

The demographic drivers of local population dynamics in two rare migratory birds

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Abstract The exchange of individuals among populations can have strong effects on the dynamics and persistence of a given population. Yet, estimation of immigration rates remains one of the greatest challenges for animal demographers. Little empirical knowledge exists about the effects of immigration on population dynamics. New integrated population models fitted using Bayesian methods enable simultaneous estimation of fecundity, survival and immigration, as well as the growth rate of a population of interest. We applied this novel analytical framework to the demography of two populations of long-distance migratory birds, hoopoe *Upupa epops* and wryneck *Jynx torquilla*, in a study area in south-western Switzerland. During 2002–2010, the hoopoe population increased annually by 11%, while the wryneck population remained fairly stable. Apparent juvenile and adult survival probability was nearly identical in both species, but fecundity and immigration were slightly higher in the hoopoe. Hoopoe population growth rate was strongly correlated

with juvenile survival, fecundity and immigration, while that of wrynecks strongly correlated only with immigration. This indicates that demographic components impacting the arrival of new individuals into the populations were more important for their dynamics than demographic components affecting the loss of individuals. The finding that immigration plays a crucial role in the population growth rates of these two rare species emphasizes the need for a broad rather than local perspective for population studies, and the development of wide-scale conservation actions.

Keywords Bayesian · Correlation · Demography · Integrated population model · *Jynx torquilla* · *Upupa epops*

Introduction

The focus of conservation is often a specific, declining population (Norris 2004) which is geographically open, i.e., subject to unknown immigration and 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, 2010a).

Identification of the spatial scale at which populations are influenced is important for defining informed conservation management units and implementing appropriate action (Baillie et al. 2000; Zannèse et al. 2006; Sirami et al. 2008). Identification of the main demographic processes involved in local population dynamics can help to identify the spatial scale at which population dynamics operate. If local reproduction has strong effects on local population

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dynamics, the spatial scale of dynamics and thus required conservation action will also be local. If local population dynamics depends more on survival, the scale depends on whether or not the species is migratory. For resident species, the scale will still be local, while in migratory species, it may extend to stopover and/or wintering sites, depending on where most of mortality occurs. Finally, when immigration is crucial for local population dynamics, conservation planning must take place at a greater than simply local scale, i.e. beyond the focal population.

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 losses (death, emigration) can be specified, but only a part of the gains (i.e. local recruitment) is known; recruitment from outside of the study population cannot be directly estimated. This prevents a comprehensive assessment of the population dynamics. This difficulty is often overcome by assuming that emigration equals immigration, which renders it impossible to quantify the relative contributions of the two dispersal processes to the dynamics of the population. Other approaches have assumed that all newly identified individuals in a population are recent immigrants (Møller 2002) or that all locally born individuals can be marked (O’Hara et al. 2009). Due to imperfect detectability, the former assumption will be wrong in most situations: newly detected individuals might have immigrated into a study population at variable times prior to first detection. It is also unlikely that all locally-born young can be marked because usually not all breeding sites can be found. With reverse-time capture–recapture modelling, it is possible to estimate total recruitment into populations (i.e. local recruitment plus immigration), but this requires the effort-intensive robust design sampling protocol for separating the two components of population dynamics (Nichols et al. 2000). A recently developed integrated population model (Abadi et al. 2010b) allows one to estimate immigration without requiring the robust design of data collection and without relying on the above two strong assumptions. This novel framework allows one to estimate and model all demographic components of population growth. Thus, it represents a major advance for demographic analyses, especially in 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* and the wryneck *Jynx torquilla*, 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 ground-feeding insectivores that search for prey in sparse vegetation [wryneck: ants (often *Lasius* sp.), Freitag 1996; hoopoe: molecrickets (*Gryllotalpa gryllotalpa*), Fournier and Arlettaz 2001; Arlettaz et al. 2010a; Schaub et al. 2010b]; both are secondary cavity breeders; they overwinter in the savannahs of the Sahel belt in Africa (Glutz von Blotzheim and Bauer 1980; Reichlin et al. 2009; Bächler et al. 2010); finally, they start to breed in their first year of life and produce many young. Knowledge about the demography of both species 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 in the breeding season affects reproductive success (Geiser et al. 2008; Arlettaz et al. 2010a).

We studied the population dynamics of hoopoes and wrynecks in the Upper Rhône valley (Valais, SW Switzerland) in the west-central Alps. The hoopoe population is isolated and has strongly increased recently (Arlettaz et al. 2010b), while the studied wryneck population is part of a continuously distributed, larger population that seems to have remained more or less stable. Our goals were (1) to estimate the demographic rates for each species, (2) to identify the demographic rates contributing most to the variation of the local population growth rate, and finally (3) to contrast the demography of two sympatric species with different population trends. We discuss our results with respect to the spatial scale of population dynamics and the respective geographic structure (isolated, continuous). We used integrated population models fitted in the Bayesian framework to simultaneously estimate all relevant demographic parameters (apparent survival, fecundity, immigration) from our two local, open populations. We extended this model hierarchically by assuming that the annual demographic rates were the realization of a random process with a mean and a variance that we estimated, to obtain the best possible annual estimates of the demographic parameters while accounting for uncertainty due to the sampling process. To evaluate the effects of the different demographic rates on population dynamics, we correlated the annual estimates with the estimated population growth rates. This approach allows a full accounting of all components of population demography, leading to a sharper appraisal of the phenomena driving demographic trajectories, which may prove decisive for informing conservation action.

Materials and methods

Study species and study site

The hoopoe and the wryneck are two small (approx. 75 and 35 g, respectively) birds of semi-open farmland. They are on the Red List of endangered species in Switzerland

(Keller et al. 2001). Breeding takes place from April to August. Many hoopoes produce two regular broods per breeding season, while this is less frequent in wrynecks. Our main study area (62 km²) is situated in 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 intensive fruit tree plantations and vineyards. About 700 nest boxes were installed in small agricultural shacks between 1998 and 2001 in an attempt to restore a local hoopoe population (Arlettaz et al. 2010b). Although the nest boxes have a large cavity size to suit hoopoes' needs, they have also been occupied by nesting wrynecks. Hoopoes depend exclusively on these nest boxes in the study area as there are virtually no other cavities of suitable size available. This is different for the wryneck that occupies smaller cavities than our nest boxes, both within and outside of the study area, e.g., in tree cavities or crevices under the roof of agricultural shacks, or in piles of wood and poles.

