishing credibility and confidence of the integrated population model.

Overall, the developed integrated population models are a very promising tool to better understand the population dynamics of wildlife species. This understanding is an essential step on the way to save populations of declining species or to manage populations of harvested species.

6.3 References

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A

Supporting Information

Appendix for Chapter 1

	Individual A					Individual B					Individual C				
	time					*time*					*time*				
	1	*2*	*3*	*4*	*5*	*1*	*2*	*3*	*4*	*5*	*1*	*2*	*3*	*4*	*5*
Juv	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0
1y	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
2+y	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1
Dead	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Offspring	1	2	0	0	0	0	0	0	0	0	0	0	2	3	3

Figure A1.1: *Life histories of three individuals (A, B, and C) over a five year study period. Individual B and C are the two offspring of individual A that were born in year 2. Columns represent study years, rows represent the state of the individual and the number of newborn it has produced. Individual A was 1 year old and produced 1 offspring in year 1, it was still alive in year 2 (now it is in age class 2+) where it produced 2 offspring, it was still alive in year 3 but had no offspring, and it dies between year 3 and 4. Individual B died between year 2 and 3. Individual C was still alive at the end of the study and it produced 2, 3 and 3 offspring in years 3, 4 and 5 respectively.*

Table A1.1: *Relative bias (rel. bias), precision (std. error: standard error) and accuracy (MSE: mean squared error) of the parameter estimates obtained with integrated and separate analyses (CR: capture-recapture, RS: reproductive success, PS: population survey) for different sample sizes under independent and dependent scenarios.*

	Juvenile survival rate			Adult survival rate			Fecundity rate		
	rel. bias	std. error	MSE	rel. bias	std. error	MSE	rel. bias	std. error	MSE
Independent, small									
CR, PS and RS	0.0890	0.0470	0.0025	-0.0228	0.0943	0.0090	-0.0094	0.2312	0.0541
CR and PS	0.2560	0.0813	0.0092	0.0274	0.1026	0.0107	-0.0712	0.9801	0.9949
CR only	0.2515	0.0817	0.0092	0.0094	0.1080	0.0117	-	-	-
RS only	-	-	-	-	-	-	-0.0037	0.2337	0.0547
Dependent, small									
CR, PS and RS	0.0705	0.0480	0.0025	-0.0250	0.0990	0.0100	-0.0009	0.2333	0.0544
CR and PS	0.273	0.0914	0.0113	0.0316	0.1034	0.0109	-0.0867	0.9299	0.9155
CR only	0.2740	0.0919	0.0114	0.0162	0.1090	0.0119	-	-	-
RS only	-	-	-	-	-	-	0.0045	0.2372	0.0564
Independent, medium									
CR, PS and RS	0.0050	0.0174	0.0003	0.0034	0.0372	0.0014	-0.0018	0.0884	0.0078
CR and PS	0.0295	0.0250	0.0007	0.0162	0.0433	0.0019	-0.0296	0.4515	0.2098
CR only	0.0280	0.0249	0.0007	0.0102	0.0430	0.0019	-	-	-
RS only	-	-	-	-	-	-	-0.0004	0.0895	0.0080

Table A1.1 – *continued from previous page*

	Juvenile survival rate			Adult survival rate			Fecundity rate		
	rel. bias	std. error	MSE	rel. bias	std. error	MSE	rel. bias	std. error	MSE
Dependent, medium									
CR, PS and RS	0.0095	0.0183	0.0003	-0.0056	0.0377	0.0014	-0.0004	0.0923	0.0085
CR and PS	0.0355	0.0263	0.0007	0.0066	0.0418	0.0018	-0.0258	0.3877	0.1548
CR only	0.0345	0.0263	0.0007	0.0001	0.0415	0.0017	-	-	-
RS only	-	-	-	-	-	-	0.0006	0.0942	0.0089
Independent, large									
CR, PS and RS	0.0050	0.0125	0.0002	-0.0014	0.0251	0.0006	-0.0006	0.0627	0.0039
CR and PS	0.0145	0.0189	0.0004	0.0032	0.0297	0.0009	-0.0050	0.3208	0.1031
CR only	0.0140	0.0189	0.0004	0.0002	0.0297	0.0009	-	-	-
RS only	-	-	-	-	-	-	-0.0002	0.0633	0.0040
Dependent, large									
CR, PS and RS	0.0010	0.0127	0.0002	-0.0008	0.0276	0.0008	-0.0015	0.0593	0.0035
CR and PS	0.0100	0.0182	0.0003	0.0036	0.0313	0.0010	-0.0055	0.2869	0.0825
CR only	0.0101	0.0183	0.0003	0.0008	0.0313	0.0010	-	-	-
RS only	-	-	-	-	-	-	-0.0012	0.0602	0.0036

Table A2.1: **Appendix for chapter 2:** *Mean and standard error (SE) of demographic rates of little owl females obtained from capture-recapture and fecundity data analyzed with the "two steps" approach (Schaub et al. 2006). Note that we report the average immigration rate across years in order to match the result as much as possible with those from the integrated models.*

	Juvenile survival		Adult survival		Fecundity		Immigration	
Year	mean	SE	mean	SE	mean	SE	mean	SE
1978	0.0407	0.0003	0.5814	0.0069	1.9510	0.4380	0.2660	0.0220
1979	0.0410	0.0003	0.5817	0.0052	2.1520	0.5650	0.2660	0.0220
1980	0.0414	0.0002	0.5828	0.0040	2.6310	0.5990	0.2660	0.0220
1981	0.0421	0.0002	0.5848	0.0033	1.7180	0.4120	0.2660	0.0220
1982	0.0429	0.0002	0.5878	0.0030	2.4480	0.4000	0.2660	0.0220
1983	0.0439	0.0002	0.5917	0.0029	2.6180	0.4240	0.2660	0.0220
1984	0.0450	0.0002	0.5966	0.0030	2.1060	0.4700	0.2660	0.0220
1985	0.0463	0.0002	0.6025	0.0031	2.6810	0.5650	0.2660	0.0220
1986	0.0477	0.0003	0.6093	0.0032	2.4980	0.5990	0.2660	0.0220
1987	0.0493	0.0003	0.6171	0.0033	2.4580	0.5650	0.2660	0.0220
1988	0.0511	0.0003	0.6258	0.0033	2.2370	0.5650	0.2660	0.0220
1989	0.0531	0.0003	0.6355	0.0033	2.0500	0.5120	0.2660	0.0220
1990	0.0552	0.0003	0.6460	0.0032	2.3980	0.4700	0.2660	0.0220
1991	0.0577	0.0003	0.6574	0.0031	2.5970	0.5110	0.2660	0.0220
1992	0.0603	0.0003	0.6695	0.0031	2.7210	0.5110	0.2660	0.0220
1993	0.0633	0.0003	0.6822	0.0032	2.7280	0.5110	0.2660	0.0220

Table A2.1 – *continued from previous page*

	Juvenile survival		Adult survival		Fecundity		Immigration	
Year	mean	SE	mean	SE	mean	SE	mean	SE
1994	0.0666	0.0004	0.6954	0.0035	1.5490	0.5360	0.2660	0.0220
1995	0.0704	0.0004	0.7089	0.0040	1.7510	0.6400	0.2660	0.0220
1996	0.0746	0.0005	0.7225	0.0047	2.6150	0.7570	0.2660	0.0220
1997	0.0793	0.0006	0.7359	0.0056	2.1630	0.7580	0.2660	0.0220
1998	0.0847	0.0008	0.7491	0.0066	2.5930	0.5990	0.2660	0.0220
1999	0.0908	0.0012	0.7617	0.0077	2.4440	0.4890	0.2660	0.0220
2000	0.0979	0.0017	0.7738	0.0087	2.1310	0.4530	0.2660	0.0220
2001	0.1060	0.0026	0.7851	0.0098	2.1610	0.4370	0.2660	0.0220
2002	0.1153	0.0039	0.7957	0.0107	1.8790	0.3790	0.2660	0.0220

Table A2.2: *Mean and standard deviation (SD) of demographic rates of little owl females obtained from capture-recapture data, population counts and fecundity data analyzed with the integrated population model.*

	Juvenile survival		Adult survival		Fecundity		Immigration	
Year	mean	SD	mean	SD	mean	SD	mean	SD
1978	0.0462	0.0136	0.5474	0.0514	1.8032	0.3504	0.2934	0.0621
1979	0.0474	0.0135	0.5547	0.0488	2.1538	0.4788	0.2934	0.0621
1980	0.0487	0.0135	0.5621	0.0464	3.1935	0.6545	0.2934	0.0621
1981	0.05	0.0134	0.5694	0.0442	1.5102	0.2984	0.2934	0.0621
1982	0.0513	0.0134	0.5766	0.0423	2.6047	0.381	0.2934	0.0621
1983	0.0527	0.0134	0.5839	0.0407	2.8886	0.422	0.2934	0.0621
1984	0.0541	0.0134	0.5911	0.0394	2.0178	0.4005	0.2934	0.0621
1985	0.0556	0.0134	0.5982	0.0384	3.229	0.5937	0.2934	0.0621
1986	0.0571	0.0136	0.6053	0.0379	2.9226	0.5852	0.2934	0.0621
1987	0.0587	0.0137	0.6124	0.0377	2.6863	0.5687	0.2934	0.0621
1988	0.0603	0.0139	0.6194	0.0379	2.2591	0.5115	0.2934	0.0621
1989	0.062	0.0142	0.6263	0.0384	1.9454	0.4185	0.2934	0.0621
1990	0.0637	0.0146	0.6331	0.0392	2.5754	0.4347	0.2934	0.0621
1991	0.0655	0.015	0.6399	0.0403	2.8995	0.5221	0.2934	0.0621
1992	0.0674	0.0155	0.6466	0.0417	3.1741	0.5539	0.2934	0.0621
1993	0.0693	0.0161	0.6532	0.0433	3.1865	0.5441	0.2934	0.0621

