ECOGRAPHY

Integrated population model reveals that kestrels breeding in nest boxes operate as a source population

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The identification of the source–sink status of a population is critical for the establishment of conservation plans and enacting smart management decisions. We developed an integrated population model to formally assess the source status of a kestrel *Falco tinnunculus* population breeding in nest boxes in Switzerland. We estimated juvenile and adult survival, reproduction and net dispersal (emigration/immigration) by jointly analyzing capture–recapture, dead recovery, breeding monitoring and population survey data. We also investigated the role of nest boxes on kestrel demography and assessed the contributions of vital rates to realized population growth rates. The results indicate that the kestrel population breeding in nest boxes has acted as a source over the 15 years of the study duration. A quantitative approach suggests that a substantial number of individuals have emigrated annually from this population likely affecting the population dynamics outside the management area. Variation in fecundity explained 34% of the temporal variability of the population growth rate. Moreover, a literature review suggests that kestrel pairs produce on average 1.4 chicks more per breeding attempt in nest boxes compared to natural open nests. Together, these findings suggest that fecundity was an important driver for the dynamics of this population and that nest boxes have contributed to its raise. Nest boxes are regularly used as an efficient tool for conservation management. We suggest that such a conservation action can result in the establishment of a source population being beneficial for populations both inside and outside the managed area.

Keywords: emigration, Eurasian kestrel, *Falco tinnunculus*, integrated population model, population dynamics, population management

Introduction

In an increasingly fragmented world, efficient conservation measures require a profound understanding of spatial population dynamics (Fahrig and Merriam 1994). A key concept in this perspective is the source–sink system which proposes the existence of two population types that differ in the net balance between reproduction and survival (Pulliam 1988, Loreau et al. 2013). In a source population births exceed deaths. Such a population could be a net exporter of individuals, i.e. the maintenance of this population is possible even if the number of emigrants exceeds the number of

immigrants. In contrast, in a sink population the number of deaths exceeds the number of births and its long-term maintenance depends on immigrants that must outnumber the emigrants.

The identification of the source–sink status of a population is a major step to establish a conservation plan and to take smart management decisions (Hernández-Matías et al. 2013, Kirol et al. 2015). Wildlife management ignoring source–sink status could be inefficient or remain unsuccessful. For example attractive sinks, also called ecological traps, can destabilize a spatially structured population leading to a rapid decline and extinction over a wide area (Delibes et al. 2001). Knowledge about source–sink systems is imperative to accurately define the ecological niche of a species (Pulliam 1988), conduct population viability analyses (Hernández-Matías et al. 2013), develop sustainable harvesting strategies (Naranjo and Bodmer 2007) or take decisions regarding prioritization of habitats for conservation (Kirol et al. 2015).

Nest box deployment is a frequent conservation action for cavity breeding species (White et al. 2005, Harley 2006, Savard and Robert 2007, Catry et al. 2009, Arlettaz et al. 2010, Libois et al. 2012, Brazill-Boast et al. 2013). When a population is limited by nest site availability, a situation which is likely common (Newton 1994), providing artificial nests may increase population size. Furthermore, reproductive performance is generally higher in nest boxes than in natural nests, at least in birds (Møller 1989). Several studies have documented the positive effect of such management on local population dynamics (Libois et al. 2012, Altwegg et al. 2014, Sutherland et al. 2014). However, no study has yet investigated if the provision of artificial nests may promote the creation of source populations. Such a perspective is attractive as it suggests that nest boxes may support both the managed populations as well as populations outside the managed area.

The assessment of the source–sink state of a population is challenging. The simple observation of population sizes or densities is not sufficient to distinguish between sources and sinks. Indeed large populations may be sinks maintained by small source populations (Pulliam 1988) and density could be decoupled from habitat quality (Van Horne 1983). A convincing assessment requires a quantitative approach including demographic rates. The comparison between the realized population growth rate (λ_{real}) and the theoretical population growth rate (λ) calculated from survival and reproduction has often been used to diagnose whether a population is a sink or a source (Pulliam 1988, Runge et al. 2006). According to this logic, a stable population ($\lambda_{real} = 1$) for which reproduction overcompensates mortality, i.e. $\lambda > 1$ is a source. However, λ could be biased owing to the difficulty of estimating true survival. Most of the time, the estimated survival probability from open populations is apparent survival, i.e. mortality is confounded with permanent emigration. Thus, the population growth rate is underestimated which may lead to the erroneous conclusion that the population is a sink. In these cases detailed demographic data with which true survival, reproduction and dispersal rate (at least emigration) can be estimated are required to distinguish sources from sinks

(Runge et al. 2006). However, estimating all these parameters for the same population is highly challenging and few studies have been able to investigate source–sink dynamics with this level of accuracy (Weegman et al. 2016). A review examining 90 source–sink assessments taken from 73 studies found that only one combined emigration with survival and reproduction (Furrer and Pasinelli 2016).