Demographic data

From 2002 to 2010, we collected three types of demographic data: capture–recapture data, data on fecundity and population survey data. For capture–recapture data, we ringed all nestlings in our nest boxes (ringed nestlings: sample size of hoopoe, $n_H = 4,124$; sample size of wryneck, $n_W = 1,970$) and all adults that we managed to catch using mist-nets, traps, or that were taken directly from nest boxes after hatching ($n_H = 492$, $n_W = 621$). Wrynecks react strongly to the playback song of conspecifics; hence, to increase sample size, we also tape-lured, mist-netted and ringed wrynecks during the pre-breeding season in April. Adult hoopoes were sexed in the field ($n_{H,male} = 221$, $n_{H,female} = 271$) based on the conspicuous uropygial gland, which is filled with a dark, predator-repelling substance in breeding females only (Martín-Vivaldi et al. 2009). Adult wrynecks captured between 2002 and 2008 ($n_{W,male} = 214$, $n_{W,female} = 221$) and a subsample of nestlings of both species from 2002 to 2008 ($n_H = 207$; $n_W = 155$) were sexed genetically based on blood samples. The 95% Bayesian credible intervals of the proportion of male nestlings included 0.5 in both species (hoopoe: 0.40–0.54; mean: 0.47; wryneck: 0.45–0.60; mean: 0.52), indicating no deviation from an even sex ratio. Thus, for the capture–recapture data, we assigned unsexed nestlings equally to either sex, keeping the overall annual sex-ratio at 1:1 (Nichols et al. 2004). A total of 186 adult wrynecks were not sexed.

To obtain data on fecundity, we intensively monitored all broods in nest boxes. Both species regularly produce two broods per season, so for each female (identified by its ring number) we calculated the total number of fledglings

produced in a given year (fledged nestlings of known females: hoopoe: $n_{\text{nestlings}} = 3,296$ in 511 female years; wryneck: $n_{\text{nestlings}} = 1,522$ in 244 female years). For the wryneck, we also included broods where the sex of the captured parent(s) was unknown (47 broods). This can be justified by the fact that partners in this species usually stay together when producing 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. Thus, our estimate of fecundity is an estimate of the total number of fledglings produced per female and 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 annual number of simultaneous broods found in the nest boxes. 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 declining number of broods during our study period (2002: 72; 2010: 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 used Bayesian, dynamic site-occupancy modelling (Royle and Kéry 2007) to estimate population trends in the local distribution at a 1-km² scale (Kéry et al. 2010). We used opportunistic observations from the whole Canton of Valais stored in the information service database of the Swiss Ornithological Institute, which contains haphazard observations, and also their breeding bird survey database. From 2002 to 2010, wrynecks were recorded in 210 1-km² quadrats. For each quadrat, year and breeding season (16 April until 29 July), we deduced day-based detection histories containing a 1 if a wryneck had been recorded and a 0 if any other species, but no wryneck, had been recorded. Site–day units without any recorded sightings in either data base were treated as missing values (see Kéry et al. (2010) for more information). Dynamic occupancy models yield estimates of the proportion of occupied sites as a function of initial occupancy probability, site colonisation and extinction probabilities, while accounting for (and estimating) the imperfect detection of a species at an occupied site (Royle and Kéry 2007). We used WinBUGS to fit a model with year effects in the dynamic parameters and year and quadratic seasonal effects in detection probability (for details, see Appendix 2). The annual number of occupied sites along with its posterior standard deviation was used as a population index and a measure of the observation error, respectively, in the integrated model of the wryneck.

Occupancy dynamics should represent a valid index for population trends in the wryneck provided that its breeding

density is not much larger than one breeding pair per 1 km². Furthermore, the larger area where the occupancy data were gathered (210 km²) must provide a representative measure of population trend also for the study area. Density measures over large areas are difficult to get in wrynecks. In habitats of high quality, the density can be at least 1.48 pairs per 1 km² (own data from the study area), while over larger areas, including habitats of lower quality, the density is certainly lower. Thus, we assume that occupancy was a valid surrogate for abundance in our study. To assess whether occupancy dynamics is spatially synchronous, we split the occupancy data in two parts according to altitude; only the lower part includes the study area. We found that the difference in the rate of occupancy change between the two parts was small. The 95% credible intervals of the difference in occupancy rate included 0 in all years. Hence, we assumed that occupancy dynamics obtained from the complete canton was also representative for the study area.

Integrated population model

We used integrated population modelling to estimate demographic parameters (Schaub and Abadi 2011). In this framework, the different sources of demographic information are combined into a single model, resulting in improved precision of parameter estimates, and often in 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, 2010a; Cave et al. 2009; Abadi et al. 2010a; Kéry and Schaub 2011: chapter 11). Recently, this framework was extended to estimate immigration rate (Abadi et al. 2010b), which makes the model particularly useful for our purpose.

Implementing integrated population models 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; Kéry and Schaub 2011: chapter 7). Fecundity was modelled 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 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 1 year of age. A deterministic

version of the model can be written as a matrix projection model (Caswell 2001), as

$$\begin{bmatrix} N_{1,t+1} \\ N_{2+,t+1} \end{bmatrix} = \begin{bmatrix} f_t \phi_{ju,t} s + \omega_t & f_t \phi_{ju,t} s + \omega_t \\ \phi_{ad,t} & \phi_{ad,t} \end{bmatrix} \begin{bmatrix} N_{1,t} \\ N_{2+,t} \end{bmatrix}$$

where $N_{1,t}$ is the number of 1 year old females and $N_{2+,t}$ is the number of females older than 1 year. The juvenile and adult apparent survival probabilities of a female at time t , $\phi_{ju,t}$ and $\phi_{ad,t}$ denote the probability that a female survives and does not emigrate permanently between year t and $t + 1$. Fecundity at time t is denoted f_t and ω_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 . Finally, s is the proportion of female fledglings. Immigration was restricted to the class of 1-year-old individuals, thus we assumed that natal dispersal occurred, but that there was no breeding dispersal. While no doubt an approximation to reality, this can be justified because natal dispersal is much stronger than breeding dispersal in most bird species (Paradis et al. 1998).

To account for demographic stochasticity, we used Poisson and binomial distributions to describe the dynamics of the true population size over time (Abadi et al. 2010b). Thus, the number of 1-year-old females ($N_{1,t+1}$) in year $t + 1$ is given by the sum of the number of local recruits and immigrants

$$N_{1,t+1} = N_{R,t+1} + N_{Im,t+1}$$

where

$$N_{R,t+1} \sim \text{Po}((N_{1,t} + N_{2+,t})f_t \phi_{ju,t} s) \text{ and}$$

$$N_{Im,t+1} \sim \text{Po}((N_{1,t} + N_{2+,t})\omega_t).$$

The number of females older than 1 year ($N_{2+,t+1}$) is given by

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

The number of immigrants could also be modelled directly (i.e. $N_{Im,t} \sim \text{Po}(\xi_t)$, where ξ_t is the expected number of immigrants). Both parameterisations of immigration (i.e. as a rate or as a number) perform similarly well (D. Fletcher and M. Schaub, unpublished data), but specification of immigration as a rate has the advantage that this rate is also a parameter in the projection matrix model. Immigration rate is estimated accurately if the other demographic rates are estimated without bias (D. Fletcher and M. Schaub, unpublished data).