Table A2.2 – *continued from previous page*

	Juvenile survival		Adult survival		Fecundity		Immigration	
Year	mean	SD	mean	SD	mean	SD	mean	SD
1994	0.0713	0.0167	0.6597	0.045	0.8213	0.2876	0.2934	0.0621
1995	0.0734	0.0175	0.6661	0.0468	1.0477	0.3789	0.2934	0.0621
1996	0.0755	0.0184	0.6725	0.0487	3.4095	0.8145	0.2934	0.0621
1997	0.0777	0.0193	0.6787	0.0507	2.0796	0.6293	0.2934	0.0621
1998	0.08	0.0204	0.6849	0.0527	3.0363	0.6189	0.2934	0.0621
1999	0.0823	0.0215	0.6909	0.0548	2.6212	0.4544	0.2934	0.0621
2000	0.0847	0.0228	0.6969	0.0569	1.9978	0.379	0.2934	0.0621
2001	0.0872	0.0241	0.7027	0.0589	2.0006	0.3624	0.2934	0.0621
2002	0.0898	0.0256	0.7085	0.0609	1.6498	0.2861	0.2934	0.0621

Table A2.3: *Mean and standard deviation (SD) of demographic rates of little owl females obtained from capture-recapture data and population counts analyzed with the integrated population model.*

	Juvenile survival		Adult survival		Fecundity		Immigration	
Year	mean	SD	mean	SD	mean	SD	mean	SD
1978	0.0443	0.0134	0.5451	0.0528	2.5838	1.4168	0.2875	0.0622
1979	0.0455	0.0133	0.5527	0.0504	2.6726	1.4368	0.2875	0.0622
1980	0.0467	0.0133	0.5603	0.0482	2.8028	1.4044	0.2875	0.0622
1981	0.048	0.0132	0.5678	0.0462	2.8297	1.3596	0.2875	0.0622
1982	0.0493	0.0132	0.5753	0.0444	2.6153	1.4534	0.2875	0.0622
1983	0.0507	0.0133	0.5828	0.0429	2.6338	1.4607	0.2875	0.0622
1984	0.0521	0.0133	0.5902	0.0417	2.6145	1.4572	0.2875	0.0622
1985	0.0536	0.0134	0.5976	0.0408	2.4781	1.4186	0.2875	0.0622
1986	0.0551	0.0135	0.6049	0.0402	2.6963	1.4137	0.2875	0.0622
1987	0.0567	0.0137	0.6122	0.0399	2.6117	1.4099	0.2875	0.0622
1988	0.0583	0.0139	0.6194	0.0399	2.7006	1.4083	0.2875	0.0622
1989	0.06	0.0141	0.6266	0.0403	2.7267	1.369	0.2875	0.0622
1990	0.0617	0.0144	0.6336	0.0409	2.5933	1.4026	0.2875	0.0622
1991	0.0635	0.0148	0.6406	0.0418	2.6186	1.4499	0.2875	0.0622
1992	0.0653	0.0153	0.6475	0.0429	2.5212	1.4116	0.2875	0.0622
1993	0.0673	0.0158	0.6544	0.0442	2.5077	1.412	0.2875	0.0622

Table A2.3 – *continued from previous page*

	Juvenile survival		Adult survival		Fecundity		Immigration	
Year	mean	SD	mean	SD	mean	SD	mean	SD
1994	0.0692	0.0164	0.6611	0.0456	2.445	1.4126	0.2875	0.0622
1995	0.0713	0.0171	0.6677	0.0472	2.468	1.4306	0.2875	0.0622
1996	0.0734	0.0179	0.6743	0.0489	2.5338	1.4302	0.2875	0.0622
1997	0.0756	0.0187	0.6807	0.0506	2.7237	1.4288	0.2875	0.0622
1998	0.0779	0.0197	0.6871	0.0524	2.8842	1.3774	0.2875	0.0622
1999	0.0802	0.0207	0.6933	0.0542	2.7933	1.3892	0.2875	0.0622
2000	0.0826	0.0218	0.6995	0.0561	2.6779	1.3887	0.2875	0.0622
2001	0.0851	0.0231	0.7055	0.0579	2.7245	1.3932	0.2875	0.0622
2002	0.0877	0.0244	0.7115	0.0597	2.7328	1.4227	0.2875	0.0622

Appendix for Chapter 3

Table A3.1: *Model selection results of demographic rates of wrynecks with data from 2002-2008 based on the deviance information criterion (DIC). The model deviance, the effective number of parameters (pD), and the difference between the DIC of the current model and the best model (ΔDIC) are provided.* ϕ_{ju} *and* ϕ_{ad} *are juvenile and adult apparent survival probabilities, respectively, p is the recapture probability, f is fecundity, i is the immigration rate, (t) stands for year-specific rates - treated as random factor for survival, fecundity and immigration rates but as fixed factor for recapture rates; (.) stands for constant, and (s) for the sex effect.*

Model number	Model notation	Deviance	pD	ΔDIC
1	$\phi_{ju}(t), \phi_{ad}(t), p(t), f(t), i(t)$	300.48	25.00	24.10
2	$\phi_{ju}(t), \phi_{ad}(t), p(t+s), f(t), i(t)$	306.46	26.20	31.30
3	$\phi_{ju}(t), \phi_{ad}(t+s), p(t), f(t), i(t)$	305.44	25.20	29.30
4	$\phi_{ju}(t), \phi_{ad}(t+s), p(t+s), f(t), i(t)$	311.28	26.80	36.70
5	$\phi_{ju}(t+s), \phi_{ad}(t), p(t), f(t), i(t)$	306.19	26.20	31.00
6	$\phi_{ju}(t+s), \phi_{ad}(t), p(t+s), f(t), i(t)$	311.93	27.10	37.60
7	$\phi_{ju}(t+s), \phi_{ad}(t+s), p(t), f(t), i(t)$	311.07	27.30	36.90
8	$\phi_{ju}(t+s), \phi_{ad}(t+s), p(t+s), f(t), i(t)$	317.09	27.70	43.40
9	$\phi_{ju}(t), \phi_{ad}(t), p(.), f(t), i(t)$	276.26	25.10	0.00
10	$\phi_{ju}(t), \phi_{ad}(t+s), p(.), f(t), i(t)$	281.03	25.90	5.60
11	$\phi_{ju}(t+s), \phi_{ad}(t), p(.), f(t), i(t)$	282.13	26.40	7.10
12	$\phi_{ju}(t+s), \phi_{ad}(t+s), p(.), f(t), i(t)$	286.66	27.10	12.30
13	$\phi_{ju}(t), \phi_{ad}(t), p(s), f(t), i(t)$	282.54	26.20	7.30
14	$\phi_{ju}(t), \phi_{ad}(t+s), p(s), f(t), i(t)$	286.47	27.00	12.10
15	$\phi_{ju}(t+s), \phi_{ad}(t), p(s), f(t), i(t)$	282.24	26.20	7.00
16	$\phi_{ju}(t+s), \phi_{ad}(t+s), p(s), f(t), i(t)$	292.50	28.20	19.30

Table A3.2: *Estimates of posterior mean with 95% credible intervals (CRI) and temporal variance ($\hat{\sigma}^2$) of demographic rates obtained from the best model (Model 9, Table 5.1) for wryneck from Valais (2002-2008).*

Demographic rates	Mean (95% CRI)	$\hat{\sigma}^2$
Juvenile survival	0.1205 (0.0741, 0.1795)	0.001
Adult survival	0.4109 (0.2533, 0.6193)	0.027
Fecundity	6.1645 (5.3969, 6.9300)	0.464
Immigration	0.2232 (0.0004, 0.5159)	0.179
Population growth rate	0.9867 (0.9407, 1.0350)	-

B

Habitat selection modeling

B1 Patches of bare ground as a staple commodity for declining insectivorous farmland birds

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Summary

This study shows that patches of bare ground are an essential foraging habitat feature for rapidly declining, ground-foraging insectivorous farmland bird species in temperate Europe, yet modern intensive agriculture offers a too dense, continuous vegetation cover condemning ground-foraging, while no agri-environment scheme currently promotes bare ground patches.

Conceived to combat widescale biodiversity erosion in farmland, agri-environment schemes have largely failed to deliver their promises despite colossal investments of taxpayer money (1, 2). While several common species have reacted positively to these measures (3, 4) , rare species further declined in most countries owing to continued intensification of agricultural practices (5-9). Particularly concerning is the status of insectivorous farmland birds that forage on the ground. Although some species-specific restoration projects have led to local population recoveries (10), general agri-environmental policies have failed to promote them so far (1, 11). Here we show that four declining insectivorous bird species specialized in ground foraging, and typical of different agricultural habitats, preferably forage in habitat mosaics consisting of patches of grass and bare ground with an optimum of 30-70% bare ground at the foraging patch scale. These birds survive even in intensively cultivated farmland, providing a suitable ground vegetation structure. As a staple commodity, bare ground is currently not favored by conventional agri-environment schemes. Based on our modeling of species-specific habitat preferences, we urge the development of new agri-environment schemes that provide bare patches throughout grassy farmland.