The development of integrated population models (IPM) over the last decade offers new opportunities to investigate the source–sink status of populations. These models jointly analyze different demographic datasets on the same population (Besbeas et al. 2002). A typical example is the joint analyses of capture–recapture, fecundity and population survey data (Schaub and Abadi 2011). IPMs are powerful tools to make inference about dispersal parameters (immigration, emigration) (Abadi et al. 2010) and have been recently used to assess the source–sink status (Weegman et al. 2016, Millsap 2017). These studies estimated explicitly the migration rate to assess whether the populations were net exporters or net importers.

In our study, we investigated the source–sink status of a Eurasian kestrel *Falco tinnunculus* (hereafter kestrel) population breeding in nest boxes in Switzerland. This species had been decreasing in the second part of the last century in Switzerland as in most of the European countries (BirdLife 2017). Kestrel populations are expected to be limited locally by nest-site availability, especially in very open landscapes lacking natural cavities and niches on buildings (Village 1990, Fargallo et al. 2001). Therefore, as a conservation measure, nest box deployment has been initiated in several areas across Switzerland. A previous study has shown that nest box deployment resulted in an increase of the local population (Jeanmonod and Broch 2001). In the current paper we assess if the kestrel population breeding in nest-boxes has operated as a source. To investigate this hypothesis, we used an integrated population model combining capture–recapture data, dead-recoveries, reproductive monitoring and population survey data. We 1) estimated population growth rate, survival, reproduction and net dispersal to determine if this population was a net exporter of individuals over the study duration (2002–2016). We 2) assessed the potential role of nest boxes on kestrel demography. For this purpose we conducted a review to investigate the effect of nest types on breeding performance of kestrels and used simulated demographic projection controlling for the effect of nest types on fecundity. Finally using life table response experiments, we 3) assessed the respective contribution of the demographic rates to the observed population growth. We discuss the ability of the studied nest box population to have contributed to the dynamics of neighboring populations.

Material and methods

Study species

The kestrel is a small raptor widespread in open landscapes throughout the Palearctic. In Switzerland kestrels are found

throughout the country from lowland agricultural land-scapes to alpine grass lands. Common voles (*Microtus* sp.) are often the most important prey, but kestrels are opportunistic and can forage also on reptiles, small birds and insects (Costantini et al. 2005). Under natural conditions, kestrels breed mainly on trees in disused stick-nests of larger bird species (typically corvids) or in cavities on cliffs and trees. In anthropogenic environments kestrels also use cavities on buildings, pylons and other man-made structures (Village 1990). Kestrels easily accept nest boxes and even seem to prefer them when available (Valkama and Korpimäki 1999, Fargallo et al. 2001). As a monogamous species, both parents participate in parental care but roles of males and females clearly differ. The female lays a single clutch per year containing 4–6 eggs. She incubates them for 30 d and broods the young during two weeks after hatching. During this time, the male delivers food to both the female and the nestlings. In case of failure, there is usually no replacement brood. The chicks leave the nest at around 30 d and are guided by both parents for another 2–4 weeks (Village 1990). Some individuals start to reproduce when they are one year old, but a large proportion is assumed to start reproductive life only when two years old (Village 1990).

Study area and population trend

In Switzerland, nest boxes have been occasionally provided for kestrels since the 50s but massive deployment mainly by groups of volunteers or regional nature organizations began in the late 90s. A large-scale monitoring project of nest boxes started in 2002 with about 1000 nest boxes distributed throughout the country from the west (Geneva) to the northeast (St-Gallen) (Fig. 1). Progressively more nest boxes have been installed until 2015 to reach a number of 3300. Given an average nest box occupation rate of 37%, this set of nest boxes has supported a breeding kestrel population of 400 to more than 1200 pairs over the study period. Nest boxes have been installed on buildings in lowland agricultural landscapes where natural nest sites for kestrel are rare. Thus in our study area breeding occurs almost exclusively in nest-boxes.