The observation process describes the relationship between the observed population counts (hoopoe) or the estimated number of occupied sites (wryneck) in year t (y_t) with the true population size. For this, we assumed a log-Normal distribution, i.e. $\log(y_t) \sim N[\log(N_{1,t} + N_{2+,t}), \sigma_{\text{obs}}^2]$, where σ_{obs}^2 is the observation (residual) variance. In

the hoopoe, the observation variance is an unknown parameter that is estimated. In the wryneck, the observation variance is a known quantity (from the dynamic occupancy model) that varies over time.

We used a hierarchical formulation of the integrated model to get the best possible annual estimates of the demographic rates that are not inflated by sampling variation. In this formulation, the annual estimates are thought to originate from a random process with a common mean and a constant temporal variance. For the logit of apparent survival probabilities, we assumed

$$\text{logit}(\phi_t) = \beta_0 + \varepsilon_t, \text{ with } \varepsilon_t \sim N(0, \sigma_\phi^2),$$

where β_0 is the mean annual survival on the logit scale and σ_ϕ^2 is the temporal variance of apparent survival on the logit scale. For the log of fecundity and immigration rate, we assumed

$$\log(f_t) = \alpha_0 + \tau_t, \text{ with } \tau_t \sim N(0, \sigma_f^2), \text{ and}$$

$$\log(\omega_t) = \gamma_0 + v_t, \text{ with } v_t \sim N(0, \sigma_\omega^2).$$

Again, α_0 and γ_0 are the mean fecundity and immigration rates, respectively, on a log scale, and σ_f^2 and σ_ω^2 the temporal variances of fecundity and immigration, respectively, on the log scale.

Assuming independence between the different datasets, 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 detailed description of the likelihood of the integrated population model used here is given by Abadi et al. (2010b). One concern in implementing the integrated population model is the assumption of independence, because individuals may appear in more than one dataset. However, a recent simulation study using the same data types as used here suggests that ignoring such a dependence only results in a slight inflation of the precision of the parameter estimates (Abadi et al. 2010a). Furthermore, the degree of non-independence is likely very weak in the wrynecks because the population survey covered a larger area and thus different individuals than the main study area where demographic data were collected.

The likelihood of the capture–recapture data of the males was constructed in the same way as that for the females. However, it was not part of the joint likelihood, unless the sexes were constrained to have identical parameters (see below).

We used the Bayesian approach to inference and Markov chain Monte Carlo (MCMC) simulation for parameter estimation (Gilks et al. 1996). This approach required defining prior distributions for all model parameters. We specified informative priors for the proportion of female

nestlings (s), based on the sex determination in a subset of nestlings. We used the beta distribution with parameters a and b [$\beta(a, b)$], where a is the number of female and b the number of male nestlings that were genetically sexed. For all other parameters, we chose priors intended to be vague, i.e. to contain little information, so that the inference was dominated by the information in the data. See Appendix S1 (Supplementary Material) for the precise specification of the priors for all parameters. Some experimentation with different prior choices suggested they had virtually no impact on the parameter estimates, indicating that the inferences were determined by the information in the data.

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 and discarding the first 20,000 as burn-in, which suggested the chains had converged. We finally ran one single chain for 1,100,000 iterations, discarded the first 100,000, and thinned such that every 100th observation was retained for parameter estimation. All analyses were conducted in WinBUGS (Lunn et al. 2000), run from R 2.9.1 (R Development Core Team 2009) via the R2WinBUGS package (Sturtz et al. 2005). R and WinBUGS code and data are available in Appendix S1 (Supplementary Material).

We aimed for inference based on a simple model. We considered in the models random 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 probability differed between sexes and was time-dependent or constant. For model selection, there is a Bayesian equivalent of AIC, the deviance information criterion (DIC; Spiegelhalter et al. 2002). However, there are doubts over the applicability of DIC for hierarchical models (Millar 2009). Therefore, we performed model selection using the capture–recapture data only for the CJS model and under consideration of fixed instead of random temporal effects. We compared 16 different models that included or excluded sex effects in apparent survival as well as sex and time effects in recapture probabilities. Sex of wrynecks was unknown for all individuals captured since 2009, hence we tested for a sex effect using the data up to 2008 (see Appendix S2, Supplementary Material). We used then the same structure for recapture and survival as in the DIC best model for estimating demographic rates with the integrated population model.

There is no goodness-of-fit test developed yet for integrated population models. For a partial fit assessment, we

Table 1 Estimates of posterior mean (median for fecundity and immigration as the back-transformation from the log scale gives the median) and temporal variance ($\hat{\sigma}^2$) with 95% credible intervals (CI)

Demographic rates	Hoopoe		Wryneck	
	Mean/median	$\hat{\sigma}^2$	Mean/median	$\hat{\sigma}^2$
Juvenile survival	0.121 (0.092, 0.158)	0.0014 (0.0002, 0.0069)	0.115 (0.081, 0.156)	0.0005 (0.0000, 0.0054)
Adult survival	0.384 (0.346, 0.431)	0.0011 (0.0000, 0.0109)	0.383 (0.276, 0.503)	0.0137 (0.0001, 0.0878)
Fecundity	6.527 (5.989, 7.110)	0.4473 (0.0574, 2.1104)	6.221 (5.772, 6.670)	0.1308 (0.0003, 1.0421)
Immigration	0.283 (0.126, 0.454)	0.0153 (0.0002, 0.1810)	0.251 (0.062, 0.484)	0.0410 (0.0001, 0.5404)
Population growth rate	1.110 (1.054, 1.138)	–	0.993 (0.965, 1.022)	–

in parentheses of demographic rates obtained from the integrated population model for hoopoe *Upupa epops* and wryneck *Jynx torquilla* from Valais (2002–2010)

performed a goodness-of-fit test for the CJS model using chi-squared decompositions in the software U-CARE (Choquet et al. 2009). These tests did not indicate any lack of fit for either species (hoopoe: $\chi^2_{35} = 35.23$, $P = 0.46$; wryneck: $\chi^2_{16} = 13.81$, $P = 0.61$).