Farming practices have changed radically since World War II, provoking an unprecedented crisis for farmland biodiversity. Firstly, the total area devoted to agricultural production has increased, which was achieved through the conversion of pristine habitats into grassland or arable land (12). Secondly, natural elements constituting the matrix of traditional agricultural landscapes have vanished: wetlands have been drained, streams channelized or put into underground pipes, while patches of forest, hedges and grassy field margins have been eradicated (13). Thirdly, fertilizers have substantially augmented the yield per land area and time units: the resulting sward densification has changed both micro-climatic conditions within grassland, lowering invertebrate abundance and reducing accessibility for many organisms (14, 15). Fourthly, the systematic application of pesticides and herbicides has eliminated many forms of life which were not directly useful for agricultural production (16). Overall, this extraordinary agricultural development has dramatically increased the human share of net primary productivity at the biosphere scale. The diversion of the net primary productivity (currently about 50% of continental NPP (17)) for the sake of a single species, *Homo sapiens*, has certainly benefited a rapidly growing human population by substantially augmenting the supply of commodities, but it has also provoked a general collapse of biodiversity. New policies aimed at restoring farmland biodiversity have thus been launched in most developing countries. The basic idea is to restore natural elements within the agricultural matrix, to set aside part of the land (i.e. to render part of the net primary productivity again available to living forms other than humans) and finally to extensify agricultural practices through a reduction of the application of agrochemicals and fertilizers in order to better preserve water, soil and air. Implemented in several countries, these measures have so far had only moderate effects on biodiversity (1, 7, 8): common species at the lower trophic levels have actually benefited locally, whilst rare species, which are often situated higher up along the food chain, stayed at rest or declined further.

Farmland birds have suffered massive population declines over the past decades (6), especially in the industrialized countries, and this trend continues (5). At the time they were launched, agri-environment schemes gave much hope for an improvement of farmland birds' status. Yet, more than one decade after the widespread implementation of agri-environment policies, few examples of population recoveries have been documented. Most studies have detected limited or moderate effects (7, 8), which led to intense public debates about the relevance of agri-environment schemes for promoting biodiversity in general (1). Ground-foraging insectivorous birds have been especially affected by agricultural changes (18) and they typically do not respond positively to existing agri-environment schemes (8). The reason for this can be twofold. First, food biomass supplied by current agri-environment schemes can be insufficient to compensate for losses due to the intensification of farming practices (14), i.e. a suitable food supply has not been restored for these birds. Second, resources may be present in sufficient quantity but remain largely inaccessible due to changes in vegetation structure (19). Both factors are not mutually exclusive. In this study, we assessed fine-grained habitat selection in four declining species of European ground-feeding insectivorous birds in various types of high intensity farmland. At our study sites, these birds – that historically had their population strongholds in traditional, low intensity farmland – still survive in high intensity agricultural matrices (fruit tree plantations, orchards and vineyards). By recognizing convergences in basic ecological requirements between species and across farmland habitat types we ought to identify a reason why current agri-environment schemes fail to promote these terrestrially feeding insectivorous birds, and to recommend novel management measures for improving the schemes.

Because detectability of ground-foraging birds is generally low and declines with increasing vegetation cover, we relied on radiotracking for three out of four of our study species (exception: common redstart). This ensured unbiased results regarding the relationship between ground vegetation structure and foraging behavior. We recorded vegetation structure within 1 m radius of all identified 1,471 foraging locations of 33 adult individuals provisioning food to chicks (13 hoopoes *Upupa epops*, 8 wrynecks *Jynx torquilla*, 7 woodlarks *Lullua arborea*, 5 common redstarts *Phoenicurus phoenicurus*) in study areas in Southwestern (Valais near Sion, 46 °41′ N, 7 °22′ E) and Northern Switzerland (Basel, 47 °33′ N, 7 °35′ E).The dominant habitats were intensively farmed fruit tree plantations (hoopoe, wryneck), intensively cultivated vineyards (woodlark) and high-stem orchards in dense grassland (common redstart). Individual home ranges were delineated as the minimum convex polygons encompassing all foraging locations of a given individual, within which we additionally recorded vegetation structure of randomly selected points (*n* equalling the number of observation locations). We analysed the data separately for each species, applying a hierarchical logistic regression model implemented in a Bayesian framework using Markov chain Monte Carlo (MCMC) simulation. The reliance on a hierarchical design (20) circumvented the problem of traditional habitat selection analyses of having to run separate analyses for the different individuals to obtain data independency, while enabling the recognition of species-specific pattern across individuals. Furthermore, this approach allows fitting a functional response for each individual and then derives a marginal (population level) response.

The habitat selection analysis showed that both variables characterizing the ground vegetation structure, the proportion of bare patches on the ground and vegetation height, were important determinants for species foraging occurrence (21). In all species, there existed a quadratic relationship between occurrence of foraging birds and amount of bare ground, with an optimum around 30-70% of bare ground at the foraging patch scale (1 m radius circles; Figure B1.1). Within species, the shape of the functional response curve was similar in all individuals and it was constant across habitat types (21), identifying bare patches as a staple commodity for these individuals and species. The vegetation height was examined for three species, and it was clearly of lesser importance than the amount of bare ground, as evidenced by the predictions (Figure B1.1). Furthermore, species reacted differentially to varying vegetation height. Woodlarks and hoopoes favored places with shorter swards while wrynecks showed no preference for a particular sward height.

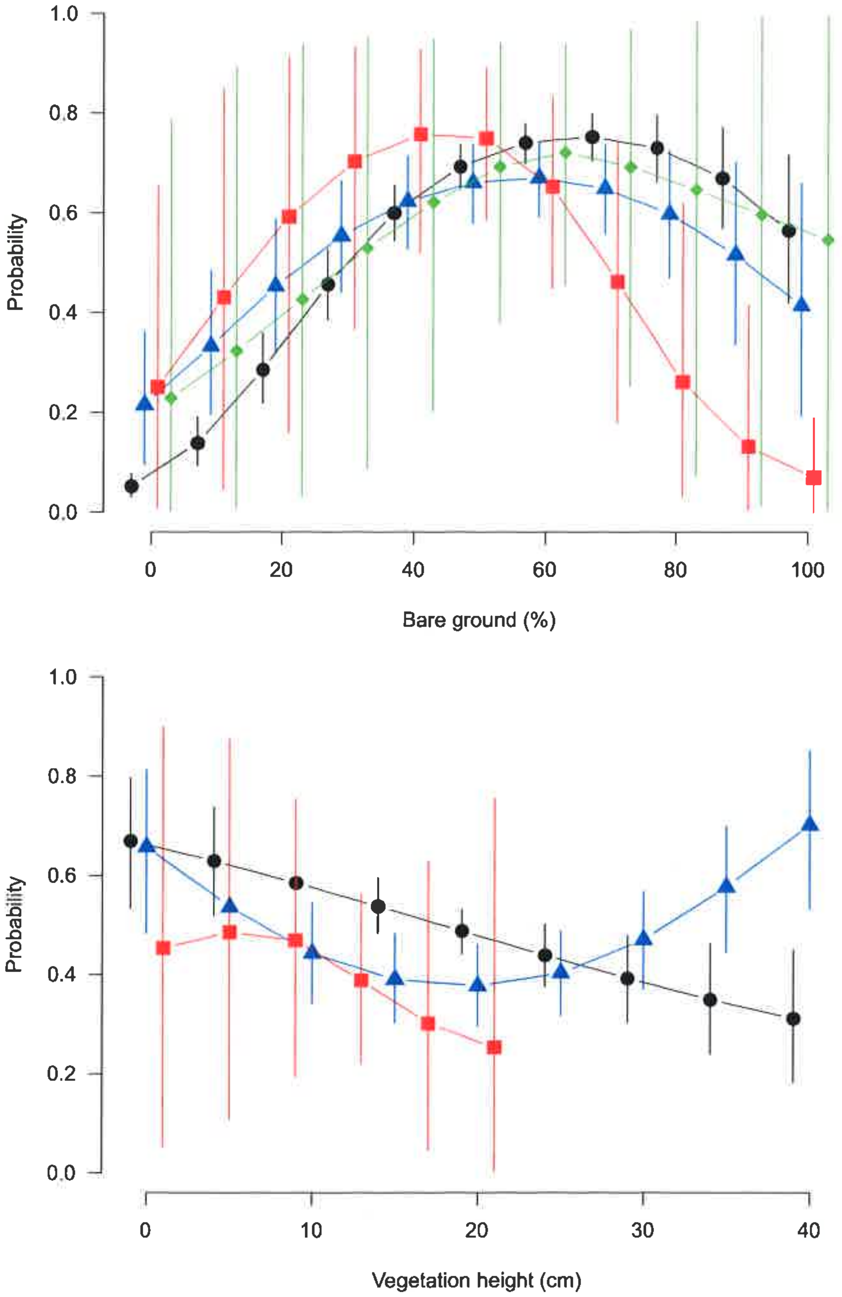

Figure B1.1: *Marginal selection probability of foraging locations in relation to amount of bare ground and vegetation height of four farmland bird species. Predictions are revealed from the best models (see Table B1.2) and refer to hoopoes (black dots), wrynecks (blue triangles), woodlarks (red squares) and common redstarts (green diamonds). Note that selection probabilities below 0.5 indicate avoidance, selection probabilities above 0.5 indicate preference. Points are posterior means, vertical lines show the limits of the 80% credible intervals.*

A common preference for bare ground in the four study bird species across the different types of farmland habitats clearly indicates the importance of food availability for habitat selection (22, 23). Thus, food availability (i.e. prey abundance modified by its accessibility) is *per se* a crucial, limiting resource for ground-feeding insectivorous birds (24). On one hand, ground vegetation provides the invertebrate food biomass (playing the role of the kitchen) to the birds, which can pick up prey items from the bare patches (the dining room) on which they can easily manoeuvre in the absence of obstacles (25, 26). The question arises then how abundant the prey supply must be in the ground vegetation and how patches of bare ground must be arranged within the agricultural matrix to offer suitable conditions for these birds. The fact that we worked in high intensity farmland (dwarf fruit plantations and vineyards which are regularly treated with pesticides) suggests that prey abundance may be less important than previously thought. An experimental examination also showed that birds preferred sparsely vegetated patches with low food supply over densely vegetated patches with high food supply (27). We think, however, that the best compromise is obtained when ground vegetation harbors abundant populations of invertebrates, which is rarely the case when the grass is either maintained short or is lacking completely on the whole surface (poorly provisioned kitchen) (28). This compromise can be achieved by a spatially fine-grained mosaic of patches of grass and bare ground within the agricultural matrix. Interestingly, current management of fruit tree and vine plantations at the Valais study sites seem to offer such an appropriate mosaic at the foraging patch scale. About 30-50% of the grass layer is destroyed by herbicide application or mechanical removal of grass along tree or vine lines to avoid competition for water between ground vegetation and fruit plants. The current proportions of bare ground and grass at the site scale seem to offer optimal conditions for these rare birds which have good populations in fruit tree and vine plantations. Current management should therefore preferably continue. For other farmland habitats characterized by a dense and continuous grass cover (grasslands and orchards above meadows) further studies are necessary to evaluate the optimal arrangement of vegetated and bare patches at the site scale.