Assessing the impact of demography on dynamics

We correlated the estimated annual population growth rates with each of the demographic rates. The strength of this correlation provides an indication of the strength of the contribution of the temporal variation of one demographic parameter to the temporal variation in population growth (Robinson et al. 2004; Freeman et al. 2007) during the study period. To do so, we computed the posterior distributions of the correlations coefficients. Since most of these posterior distributions were very skewed, we used the mode to describe them (instead of posterior means as for the other parameters). We also calculated the probability that the correlation coefficients were positive.

Results

Temporal patterns in demographic rates and test for sex effects

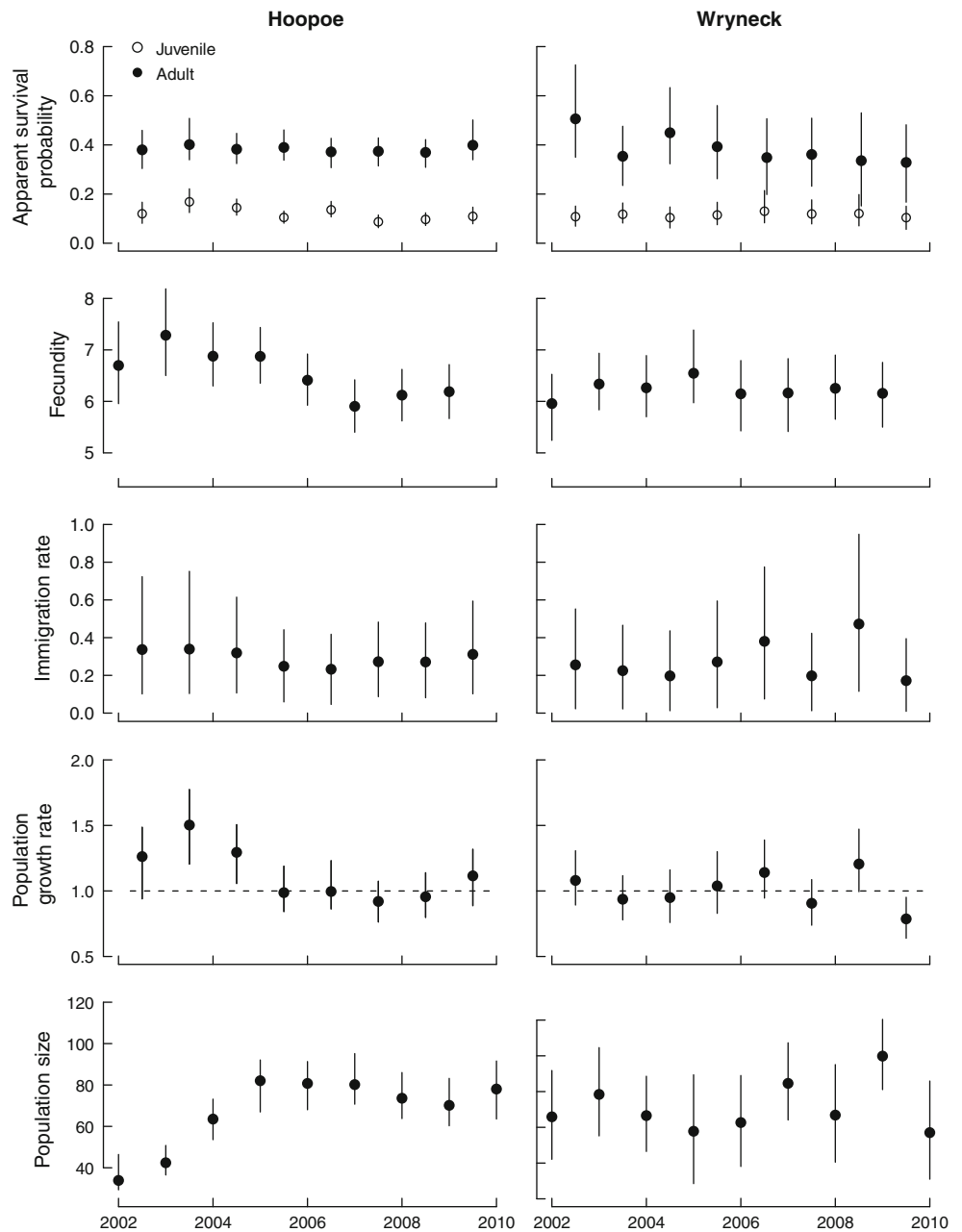
Model selection for the capture–recapture component suggested that apparent survival in hoopoes was best modelled without a sex effect, but that recapture probabilities contained a sex effect and an additive year effect (Appendix S3, Table S1, Supplementary Material). In contrast, in wrynecks, there was no evidence for sex-specific differences in apparent survival or recapture probabilities (Appendix S3, Table S2, Supplementary Material). The estimates of the demographic parameters under the integrated population models show that the demography of the two species was surprisingly similar, with a slightly higher productivity (+5%) and a higher immigration rate (+18%) for hoopoes, compared with wrynecks (Table 1).

Population growth in hoopoes was clearly positive (population growth rate: 1.11, 95% credible intervals: 1.05–1.14), while that of the wryneck was very close to 1 (0.99, 0.95–1.02). The population growth rates varied strongly among years (Fig. 1). While the hoopoe population strongly increased from 2002 to 2005 ($\lambda > 1$) and then remained fairly stable ($\lambda \sim 1$), the wryneck population fluctuated during the entire study period. The temporal pattern of demographic rates showed a decline in hoopoe fecundity and wryneck adult survival during the course of the study, but no obvious trends in the other rates (Fig. 1).

Correlations of demographic rates with population growth rate

The modes of the correlation coefficients of all demographic rates with the population growth rate were positive in the hoopoe. Juvenile apparent survival and fecundity had higher correlation coefficients than immigration and adult apparent survival (Fig. 2). Based on the posterior distributions of the correlation parameters, we could be 0.99 certain that there was a positive association between growth rate and juvenile survival and fecundity, compared to a >0.8 probability for immigration and a >0.7 probability for adult survival. In the wryneck, immigration was positively correlated with the population growth rate, while the correlations of apparent juvenile and adult survival with population growth were weaker and that of fecundity with population growth close to zero (Fig. 2). The probability of a positive correlation was >0.9 for immigration, >0.7 for juvenile survival and >0.5 for adult survival and fecundity. The probabilities that the correlation coefficients between growth rate and vital rates were higher in hoopoes than in wrynecks were 0.85, 0.53, 0.93 and 0.29 for juvenile survival, adult survival, fecundity and immigration, respectively. This shows that the contributions of fecundity and juvenile survival to population growth were more likely to differ between the two species than the contributions of immigration and adult survival.

Fig. 1 Estimates of annual demographic parameters, population growth rates and population sizes (population index for the wryneck) obtained from the integrated population model along with 95% credible intervals for hoopoe *Upupa epops* (left panel) and wryneck *Jynx torquilla* (right panel)



Discussion

We conducted a comprehensive demographic assessment of the population dynamics of two sympatric long-distance migrant bird species: hoopoe and wryneck. Our study showed that the two species were very similar in terms of the mean demographic rates, but suggested that the driving forces in their population dynamics were different. The observed population fluctuations in the hoopoe were most strongly correlated with variation in fecundity and juvenile survival, and there was also an important contribution of immigration. In contrast, wryneck population dynamics was likely to be a result of variation in immigration. The

correlations of population growth with fecundity and with juvenile survival were likely different between species, with the hoopoe having stronger correlations.

Integrated population models can achieve a detailed accounting of all demographic components underlying the dynamics of a population. This includes one of the most elusive demographic component, immigration, which is hard to estimate reliably. The price to be paid is the relatively low precision in the estimation of immigration. Our model assumes that all immigrants are 1-year-old birds. This is not a strong assumption: apparent survival and fecundity of 1-year-old birds and older birds did not differ, and the immigration rate would be the same had we

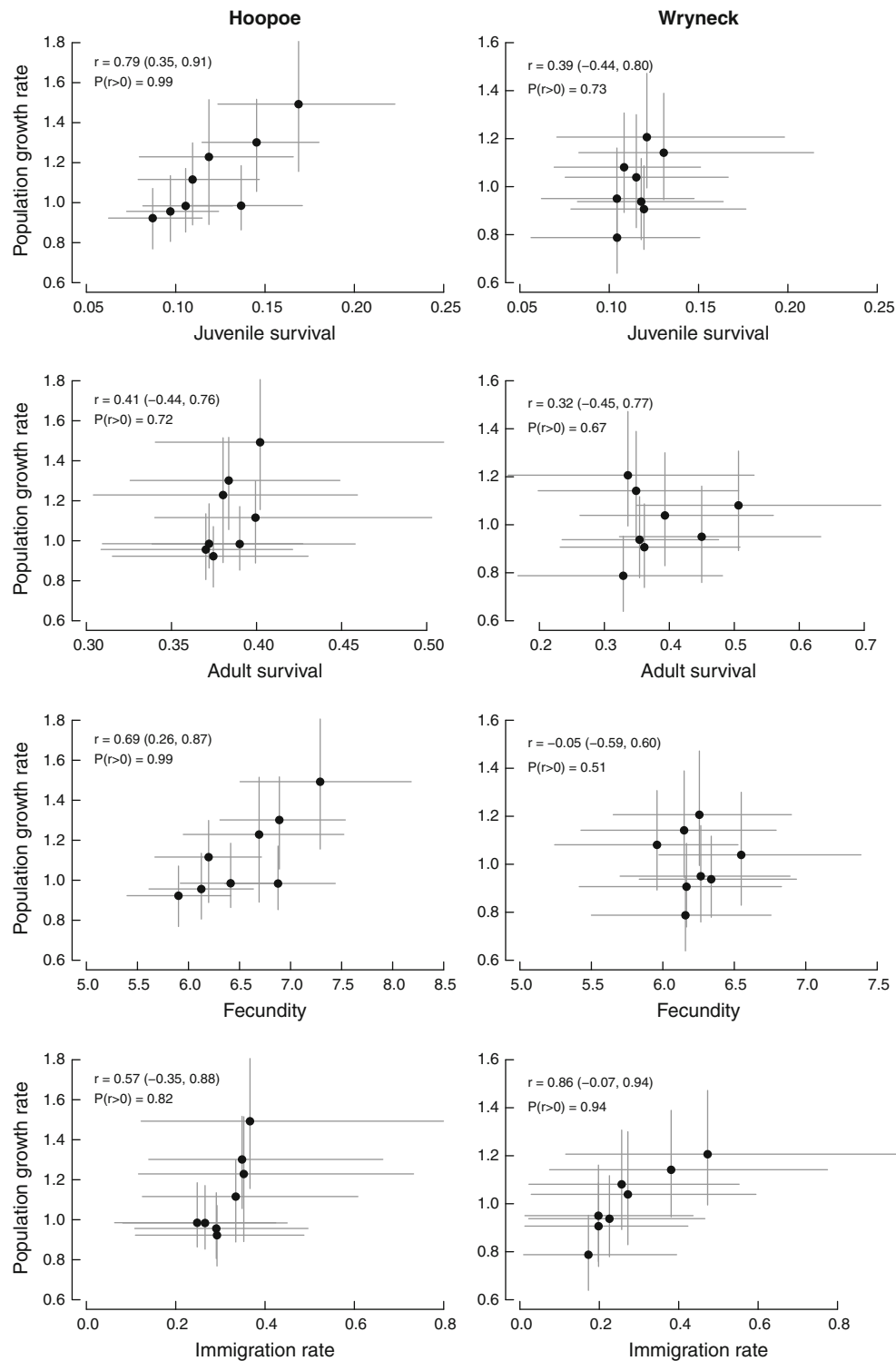


Fig. 2 Annual estimates of demographic rates plotted against the annual estimates of population growth in hoopoe and wrynecks. The dots show the posterior means and the horizontal and vertical lines show the limits of the 95% credible intervals. Also given are the

posterior mode and the 95% credible intervals of the correlation coefficients (r) as well as the probability that the correlation coefficient is positive [$P(r > 0)$]

assumed that all immigrants were older than 1 year. Hence, the assumption appears to have an effect on the inference, but not on the estimate itself. The reliance on a hierarchical

formulation for annual rates allowed us to estimate the temporal variance of the demographic rates, and to get better estimates of the annual demographic rates (Gelman

and Hill 2007). Using a hierarchical model, the estimated annual parameters are shrunken towards the mean, and the degree of shrinkage depends on the precision (Burnham and White 2002). This is a desirable property, as the impact of uncertain parameters is reduced. The hierarchical model is more parsimonious compared to a model where for each year an independent parameter is estimated; nevertheless, the estimates of temporal variability and of the immigration rate in particular were not very precise. The method applied here would yield more precise results with longer study duration.