We conclude that the dense sward that characterizes both modern, fertilized grassland and most grassy ecological compensation areas (low-intensity and extensive meadows, set aside, wildflower areas, etc.) in restored agricultural matrices does not match the requirements of most ground-feeding insectivorous bird species. This calls for a dramatic change of management to restore appropriate cultivated landscapes. More open vegetation can be achieved despite general nitrogen and carbon enrichment on the soil surface (29, 30). Firstly, by extensifying grassland management (less fertilization and irrigation) patches of bare ground can be reinstated within cultivated habitats. Secondly, a mechanical removal of the ground vegetation cover could be conducted in grassy habitats where extensification is difficult to achieve (e.g. set aside and wildflower areas). By integrating these measures, future agri-environment schemes could benefit threatened species of insectivorous farmland birds as well as many other organisms that profit from habitat heterogeneity at the site scale. As shown at our study sites, modern high-intensity farming may offer more scope for the survival of rare and endangered birds than previously thought, providing that suitable structural habitat conditions exist which are compatible with the species' needs.

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31. We thank all the farmers who allowed us to work on their land and John Dwyer for comments on the manuscript.

Supporting information

Material and methods

Radio-tracking, sample size and habitat mapping

Radio-tracked birds were equipped with light radiotags (BD-2-P with activity sensor, 0.9 - 1.4 g, Holohil Systems Ltd., Canada) that were fitted using a leg-loop harness (S1). We localized foraging birds using the homing-in technique (S2). For common redstarts, foraging locations were obtained from visual observation because the species sit-and-wait foraging tactic renders it more conspicuous and the identification of the feeding location is independent from the ground vegetation structure. Sample sizes are given in Table B1.1. At each point (observation or random) we estimated the proportion of bare ground visible when looking vertically onto the ground, and the average height of the ground vegetation (yet, vegetation height was not measured in the common redstart study). We also recorded the habitat type (fruit tree plantation, orchard, vineyard, meadow, pasture, wood, and cropland) to which the points belonged to.

Statistical model

We used a hierarchical logistic regression model implemented in a Bayesian framework to analyse the binary response variable (y). For each individual j ($j = 1 \dots J$) and each observation i ($i = 1 \dots I$), the dependent variable $y_{i,j}$ follows a Bernoulli distribution:

$$y_{i,j} \sim Bern(\mu_{i,j})$$

The expected value $\mu_{i,j}$ is modeled by variables describing the structure of the ground vegetation using the logit link function:

$$logit(\mu_{i,j}) = \alpha_j + \beta_j bare_{i,j} + \gamma_{i,j} bare_{i,j}^2 + \delta_j height_{i,j} + \varepsilon_j height_{i,j}^2$$

The individual slope parameters are then modeled independently from each other with a normal distribution to estimate the population mean and variance of the slope parameters:

$$\alpha_j \sim N(\mu_\alpha, \sigma_\alpha^2)$$

$$\beta_j \sim N(\mu_\beta, \sigma_\beta^2)$$

$$\gamma_j \sim N(\mu_\gamma, \sigma_\gamma^2)$$

$$\delta_j \sim N(\mu_\delta, \sigma_\delta^2)$$

$$\varepsilon_j \sim N(\mu_\varepsilon, \sigma_\varepsilon^2)$$

The current model considered individual random effects for the intercept as well as individual random slopes, thus allows to model individual functional responses.

We specified non-informative priors for all parameters to be estimated. We used $N(0, 1000)$ priors for the slope parameters and uniform priors $U(0, 100)$ on the standard deviations for the variance parameters (S3). To calculate the posterior distributions of the parameters of interest, we used MCMC simulations implemented in WinBUGS (S4) executed from R (R Development Core Team 2004) with package R2WinBUGS (S5). We ran 5 independent chains, with 50,000 iterations after 10,000 initial burn-in iterations, and checked the convergence using the Brooks-Rubin-Gelman diagnostic (S6). Convergence was satisfactory for all parameters ($R < 1.05$). We saved every 50^{th} MCMC sample and based inference on the remaining 1,000 posterior samples. For predictive graphs, we ran 1 chain with 110,000 iterations and a burn-in period of 10,000 iterations, and saved every 50^{th} observation. The explanatory variables were all standardized (mean = 0, sd = 1) prior to analysis.

Additional results

For each major habitat category of hoopoe (fruit tree plantation, grassland, all remaining habitat types together) and wryneck (fruit tree plantation, all remaining habitat types together) we first ran the basic model as defined above. This allowed us to evaluate whether the relationships between occurrence and vegetation structure were consistent among broad habitat categories. We found that this was the case (Figure B1.2), and thus did not consider habitat categories in subsequent analyses. For woodlarks and common redstarts the vast majority of locations occurred in one habitat type only (vineyard and orchard, respectively).

Second, we fitted different models that included different combinations of effects of bare ground and its square, as well as vegetation height and its square. The models were then ranked according to the deviance information criterion (DIC) (S7). Squared effects were included, because of a likely trade-off between food abundance and accessibility, with vegetation density and height which would result in optima curves. Model selection summary is provided in Table B1.2, parameter estimates in Table B1.3.

Based on the best models we calculated predictive distributions to evaluate goodness-of-fit. We compared observed values with predicted values using χ^2-diagnostics and report Bayesian *P*-values. If the fit of the model is good, Bayesian P-values around 0.5 are expected (S8).

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Table B1.1: *Sample sizes, locations and the use of radio-tags for the four studies: number of individuals, total number of observations and random points, and mean number of observations and random points per individual.*

	Hoopoe	Wryneck	Woodlark	Common redstart
Number of individuals (males)	13 (13)	8 (3, 2 unknown sex)	7 (5)	5 (3)
Total number of observation points (random points)	552 (496)	145 (141)	504 (504)	270 (270)
Mean number of observation points per individual (range)	42 (10 - 55)	18 (6 - 20)	72 (58 - 96)	54 (28 - 95)
Mean number of random points per individual (range)	38 (9 - 54)	18 (5 - 21)	72 (58 - 96)	54 (28 - 95)
Location	Valais	Valais	Valais	Basel
Radio tags used	Yes	Yes	Yes	No

Table B1.2: *Model selection results for the effect of the proportion of bare ground (b), its square (b^2), the vegetation height (h) and its square (h^2) on the foraging selection probability of each species. Given are the deviance, the model complexity (pD) and the difference of the deviance information criterion between the best and the current model (ΔDIC). The best models are bold printed. The goodness-of-fit test of the best models were acceptable in all species (Bayesian P-values, hoopoe: 0.54, wryneck: 0.19, woodlark: 0.24, common redstart: 0.32).*

	Hoopoe			Wryneck			Woodlark			Common redstart		
Model	Deviance	pD	ΔDIC	Deviance	pD	ΔDIC	Deviance	pD	ΔDIC	Deviance	pD	ΔDIC
$b+b^2+h+h^2$	998.64	34.53	1.36	**351.32**	**18.39**	**0**	**935.82**	**32.26**	**0**	-	-	-
$b+h+h^2$	1123.13	30.56	121.88	359.73	18.85	8.86	1056.36	26.96	115.24	-	-	-
$h+h^2$	1327.08	21.25	316.51	386.66	10.54	27.48	1268.55	21.17	321.64	-	-	-
$b+b^2+h$	**1000.02**	**31.78**	**0**	357.78	16.97	5.04	951.48	26.69	10.09	-	-	-
$b+b^2$	1071.58	20.09	59.87	363.92	11.09	5.29	1052.83	18.74	103.5	**544.34**	**11.39**	**0**
b+h	1145.17	26.89	140.26	363.16	15.87	9.31	1093.14	20.45	145.51	-	-	-
b	1231.21	13.99	213.39	369.74	9.24	9.26	1185.16	12.94	230.03	551.46	9.97	5.69
h	1356.06	13.53	337.78	391.2	8.54	30.03	1315.51	13.11	360.54	-	-	-
intercept	1451.73	2.21	422.13	398.49	2.16	30.93	1399.41	2.01	433.33	750.66	2.06	196.99

Table B1.3: *Estimates of the mean model parameters and of their variability among individuals from the most complex model* (b+b^2+h+h^2) *for each species. Values in parentheses show the limits of the 95% credible intervals for each estimate.*