In hoopoes, variation of apparent juvenile survival was an important driver for the local population dynamics. This result is in line with population dynamics studies of birds (e.g. Reid et al. 2004; Robinson et al. 2004; Ezard et al. 2006; Baillie et al. 2008; Sim et al. 2011) and mammals (Gaillard et al. 2000) that found a significant contribution of the variation of juvenile survival to the variation of population growth. Apparent survival is composed of true survival and fidelity to the study population, so the variation of either true survival and/or natal dispersal might be the real driving force. Robinson et al. (2004) decomposed juvenile survival temporally and found that survival from fledgling until autumn (post-fledgling survival) was the most important phase. This might also apply to hoopoes and wrynecks. However, our data so far neither enable such a temporal decomposition nor a separation of true survival and dispersal.

Immigrants are individuals breeding in the study population but that were born outside it. Depending on the location of other populations with respect to the study population, immigrants may originate from far away, from nearby or even from within the study area. Our hoopoe population is very isolated; the next known hoopoe populations of comparable sizes are 250–350 km away (Trento, Italy; Kaiserstuhl, Germany; see Arlettaz et al. 2010b). In between, there are only scattered breeding pairs (canton of Vaud, Switzerland; Valle d'Aosta, Italy). Furthermore, we are confident that we know the Valais breeding population very well and essentially exhaustively, because hoopoes occupy almost exclusively nest boxes, which we have systematically monitored for many years (Arlettaz et al. 2010b). Thus, in the hoopoe, immigrants are most likely individuals born in populations many kilometres 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 versus possible immigrants (Reichlin et al., unpublished data). 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 originating from another population but

may include individuals born within the same local population (Reichlin et al. 2010). Consequently, the interpretation of the immigration rate of the wrynecks is different from that for the hoopoes.

The population growth rates of both species would be low in the absence of immigration (hoopoe: 0.83; wryneck: 0.74). These values well below 1 suggest that both populations are not self-sustainable and represent sinks. However, true juvenile survival is probably higher than estimated here (hoopoe: 0.09–0.17; wryneck: 0.10–0.13), i.e. closer to what is observed in birds of similar body size (about 0.2; Siriwardena et al. 1998). This may indicate that a large fraction of our juveniles emigrate from the local populations. The proportion of emigrants can roughly be estimated under a simplistic scenario where (1) no adults settle outside a local population (Greenwood and Harvey 1982), i.e. the observed apparent adult survival were the true survival (0.38 in both species); and (2) immigration is 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 can be computed. Under this hypothetical scenario, juvenile survival would have to be 0.22 and 0.20 for hoopoes and wrynecks, respectively, to yield the actual, observed population growth rates (Table 1). This would result in an emigration probability of juveniles of 0.46 in hoopoes ($1-0.12/0.22$) and 0.42 in wrynecks ($1-0.11/0.20$). 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 young individuals. For hoopoes, this system may extend over a very large area, while for the wryneck, the spatial extent is uncertain. 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, 2010a). Assessing whether the systems have the characteristics of sink–source dynamics (Dias 1996) or of balanced dispersal (McPeck and Holt 1992) would require detailed knowledge of the demographic performance of several populations, which remains a real logistic challenge for field research (Doncaster et al. 1997).

The variation of fecundity contributed strongly to the variation of the population growth in the hoopoes. At the beginning of the study period, when the population size was smaller, fecundity was higher, and then progressively declined with increasing population size (Fig. 1). Thus, part of the strong correlation between fecundity and population growth might be explained by density-dependence. By contrast, fecundity in wrynecks hardly contributed to

their population dynamics. This is somewhat unexpected, because fecundity is a part of recruitment, to which populations of short-lived species should be particularly sensitive (Saether and Bakke 2000). Breeding success in wrynecks is less affected by adverse weather than in hoopoes (Geiser et al. 2008; Arlettaz et al. 2010a), resulting in lower temporal variability of fecundity in wryneck. This may be an explanation for why the variation of population growth rate in wrynecks is less affected by the variation of fecundity than in hoopoes. Another possible explanation is that population density of wrynecks remained relatively stable. However, the observation that variation of population growth rate is little affected by the variation of fecundity does not mean that local reproduction of wrynecks is unimportant. The locally produced young that emigrate from the local population are the immigrants to other populations, which may be a crucial component for their dynamics. Thus, local reproduction is important to stabilise the system of spatially structured populations, but not so much for the individual population (Baillie et al. 2000; Schaub et al. 2006).

The variation of adult survival contributed little in either species to the variation of population growth. Adult survival is often an important component of population dynamics only in longer-lived species (Saether and Bakke 2000; Schaub et al. 2006; Schorch et al. 2009); thus, it was expected a priori that adult survival in the short-lived hoopoe and wryneck are not crucial for the local population dynamics.

The dynamics of many bird populations are synchronised across large spatial scales (e.g. Paradis et al. 2000; Jones et al. 2007; Saether 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 suggests the former mechanism (Schaub et al. 2005; Saether et al. 2007). Our demographic analysis shows that immigration and apparent juvenile survival were important drivers of local population dynamics, and thus there is the potential of larger scale population synchrony due to dispersal. Indeed, population trends of both species are known to be synchronised across different countries (Glutz von Blotzheim and Bauer 1980; but see Arlettaz et al. 2010b). Because the regulation of both studied populations also 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 hundreds of kilometres. The situation of the wryneck is less clear and requires further study.

Our study establishes that the population dynamics of two endangered sympatric species exhibiting similar life histories was strongly dependent on demographic

components affecting the number of new individuals entering the population (in situ recruitment and immigration) rather than on components affecting the number of individuals lost. The hoopoe population, which was locally on the brink of extinction before the start of our study, has been rapidly recovering after the installation of hundreds of nestboxes since 1998 which increased the number of breeding sites that locally were the most limiting factor (Fournier and Arlettaz 2001; Arlettaz et al. 2010b). The strong population increase was facilitated by high immigration from pre-existing population reservoirs of unknown geographic location and by high local fecundity. 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 habitat of suitable quality within and beyond the focal population.