	Hoopoe		Wryneck	
	Mean	Variance	Mean	Variance
Intercept	0.939 (0.544; 1.370)	0.291 (0.023; 0.938)	0.290 (-0.313; 0.932)	0.202 (0.000; 1.019)
Bare ground	1.630 (1.173; 2.103)	0.490 (0.106; 1.328)	1.198 (0.274; 2.149)	1.152 (0.052; 5.392)
Bare ground^2	-1.017 (-1.250; -0.802)	0.037 (0.000; 0.245)	-0.856 (-1.464; -0.276)	0.326 (0.000; 1.935)
Vegetation height	-0.499 (-1.213; -0.124)	1.234 (0.320; 3.483)	0.028 (-0.664; 0.821)	0.809 (0.002; 4.076)
Vegetation height^2	-0.026 (-0.272; 0.223)	0.060 (0.000; 0.276)	0.598 (-0.090; 1.336)	0.568 (0.000; 2.820)
	Woodlark		Common redstart	
	Mean	Variance	Mean	Variance
Intercept	0.956 (0.055; 1.830)	1.022 (0.097; 4.322)	3.568 (0.311; 8.053)	18.626 (0.001; 77.455)
Bare ground	-2.194 (-3.110; -1.206)	1.372 (0.203; 5.511)	3.032 (-0.012; 7.229)	15.363 (0.485; 84.915)
Bare ground^2	-1.715 (-2.680; -0.832)	1.673 (0.187; 6.492)	-3.322 (-8.780; 2.084)	32.909 (0.181; 235.871)
Vegetation height	-0.688 (-3.549; -2.132)	14.467 (1.008; 74.106)	-	-
Vegetation height^2	-0.263 (-2.053; -1.051)	3.494 (0.105; 16.286)	-	-

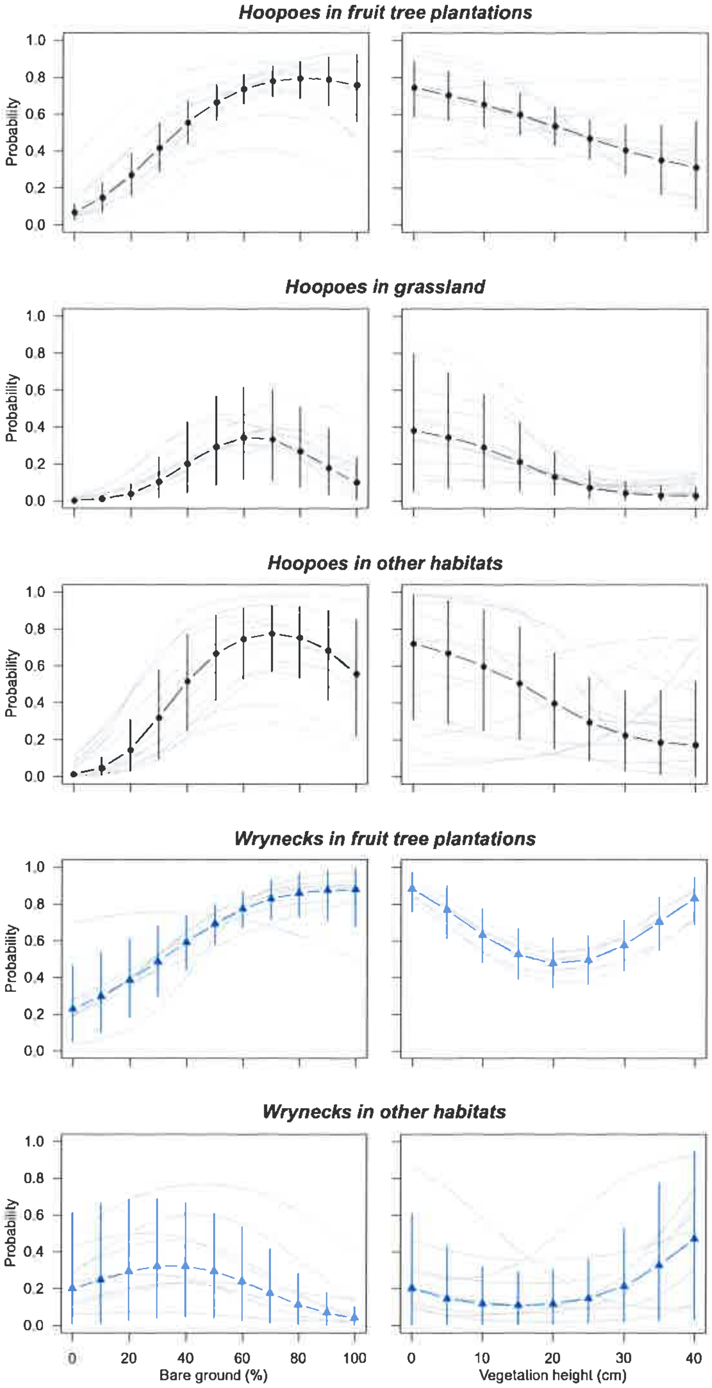

Figure B1.2: *Selection probability of habitat use in relation to amount of bare ground and vegetation height for hoopoe and wryneck in different habitat categories as revealed by the most complex model (see Table B1.2). The grey lines show the individual effects, the black and blue line shows the population (marginal) average with 80% credible intervals. Note that selection probabilities below 0.5 indicate avoidance, selection probabilities above 0.5 indicate preference.*

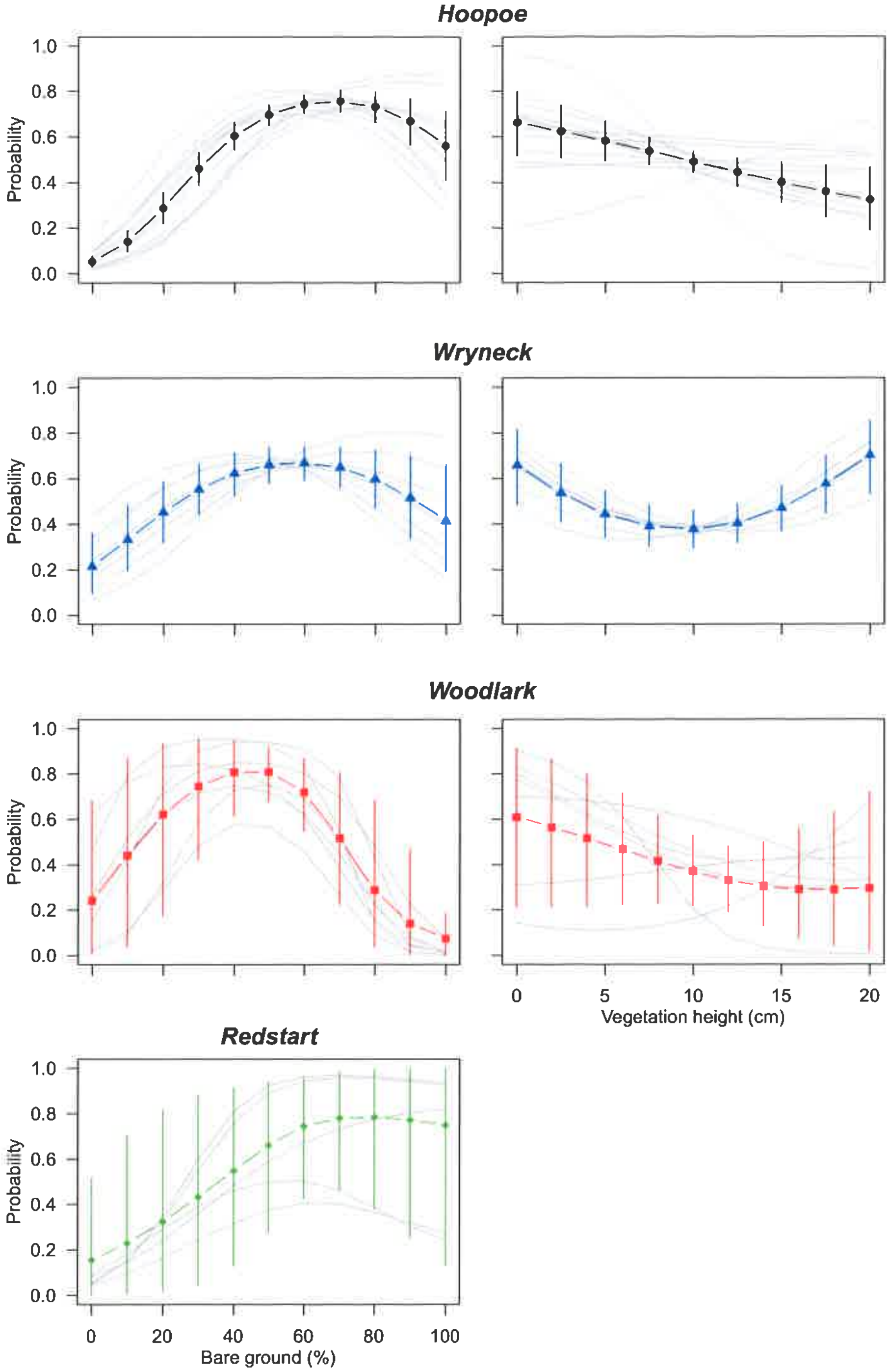

Figure B1.3: *Selection probability of habitat use in relation to the amount of bare ground and vegetation height for four farmland species as revealed by the best models (see Table B1.2). The grey lines show the individual effects, the colored lines show the population (marginal) average with 80% credible intervals. Note that selection probabilities below 0.5 indicate avoidance, selection probabilities above 0.5 indicate preference.*

B2 New vineyard cultivation practices benefit a vulnerable ground-foraging farmland bird, the Woodlark: guidelines for optimal habitat management

Arlettaz, R., Maurer, M., Mosimann-Kampe, P., Nussle, S., **Abadi, F.**, and Schaub, M. (in prep.)

Abstract

Agricultural intensification has caused a widespread collapse of farmland biodiversity. The decline of farmland birds has been related to a dramatic reduction of food availability impacting reproductive output and survival negatively. Diminished food availability results from farming practices that lessen food supply (e.g. prey diversity and biomass) and/or reduce food accessibility (e.g. too dense grass sward). Vineyards in southern Europe harbor several red-listed species. Over the past decades there has been a strong reduction in the application of insecticides in Swiss vineyards, with a progressive switch to biological control and organic protocols. Spraying of herbicides has also slightly diminished, which has led to more vegetation cover on the ground. The effect of these potentially positive environmental trends upon vertebrate biodiversity remains mostly unknown.The woodlark (*Lullula arborea*) is an endangered, short-distance migratory bird that forages and breeds on the ground. In southern Switzerland (Valais) it occurs mostly in vineyards. Using radiotracking, we analyzed habitat selection by foraging woodlarks in order to test the response of a vertebrate to modern vineyard management and to define species' optimal habitat profile for proposing adequate management guidelines. Mixed effects logistic model (visited vs random locations within home range) showed that the main habitat selection criterion was the amount of ground vegetation cover, with an optimum around 45-60%. These conditions are met mostly in vineyards managed according to the biological control protocol, but only where grass is tolerated on a corresponding proportion of the ground surface (<5% of the vineyard area in Valais). Conventional vineyards (≥95% of the vineyard area) are too bare because of systematic application of herbicides, whilst the rare organic vineyards have most of the time a too dense sward. New vineyard management is beneficial to woodlarks and should progressively replace conventional, mineral vineyards. When biological control protocol is associated with limited herbicides application, it naturally leads to an alteration of vegetated and bare ground rows, which provides an ideal 50% ground vegetation cover. Partial ground vegetation cover in organic parcels could be obtained through mechanical removal of ground vegetation. These measures are likely to benefit biodiversity in vineyards.

Key-words: Agricultural intensification; population decline; herbicides; vegetation structure; *Lullula arborea*; habitat selection; habitat restoration

Introduction

Agricultural intensification has led to a widespread decline in farmland biodiversity across many different taxa such as plants, arthropods, birds and bats (e.g. Benton et al. 2003, Britschgi et al. 2006, Donald et al. 2001, Gregory et al. 2004, Hole et al. 2005, Poulsen et al. 1998, Verhulst et al. 2004, Vickery et al. 2001, Wickramasinghe et al. 2003). Benton et al. (2002) have established that insect numbers have significantly changed over time, with a higher abundance in low intensity farming. A drastic drop in arthropod abundance has in turn affected the populations of insectivorous vertebrates (Benton et al. 2002, Brickle et al. 2000, Britschgi et al. 2006).

Habitat alteration and agrochemicals are believed to be the main factors of biodiversity reduction in farmland, affecting individual survival and reproductive output (Boatman et al. 2004, Brickle et al. 2000). According to Boatman et al. (2004) pesticides may affect food availability for birds in three ways: (1) arthropod populations could be eliminated or depleted due to insecticides, resulting in reduction of breeding productivity in adults that feed their young with insects; (2) the abundance of non-crop plants which operate as hosts for arthropods may be reduced through herbicide use; (3) herbicides can deplete or eliminate plant species that provide either green matter or seeds for herbivorous and granivorous species. Such effects were demonstrated in two farmland birds, the skylark and the corn bunting (Boatman et al. 2004, Brickle et al. 2000, respectively).

Fertilizers may also affect bird population dynamics through major changes in the fine-grained structure of ground vegetation cover. A high sward density, for instance, impedes forager's mobility, and diminishes foraging efficiency through lower prey detectability and accessibility (Butler and Gillings 2004, Atkinson et al. 2004, Vickery et al. 2001). A mosaic of dense and sparsely vegetated ground is thus likely to provide the maximum benefits for many farmland birds (Benton et al. 2003, McCracken and Tallowin 2004). Birds that feed on soil invertebrates typically prefer short grazed swards with a large amount of bare earth (Atkinson et al. 2004). Toepfer and Stubbe (2001) showed that Skylarks preferred a vegetation cover of 35-60% and a vegetation height of 25-60 cm.

In Switzerland 14,800 ha are devoted to vineyard cultivation, with one third of the area occurring in Valais (SW Switzerland). Vineyards in Valais are located mostly on the sun-exposed, right side bank of the Rhône river, up to 1000 m above sea level. Often organized in successive terraces along the slopes, the vineyards support a variety of different soil types and compositions, and are intermixed with natural elements such as patches of steppe on rocky outrcops, or fragments of xerophilous forests. This allows a great diversity of vine sorts to be grown, as well as a rich flora and fauna with often specialized plant and animal species (Sierro and Arlettaz 2003). Most of the Valais vineyards are currently cultivated according to the biological control protocol, which has led to a progressive decline of pesticide utilization over the past 15 years. A recent trend among these winekeepers is to tolerate more vegetation on the ground than it was the case in the recent past, when the entire soil surface was systematically sprayed with herbicides. However, restriction of herbicide application is not mandatory in the biological control protocol, which explains why most Valais vineyards ($\geq$ 95%) still have a very mineral appearance (these vineyards will be called hereafter "conventional vineyards"). In contrast, organic cultivation, which remains rare in the study area, is characterized by an almost continuous vegetation cover on the ground. Although progressive "greening" of vineyards will certainly be beneficial to that part of the net primary productivity which is not exploited, i.e. biodiversity, one may fear that a too dense sward will be detrimental for many terrestrial organisms because it could result in limited accessibility to essential food resources (Atkinson et al. 2004).

We used the woodlark as a model to test the response of terrestrially-feeding vertebrates to novel vineyard management methods. The woodlark is partly migratory and mostly insectivorous during the breeding season. Since the middle of the last century there has been a dramatic decline in the Swiss woodlark population (Glutz von Blotzheim and Bauer 1985, Leuzinger 1955, Schmid et al. 1998, 2001). At present, ca 250-500 breeding pairs remain, part of which in vineyards (Burkhardt and Schmid 2001). The species is thus classified as vulnerable and belongs to the 50 priority bird species of Switzerland for which action plans are currently under development (Keller et al. 2001, Bollmann et al. 2002, Keller and Bollmann 2001). In order to support efforts to preserve the species in Switzerland we investigated by radiotracking its key ecological niche preferences in vineyards, with the goal to draw optimal habitat profiles which may serve as guidelines for optimizing biodiversity-friendly vineyard management. This information may first be useful beyond the study area because declines of woodlarks have been reported in most northern and western European countries (Glutz von Blotzheim and Bauer 1985, Snow and Perrins 1998), although there is evidence for recent recoveries in some areas (Langston et al. 2007). Second, as the woodlark is a good indicator species, other elements of flora and fauna would also benefit from any conservation and restoration measures targeted to its habitat. More specifically, we addressed the following questions: 1) do woodlarks favor certain foraging micro-habitats within their home range, which may provide more feeding opportunities (more food) and/or prey accessibility? 2) what are the habitat associations of woodlarks? 3) could the recent increase of the area of vegetated vineyards benefit the species? 4) if yes, can we provide management guidelines for propping up woodlark and biodiversity in vineyards?

Material and methods

Study site

This study was conducted in the vineyards of Central Valais, between the communities of Vétroz (46 °13′ N, 7 °16′ E) and Leuk (46 °19′ N, 7 °38′ E), in which calling males had been mapped in previous surveys (Swiss ornithological institute, unpublished data).

Capture and marking techniques

All capture attempts took place between March and July 2005 (Table B2.1). Tape-luring and stuffed birds were used to attract free-ranging birds, according to own previous field experience. Capture techniques consisted of mist netting (3 mist nets placed triangularly around the tape-recorder and stuffed bird), perch traps and cage-box traps positioned on the ground along the path used by parents when feeding the chicks at the nest. Birds were ringed and sexed on the basis of the form of the cloaca peg, and the presence or absence of a breeding blot. Radio tags (BD-2 transmitters; weight: 0.90 g, Holohil Systems Ltd., Canada) were attached to the bird's back, with a self-breakable leg harness (Rappole and Tipton 1991) made up of thin elastic cord. The weight of the transmitters was less than 3.5% of body mass (Aldridge and Brigham 1988).

Radiotracking

The birds were first located by homing-in on the animal to get an approximate position. They were then searched visually with binoculars and, if necessary, by triangulation so as to assess foraging activity. Localizations took place every 15 minutes to avoid as far as possible temporal autocorrelation. Observation locations were marked in the field with a numbered, colored scotch tape label placed directly on vineyard sticks or wires. The exact position was retrieved after the radiotracking session using a Global Positioning System (GPS). We mapped the habitat within a 5 m radius around every location (see variables in Table B2.4).

Data analysis

Individual home ranges were estimated as 100% minimum convex polygons (MCP; Animal Movement module, ArcView GIS 3.3) from ascertained foraging locations. Georeferenced maps (1:10,000) derived from the Valais land survey were fitted to a geographical information system (GIS). A buffer zone of 5 m was added around the 100% MCP. Habitat selection was investigated by comparing habitat features at foraging locations with those at random locations. An equal number of random locations as visited locations was chosen within the buffered MCPs for this purpose. Random locations were uniformly distributed within the home range and were allowed to overlap because visited locations of woodlarks overlapped too. However, around each visited location, a buffer of 10 m was drawn to ensure that the random locations did not fall in the close vicinity of visited locations. The attributes of the random locations were derived in the same manner as for the woodlarks' visited locations.

We modeled the occurrence of woodlark with respect to habitat features using a maximum likelihood approach for generalized linear mixed model (GLMM) with a logit link function and a binomial distribution. This model extends the generalized linear models by the inclusion of the random effects (Williams 1982). In this study, GLMMs with random intercept terms were considered to account for the variability among individual birds. The general form of the model is given as:

$$logit(p_{ij}) = X_{ij}^{'}\beta + b_i$$

where p_{ij} is the probability of occurrence at location j for bird i, β is a vector of coefficients, X_{ij} is a design matrix of habitat predictors at location j for bird i, and b_i is a random effect for bird i which is assumed to be normally distributed with mean 0 and variance σ^2.

Our data set contained nine habitat predictors (Supporting Information Table B2.4). We first assessed the correlation between continuous predictors using Spearman correlation coefficient. To avoid collinearity we dropped predictors if their Spearman correlation coefficient was $> |0.7|$ (Hosmer and Lemeshow 1989). We then grouped the variables into main categories: vineyard management (vineyard age, vineyard type, and herbicide application), ground vegetation (ground vegetation cover and ground vegetation height), and infrastructure (wall, scrub, and roads) to reduce the total number of potential candidate models. We then constructed a total of 55 *apriori* models that considered different combinations of these main categories. In addition, we included the quadratic term of ground vegetation cover as a curvilinear relationship was expected regarding occurrence probability with respect to this variable.