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References

- Abadi F, Gimenez O, Arlettaz R, Schaub M (2010a) An assessment of integrated population models: bias, accuracy, and violation of the assumption of independence. *Ecology* 91:7–14
- Abadi F, Gimenez O, Ullrich B, Arlettaz R, Schaub M (2010b) Estimation of immigration rate in integrated population model. *J Appl Ecol* 47:393–400
- Arlettaz R, Schaad M, Reichlin TR, Schaub M (2010a) Impact of weather and climate variation on hoopoe reproductive ecology and population growth. *J Ornithol* 151:889–899
- Arlettaz R, Schaub M, Fournier J, Reichlin TS, Sierro A, Watson JEM, Braunisch V (2010b) From publications to public actions: when conservation biologists bridge the gap between research and implementation. *Bioscience* 60:835–842
- Bächler E, Hahn S, Schaub M, Arlettaz R, Jenni L, Fox WJ, Afanasyev V, Liechti F (2010) Year-round tracking of small trans-Saharan migrants using light-level geolocators. *PLoS ONE* 5:e9566
- Baillie SR, Sutherland WJ, Freeman SN, Gregory RD, Paradis E (2000) Consequences of large-scale processes for the conservation of bird populations. *J Appl Ecol* 37:88–102
- Baillie SR, Brooks SP, King R, Thomas L (2008) Using a state-space model of the British song thrush *Turdus philomelos* population to

- diagnose the causes of a population decline. In: Thomson DL, Cooch EG, Conroy MJ (eds) Modeling demographic processes in marked populations. Environmental and Ecological Statistics, vol 3. Springer, New York, pp 541–561
- Besbeas P, Freeman SN, Morgan BJT, Catchpole EA (2002) Integrating mark-recapture-recovery and census data to estimate animal abundance and demographic parameters. *Biometrics* 58:540–547
- Brooks SP, Gelman A (1998) General methods for monitoring convergence of iterative simulations. *J Comput Graph Stat* 7:434–455
- Brooks SP, King R, Morgan BJT (2004) A Bayesian approach to combining animal abundance and demographic data. *Anim Biodiv Conserv* 27:515–529
- Burnham KP, White GC (2002) Evaluation of some random effects methodology applicable to bird ringing data. *J Appl Stat* 29:245–264
- Caswell H (2001) Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Sunderland, MA
- Cave VM, King R, Freeman SM (2009) An integrated population model from constant effort bird-ringing data. *J Agric Biol Envir Stat* 15:119–137
- Choquet R, Lebreton J-D, Gimenez O, Reboulet A-M, Pradel R (2009) U-CARE: utilities for performing goodness-of-fit tests and manipulating capture–recapture data. *Ecography* 32:1071–1074
- De Valpine P, Hastings A (2002) Fitting population models incorporating process noise and observation error. *Ecol Monogr* 72:57–76
- Development Core Team R (2009) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria
- Dias PC (1996) Sources and sinks in population biology. *Trends Ecol Evol* 11:326–330
- Doncaster CP, Clobert J, Doligez B, Gustafsson L, Danchin E (1997) Balanced dispersal between spatially varying local populations: an alternative to the source-sink model. *Am Nat* 150:425–445
- Ezard THG, Becker PH, Coulson T (2006) The contributions of age and sex to variation in common tern population growth rate. *J Anim Ecol* 75:1379–1386
- Fournier J, Arlettaz R (2001) Food provision to nestlings in the hoopoe *Upupa epops*: implications for the conservation of a small endangered population in the Swiss Alps. *Ibis* 143:2–10
- Franklin AB, Gutiérrez RJ, Nichols JD, Seamans ME, White GC, Zimmerman GS, Hines JE, Munton TE, LaHaye WS, Blakesly JA, Steger GN, Noon BR, Shaw DWH, Kean JJ, McDonald TL, Britting S (2004) Population dynamics of California spotted owl (*Strix occidentalis occidentalis*): a meta-analysis. *Ornithol Monogr* 54:1–54
- Freeman SN, Robinson RA, Clark JA, Griffin BM, Adams SY (2007) Changing demography and population decline in the common starling *Sturnus vulgaris*: a multisite approach to integrated population monitoring. *Ibis* 149:587–596
- Freitag A (1996) Le régime alimentaire du Torcol fourmilier (*Jynx torquilla*) en Valais (Suisse). *Nos Oiseaux* 43:497–512
- Gaillard JM, Festa-Bianchet M, Yoccoz NG, Loison A, Toïgo C (2000) Temporal variation in fitness components and population dynamics of large herbivores. *Annu Rev Ecol Syst* 31:367–393
- Geiser S, Arlettaz R, Schaub M (2008) Impact of weather variation on feeding behaviour, nestling growth and brood survival in Wrynecks *Jynx torquilla*. *J Ornithol* 149:597–606
- Gelman A, Hill J (2007) Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, Cambridge
- Gilks WR, Richardson S, Spiegelhalter DJ (1996) Markov chain monte carlo in practice. Chapman and Hall, London
- Glutz von Blotzheim UN, Bauer KM (1980) Handbuch der Vögel Mitteleuropas, vol 9. Akademischer, Wiesbaden, Frankfurt am Main
- Greenwood PJ, Harvey PH (1982) The natal and breeding dispersal of birds. *Annu Rev Ecol Syst* 13:1–21
- Jones J, Doran PJ, Holmes RT (2007) Spatial scaling of avian population dynamics: population abundance, growth rate, and variability. *Ecology* 88:2505–2515
- Keller V, Zbinden N, Schmid N, Volet B (2001) Rote Liste der gefährdeten Brutvogelarten der Schweiz. BUWAL- Reihe Vollzug Umwelt, 57. Bundesamt für Umwelt, Wald und Landschaft (BUWAL) and Schweizerische Vogelwarte Sempach
- Kéry M, Schaub M (2011) Bayesian population analysis using WinBUGS—a hierarchical perspective. Academic, Burlington
- Kéry M, Royle JA, Schmid H, Schaub M, Volet B, Häfliger G, Zbinden N (2010) Correcting population trend estimates from opportunistic observations for observation effort using site-occupancy modeling. *Conserv Biol* 24:1388–1397
- Lambrechts MM, Blondel J, Caizergues A, Dias PC, Pradel R, Thomas DW (1999) Will estimates of lifetime recruitment of breeding offspring on small-scale study plots help us to quantify processes underlying adaptation? *Oikos* 86:147–151
- Lampila S, Orell M, Belda E, Koivula K (2006) Importance of adult survival, local recruitment and immigration in a declining boreal forest passerine, the willow tit *Parus montanus*. *Oecologia* 148:405–413
- Lande R, Engen S, Saether BE (1999) Spatial scale of population synchrony: environmental correlation versus dispersal and density regulation. *Am Nat* 154:271–281
- Lebreton J-D, Burnham KP, Clobert J, Anderson DR (1992) Modelling survival and testing biological hypotheses using marked animals—a unified approach with case-studies. *Ecol Monogr* 62:67–118
- Lunn DJ, Thomas A, Best N, Spiegelhalter D (2000) WinBUGS—a Bayesian modelling framework: concepts, structure, and extensibility. *Stat Comput* 10:325–337
- Martín-Vivaldi M, Ruiz-Rodríguez M, Soler JJ, Peralta-Sánchez JM, Mendez M, Valdivia E, Martín-Platero AM, Martínez-Bueno M (2009) Seasonal, sexual and developmental differences in hoopoe *Upupa epops* preen gland morphology and secretions: evidence for a role of bacteria. *J Avian Biol* 40:191–205
- McPeck MA, Holt RD (1992) The evolution of dispersal in spatially and temporally varying environments. *Am Nat* 140:1010–1027
- Millar RB (2009) Comparison of hierarchical Bayesian models for over dispersed count data using DIC and Bayes’ factors. *Biometrics* 65:962–969
- Møller AP (2002) North Atlantic Oscillation (NAO) effects of climate on the relative importance of first and second clutches in a migratory passerine bird. *J Anim Ecol* 71:201–210
- Murphy MT (2001) Habitat-specific demography of a long-distance, neotropical migrant bird, the Eastern Kingbird. *Ecology* 82:1304–1318
- Newton I, Marquiss M (1986) Population regulation in Sparrowhawks. *J Anim Ecol* 55:463–480
- Nichols JD, Hines JE, Lebreton J-D, Pradel R (2000) Estimation of contributions to population growth: a reverse-time capture–recapture approach. *Ecology* 81:3362–3376
- Nichols JD, Kendall WL, Hines JE, Spendlow JA (2004) Estimation of sex-specific survival from capture–recapture data when sex is not always known. *Ecology* 85:3192–3201
- Norris K (2004) Managing threatened species: the ecological toolbox, evolutionary theory and declining-population paradigm. *J Appl Ecol* 41:413–426
- O’Hara RB, Lampila S, Orell M (2009) Estimation of rates of births, deaths, and immigration from mark-recapture data. *Biometrics* 65:275–281

- Paradis E, Baillie SR, Sutherland WJ, Gregory RD (1998) Patterns of natal and breeding dispersal in birds. *J Anim Ecol* 67:518–536
- Paradis E, Baillie SR, Sutherland WJ, Gregory RD (2000) Spatial synchrony in populations of birds: effects of habitat, population trend and spatial ecology. *Ecology* 81:2112–2125
- Reichlin TS, Schaub M, Menz MHM, Mermod M, Portner P, Arlettaz R, Jenni L (2009) Migration patterns of hoopoe *Upupa epops* and wryneck *Jynx torquilla*: an analysis of European ring recoveries. *J Ornithol* 150:393–400
- Reichlin TS, Hobson KA, Wassenaar LI, Schaub M, Tolkmitt D, Becker D, Jenni L, Arlettaz R (2010) Migratory connectivity in a declining bird species: using feather isotopes to inform demographic modelling. *Divers Distrib* 16:643–654
- Reid JM, Bignal EM, Bignal S, McCracken DI, Monaghan P (2004) Identifying the demographic determinants of population growth rate: a case study on red-billed choughs *Pyrrhocorax pyrrhocorax*. *J Anim Ecol* 73:777–788
- Robinson RA, Green RE, Baillie SR, Peach WJ, Thomson DL (2004) Demographic mechanisms of the population decline of the song thrush *Turdus philomelos* in Britain. *J Anim Ecol* 73:670–682
- Royle JA, Kéry M (2007) A Bayesian state-space formulation of dynamic occupancy models. *Ecology* 88:1813–1823
- Saether BE, Bakke O (2000) Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* 81:642–653
- Saether BE, Engen S, Grotnan V, Fiedler W, Matthysen E, Visser ME, Wright J, Møller AP, Adriaensen F, Van Balen H, Balmer D, Mainwaring MC, McCleery R, Pampus M, Winkel W (2007) The extended Moran effect and large-scale synchronous fluctuations in the size of great tit and blue tit populations. *J Anim Ecol* 76:315–325
- Schaub M, Abadi F (2011) Integrated population models: a novel analysis framework for deeper insights into population dynamics. *J Ornithol*. doi:10.1007/s10336-010-0632-7 (in press)
- Schaub M, Kania W, Köppen U (2005) Variation of primary production during winter induces synchrony in survival rates in migratory white storks *Ciconia ciconia*. *J Anim Ecol* 74:656–666
- Schaub M, Ullrich B, Knöttsch G, Albrecht P, Meisser C (2006) Local population dynamics and the impact of scale and isolation: a study on different little owl populations. *Oikos* 115:389–400
- Schaub M, Gimenez O, Sierro A, Arlettaz R (2007) Use of integrated modeling to enhance estimates of population dynamics obtained from limited data. *Conserv Biol* 21:945–955
- Schaub M, Aebischer A, Gimenez O, Berger S, Arlettaz R (2010a) Massive immigration balances high anthropogenic mortality in a stable eagle owl population: lessons for conservation. *Biol Conserv* 143:1911–1918
- Schaub M, Martinez N, Tagmann-Ioset A, Weisshaupt N, Maurer ML, Reichlin TS, Abadi F, Zbinden N, Jenni L, Arlettaz R (2010b) Patches of bare ground as a staple commodity for declining ground-foraging insectivorous farmland birds. *PLoS ONE* 5:e13115
- Schorcht W, Bontadina F, Schaub M (2009) Variation of adult survival drives population dynamics in a migrating forest bat. *J Anim Ecol* 78:1182–1190
- Sim IMW, Graham WR, Ludwig SC, Grant MC, Reid JM (2011) Characterizing demographic variation and contributions to population growth rate in a declining population. *J Anim Ecol* 80:159–170
- Sirami C, Brotons L, Martin JL (2008) Spatial extent of bird species response to landscape changes: colonisation/extinction dynamics at the community-level in two contrasting habitats. *Ecography* 31:509–518
- Siriwardena GM, Baillie SR, Wilson JD (1998) Variation in the survival rates of some British passerines with respect to their population trends on farmland. *Bird Study* 45:276–292
- Spiegelhalter DJ, Best NG, Carlin BR, van der Linde A (2002) Bayesian measures of model complexity and fit. *J R Stat Soc B* 64:583–616
- Stacey PB, Taper M (1992) Environmental variation and the persistence of small populations. *Ecol Appl* 2:18–29
- Sturtz S, Ligges U, Gelman A (2005) R2WinBUGS: a package for running WinBUGS from R. *J Stat Softw* 12:1–16
- Tucker GM, Heath MF (1994) Birds in Europe their conservation status. Birdlife International, Cambridge, UK
- Ward MP (2005) The role of immigration in the decline of an isolated migratory bird population. *Conserv Biol* 19:1528–1536
- Zannè A, Morellet N, Targhetta C, Coulon A, Fuser S, Hewison AJM, Ramanzin M (2006) Spatial structure of roe deer populations: towards defining management units at a landscape scale. *J Appl Ecol* 43:1087–1097
- Zingg S, Arlettaz R, Schaub M (2010) Nest box design influences territory occupancy and reproduction in a declining, secondary cavity-breeding bird. *Ardea* 98:67–75