The models were fitted using the lmer function in the lme4 package (Bates and Sarkar 2005) in R.2.6.2. (R Development Core Team 2008). Fitted models were then compared and ordered according to their best fit to data using the Akaike Information Criterion

(AIC) (Akaike 1974) and Akaike weight (Burnham and Anderson 2002).

Results

Five male and two female woodlarks were captured and radiotracked over 88 days between March and August 2005. Home ranges were, on average (± SD), 5.22 ± 3.46 ha (range: 1 - 11.5 ha, Table B2.1).

In total we obtained 684 radio locations, i.e., on average (± SD), 98 ± 29 locations per bird (range: 62-140). Altogether, 74% (= 504 bearings, 72 ± 15 per individual, range: 58-96) were locations at which foraging could be assessed (Table B2.1). These served for the habitat selection analysis.

As there was a strong negative correlation between ground vegetation cover and amount of organic litter (Spearman correlation coefficient = -0.73), only ground vegetation cover was considered in further models (Supporting Information Table B2.4). In addition, the variable scrub was removed as it was highly skewed (with many zeros). The results of GLMM analyses showed that one model (model 4) received substantial support by the data as it had a 90% likelihood of being the best model in the set of models considered. This model includes the following variables: vineyard type and age, herbicide application, ground vegetation cover and its quadratic term, vegetation height, presence of walls and roads. It was 16.6 times more likely (0.896/0.054) than the next best model (model 55).

Vineyard management influenced species occurrence (Table B2.3): 1) vineyard age had a negative impact (Figure B2.1a); 2) woodlarks had a higher probability of occurrence in "gobelet" vineyards (plants branching low above the ground and arranged in 100-110 cm distant rows) than in plantations on wires (120-200 cm distant plantation lines, Table B2.4; Figure B2.1c); and 3) herbicide application affected occurrence probability negatively (Figure B2.1d). Occurrence probability was strongly affected by ground vegetation: 1) it was higher in vineyards with short ground vegetation (Figure B2.1b); and 2) an optimum for species occurrence probability coincided with ground vegetation cover around 55% (Figure B2.2). Finally, infrastructure also played a role, with the presence of walls and roads negatively impacting on occurrence probability (Figure B2.1e-f).

Table B2.1: *Synopsis of radiotracking activities carried out in summer 2005 with seven woodlarks.*

Individual #	Sex	Date of capture	Capture technique	Number of days with active radiotags	Number of radio-monitoring days	Total number of bearings	Bearings with foraging activity	Foraging home range (ha)
1	m	27.03.2005	Mistnet	15	14	131	96	11.51
2	f	03.05.2005	Mistnet	13	11	102	85	5.73
3	m	16.05.2005	Perch trap	14	11	85	60	4.15
4	f	17.05.2005	Mistnet	30	23	140	68	5.55
5	m	21.05.2005	Cage-box trap	8	7	62	58	1.8
6	m	02.06.2005	Cage-box trap	7	7	70	58	1.09
7	m	13.07.2005	Perch trap	23	15	94	79	6.69
Total				110	88	684	504	

Table B2.2: *The top five GLMM models explaining occurrence of woodlarks based on Akaike's Information Criterion (AIC). For each model, the values for deviance, the number of estimated parameters (K), the difference of the AIC between that model and the best model (ΔAIC), and the Akaike weight are shown.*

Model #	Variables	Deviance	K	ΔAIC	Akaike weight
4	Vineyard age + Vineyard type + Herbicide + Ground vegetation cover + (Ground vegetation cover)^2 + Vegetation height + Wall + Road	1022.07	10	0	0.896
55	Road + Vineyard age + Vineyard type + Herbicide + Ground vegetation cover + (Ground vegetation cover)^2 + Vegetation height	1029.7	9	5.628	0.054
28	Vineyard type + Herbicide + Ground vegetation cover + (Ground vegetation cover)^2 + Vegetation height + Wall + Road	1030.93	9	6.864	0.029
46	Ground vegetation cover + (Ground vegetation cover)^2 + Vineyard age + Vineyard type + Herbicide + Wall + Road	1031.61	9	7.537	0.021
51	Wall + Vineyard age + Vineyard type + Herbicide + Ground vegetation cover + (Ground vegetation cover)^2 + Vegetation height	1038.55	9	14.479	0.001

Notes: The remaining 50 models had zero Akaike weight (< 0.001).

Table B2.3: *Estimated coefficients and their standard errors for the variables of the most parsimonious model (model 4, Table B2.2).*

Variables	Estimated coefficients	Standard error
Intercept	1.644	0.539
Vineyard age	-0.211	0.078
Vineyard type (wire)	-0.975	0.23
Vegetation height	-0.091	0.029
Ground vegetation cover	0.141	0.013
(Ground vegetation cover)^2	-0.001	0.0001
Herbicide	-1.295	0.309
Wall (presence)	-0.603	0.23
Road (presence)	-1.051	0.28

To visualize effect sizes, we calculated the occurrence probability on the logit scale using the best model by bootstrapping with 1,000 replicates. For each predictor variable in turn we used the lowest and the highest observed values and calculated the occurrence probabilities while keeping the other predictor variables at their means. Again, a greater change between the maximum and minimum predicted values was observed for ground vegetation cover (3.854), followed by herbicide application (1.321), vegetation height (1.087), road (1.061), vineyard type (0.982), vineyard age (0.714), and wall (0.609). These results provide evidence for the outstanding role of ground vegetation cover in patterns of habitat selection by woodlarks.

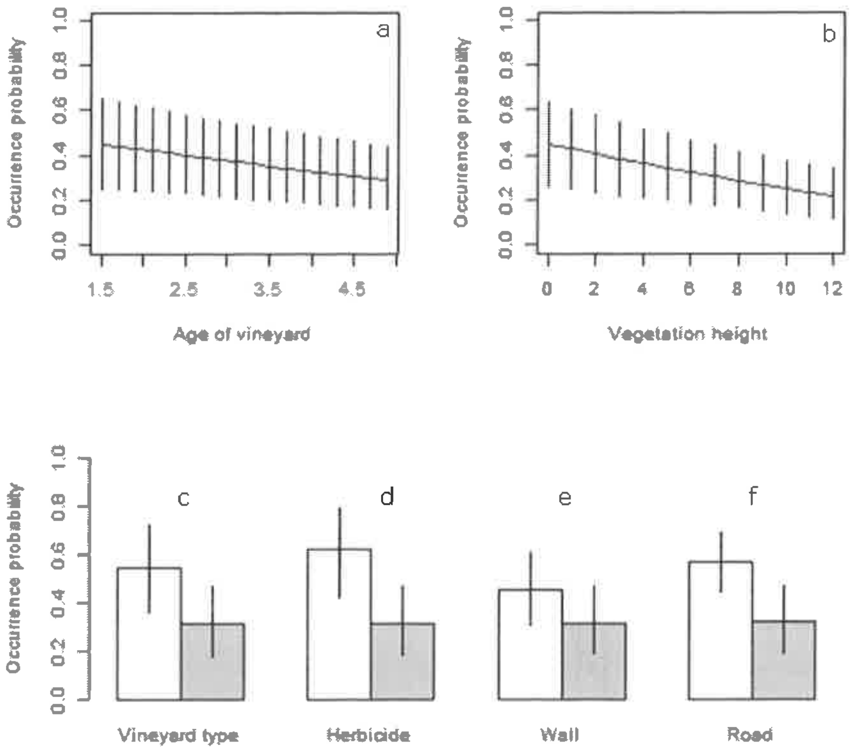

Figure B2.1: *The population-averaged occurrence probability in relation to the predictors (a-f) included in the best model (#4; Table B2.2). Vineyard age (a) represents a relative age, not years. Ground vegetation height (b) is in cm. For vineyard type (c), white indicates "gobelet" and grey indicates wires (see Supporting Information Table B2.4). For the other predictors (herbicide application, d; wall, e; and road, f), white represents absence and grey represents presence. Approximate 95% confidence intervals were constructed by bootstrapping with 1,000 replicates.*

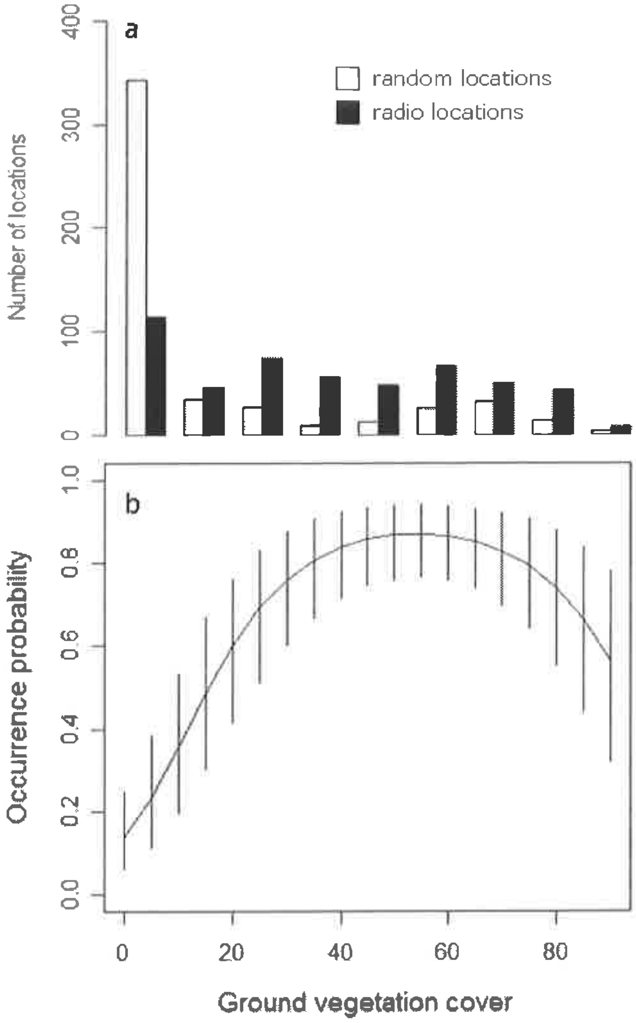

Figure B2.2: *a) Frequency distribution of radiolocations and random locations within woodlark home ranges: note the high proportion of random locations without ground vegetation cover (%), which shows the predominance of "mineral" vineyards (systematic herbicide application) in birds' home ranges. b) The population-averaged occurrence probability is shown in relation to ground vegetation cover, while other predictors are kept fixed at their average values. Approximate 95% confidence intervals were constructed by bootstrapping with 1,000 replicates. .*

Discussion

Our results support the hypothesis that new methods of vine cultivation may be beneficial to terrestrial insectivorous vertebrates, as illustrated here by the woodlark in southern Switzerland. It is primarily the proportion of ground vegetation cover, among several other variables, which drives the pattern of habitat selection in this bird species. Conventional, mineral vineyards, where herbicides are applied on the entire soil surface, still predominate in Valais, representing $\geq$ 95% of the area devoted to this culture (Sierro and Arlettaz 2003). This trend is recognizable even within woodlarks' home ranges: 69% of the random locations (which roughly represent availability) fell within a ground vegetation cover below 10% (Figure B2.2a). If the availability of mineral vineyards is generally higher in our study area than in our woodlarks' home ranges, it is because the radiotracked birds already operated a macro-scale habitat selection towards areas presenting a relatively higher proportion of vegetated vineyards. Occurrence probability declined dramatically below 20% ground vegetation cover, and a similar pattern occurred above 80% (Figure B2.2a). This defines an optimum for ground vegetation cover around 45-60% (peak at ca 55%). Interestingly, similar figures were obtained for woodlarks in the UK (optimum around 43% bare ground; Mallord et al. 2007) and skylarks in Germany (35-60%, Toepfer and Stubbe 2001). Hence, woodlarks prefer vegetated vineyards insofar as they offer a mosaic of grass and herbs interspersed with bare surfaces.

The age of vineyards has a negative effect, which may be explained by the fact that young vineyards offer a less dense vine canopy than old vineyards. As the woodlark is predominantly a species of open and semi-open landscapes, the dense vine canopy of older vineyards may deter the birds from colonizing them. Moreover, herbicide application is less intensive in young vineyards to avoid inadvertently damaging the fragile growing vines. A preference for the traditional "gobelet" vineyards compared to the "wire" vineyard system indicates that this new cultivation structure (more distance between the plants; Supporting Information Table B2.4) is not automatically associated with optimal ground vegetation management for woodlarks. Moreover, despite a higher towering above the ground, wire vineyards eventually do not offer a more open overall habitat configuration than "gobelet".

In line with the above argumentation about ground vegetation cover, the application of herbicides impacts negatively on bird habitat selection. A short vegetation also increases occurrence probability (Boatman et al. 2004). These elements confirm the conclusions of previous work about the importance of food accessibility for terrestrial insectivorous birds inhabiting grassland (Atkinson et al. 2004, 2005, Butler and Gillings 2004, McCracken and Tallowin 2004). The woodlark in Valais vineyards represents yet a totally different situation than other grassland bird species in general (same authors as above) and even than British woodlarks in particular (Mallord et al. 2007). This is because the predominant habitat conditions in the study area are not a too dense grass vegetation cover, unlike in all other studies on habitat selection of farmland birds, but a generally totally bare habitat ($\geq 95\%$ of mineral vineyards). Thus, although extensifying agriculture practices in grassland production will positively affect bird population dynamics (Benton et al. 2002, Britschgi et al. 2006, Hansen and Urban 1992), in the case of woodlarks inhabiting vineyards it is the promotion of more vegetation on the ground which may support the species: if ground vegetation is absent, then food supply remains insufficient, especially as regards arthropods which constitute the staple food of woodlarks during reproduction. Genini (2000) showed that ground-dwelling arthropods such as spiders, carabid beetles, ants and locusts have more diverse communities and more abundant populations in vegetated vineyards.

Finally, the probability of occurrence of foraging woodlarks decreases with increasing infrastructure such as walls and roads. At a regional scale, it is evident that Valais woodlarks prefer the shallow vineyard plateaux than the steep slopes arranged in terraces separated by numerous stone walls, which is not especially surprising since lark species in general favor open, flat landscapes. The negative effect of roads could indicate an avoidance of traffic or human disturbance, as demonstrated in the UK (Mallord et al. 2007).

Conventional vine cultivation practices that systematically rely on herbicides lead to an entirely mineral, i.e. hostile habitat for woodlarks and other flora and fauna elements in southern Europe. A progressive switch to new methods is thus the most promising development for the woodlark in particular and for biodiversity in general. On the other end of the management spectrum, however, organic vineyards, which mostly have a continuous and dense ground vegetation cover because herbicides are prohibited, hamper the accessibility to food resources for the woodlark, and probably also for many other species feeding on the ground. Organic winekeepers should thus envision to maintain bare ground surfaces by removing part of the ground vegetation mechanically (optimally on about half of the parcel surface). Finally, it seems that the best compromise would be achieved by practices fulfilling the biological control protocol, but insofar as ground vegetation is tolerated. Unfortunately, this is not (yet) the case of every winekeeper implementing this scheme. Those winekeepers tolerating ground vegetation in their parcels usually treat with herbicides every second row, which appears to provide the most optimal habitat configuration with 50% ground vegetation cover. By spreading this technique, wine producers would support habitat restoration for a vulnerable, emblematic species of farmland. They would also contribute to promoting a rich and diverse flora and fauna typical of arid, semi-open cultivated landscapes of southern Europe.

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Supplementary information

List of variables recorded both at the visited and random locations are shown below.

Table B2.4: *Variables recorded at visited locations (radiotracking) and random locations, which describe: location and bearing accuracy (variables 1-5), bird behavior (6-8), vineyard management (7-9), ground vegetation (10-12) and infrastructure (13-15). Variables 7-15 were used for habitat selection analysis.*

	Variable	Definition
1	Coordinate X	Coordinate X of bearing or random location
2	Coordinate Y	Coordinate Y of bearing or random location
3	GPS accuracy	Accuracy of the GPS location (m)
4	Localization accuracy	Accuracy of the bearing/visual observation (m)
5	Visible	Visual observation (0: not seen; 1: bird seen)
6	Foraging	Foraging behavior (0: no foraging; 1: foraging)
7	Vineyard age	Estimated relative age of the vineyard (width of main vine trunk, continuous)
8	Vineyard type	Distance between plant rows: short for "gobelet"[1]; long for wires; categorial)
9	Herbicide application	Yes or no (categorial; 2 levels)
10	Ground vegetation cover	Percentage of ground vegetation cover (vines not considered; continuous)
11	Ground vegetation height	Mean height of grass sward (cm; continuous)
12	Organic litter[2]	Percent coverage of organic litter on the ground
13	Wall	Presence/absence of stone or beton wall (categorial; 2 levels)
14	Scrub[3]	Presence/absence of scrub (categorial; 2 levels)
15	Road	Presence/absence (categorial; 2 levels)

Note: [1] "Gobelet" is a special arrangement of vine plants, which grow small and are not arranged with wires. This is the conventional mode, compared to vines supported by wires bent between poles. In "gobelet" vineyards, the plant lines are ca 100-110 cm distant, whilst the spacing in wire vineyards is 120-200 cm.

[2] Removed from the habitat analysis because of high correlation with ground vegetation cover

[3] Removed from the habitat selection analysis because of highly skewed distribution

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Erklärung

gemäss Art. 28 Abs. 2 RSL 05

Name/Vorname: ....

Matrikelnummer: ....

Studiengang: ....

Bachelor ☐ Master ☐ Dissertation ☐

Titel der Arbeit: ....

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LeiterIn der Arbeit: ....

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Ich erkläre hiermit, dass ich diese Arbeit selbständig verfasst und keine anderen als die angegebenen Quellen benutzt habe. Alle Stellen, die wörtlich oder sinngemäss aus Quellen entnommen wurden, habe ich als solche gekennzeichnet. Mir ist bekannt, dass andernfalls der Senat gemäss Artikel 36 Absatz 1 Buchstabe o des Gesetztes vom 5. September 1996 über die Universität zum Entzug des auf Grund dieser Arbeit verliehenen Titels berechtigt ist.

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Ort/Datum

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Unterschrift

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Academic Experience

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Professional Experience

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Publications

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Conference contributions

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Courses/workshop attended

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"Mixed Models in Statistics Course" organized by the ee doctoral program, Lausanne, Switzerland, 01-03 July 2009.

"How to sell science to good journals" organized by the ee doctoral program , Lausanne, Switzerland, 05,19,26 November 2007.

"Effective public speaking" organized by the ee doctoral program, Lausanne, Switzerland, 06,19 December 2007.

"Workshop in Hierarchical Models in Ecology" organized by University of Zurich, Switzerland, 10-14 September 2007.

"Workshop in quantitative population dynamics" organized by University of Aagon, Greece, 06-10 June 2007.

"Survival Analysis" organized by the Center for Statistics, Hasselt University and K.U.Leuven University, Belgium, 19 May 2006.

"Customer Service" organized by Ethiopian Management Institute (EMI), Ethiopia, 05-09 June 2000.

"Advanced Reinsurance Practice" organized by the London School of Insurance, Ethiopia, 20-27 October 2000.

"Advanced Introduction to Computing" organized by African Virtual University (AVU), Ethiopia, 15 October 1999 - 15 February 2000.

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