Data collection

From 2002 to 2016, volunteers collected three types of demographic data: data on fecundity, capture–recapture–recovery data and population survey data. Fecundity and capture–recapture data were obtained from the monitoring of the nest boxes during the breeding season. The timing and the frequency of the nest box checks was heterogeneous. From a total of 6187 broods, 4830 were visited for the first time before the nestlings hatched, while the remaining broods were checked for the first time after the hatching of the nestlings. Based on the broods visited before hatching, we could estimate the probability whether an initiated brood was successful, while from all monitored successful broods we could estimate the number of fledglings, here defined as the number of chicks reaching the ringing age. Broods were defined
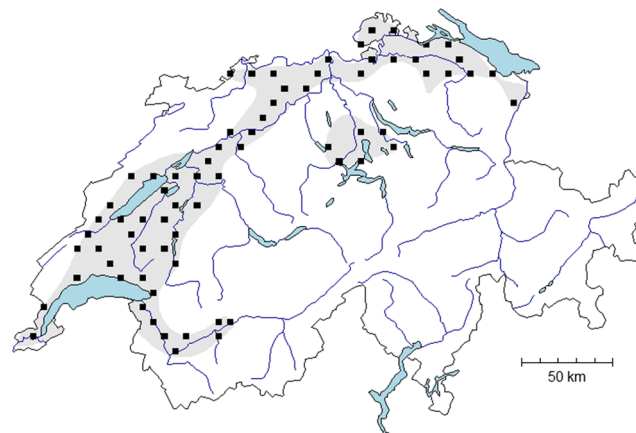

Figure 1. Map of Switzerland with the nest box deployment area (gray) and the location of the 1-km² quadrats (n = 71) where territory mappings have been conducted annually (black square).

as having failed if no individual has reached the ringing age. Most nestlings in each year were ringed with an aluminum ring at a minimal age of 15 d (n = 28 658). In addition, a total of 808 adults were captured. Most kestrels marked as adults were ringed with both an aluminum and an alphanumeric color ring. Reencounters were either recaptures with so called Bal-chatri traps close to the nest site or with a scoop net at the nest box entrance or resightings of the color marked adults within the study area. Both methods were used during the breeding season (n = 418 reencountered individuals in total). In addition, marked individuals could be found dead (dead recovery) throughout the year and within or outside the study area (n = 636). Experienced birders have conducted territory mapping on 267 1-km² quadrats which have been distributed randomly across Switzerland from 1999 to 2017 (Kéry and Schmid 2004). We selected the 71 1-km² quadrats that are located within our study area (Fig. 1). The annual numbers of detected territories in these quadrats were analyzed with a Poisson regression model to estimate the annual population index and its uncertainty.

Data analyses

We used an integrated population model (IPM) to estimate demographic parameters and make inference on population dynamics. Data on reproduction, survival as well as the estimated population index were analyzed in a single model with the benefit of obtaining more precise parameter estimates (Besbeas et al. 2002, Schaub and Abadi 2011). Furthermore IPMs allow estimating dispersal based from the difference between the demographic parameters and the observed population change (Abadi et al. 2010, Schaub and Fletcher 2015).

We started by building a population matrix model based on a pre-breeding census (Caswell 2001). The projection matrix is parameterized with the demographic parameters that will be shared by the others models, i.e. fecundity model, capture–recapture–recovery model and population index model. Demographic data included individuals of

both sexes, but the demographic rates could not be estimated sex-specific. We therefore defined a one sex population model that we parameterized with average (with respect to sex) rates. As some kestrels do not breed before they are two years old, we used two age classes, one and two years or older. The expected numbers of individuals present in the year $t+1$ are given by

$$\begin{bmatrix} N_1 \\ N_2 \end{bmatrix}_{t+1} = \begin{bmatrix} \alpha_1 S_{1,t}\gamma_t\delta_t/2 + w_t & \alpha_2 S_{1,t}\gamma_t\delta_t/2 + w_t \\ S_{2,t} & S_{2,t} \end{bmatrix} \begin{bmatrix} N_1 \\ N_2 \end{bmatrix}_t \quad (1)$$

where $N_{1,t}$ is the number of 1-year-old individuals in year t and $N_{2,t}$ is the number of two years or older individuals in year t. $S_{1,t}$ and $S_{2,t}$ are the survival probabilities between years t and $t+1$ of juveniles and adults, respectively. We assumed to estimate true survival probability due to the dominance of dead recoveries in the capture–recapture–recovery dataset (Barker 1997) and the large size of the study area (Marshall et al. 2004). α_1 is the breeding probability at age 1, i.e. the recruitment probability, α_2 is the adult breeding probability, γ_t the breeding success in year t, i.e. the probability that an initiated brood produces at least one fledging, and δ_t the productivity in the year t given success, i.e. the mean number fledglings per successful broods in year t. In this formulation, $\gamma_t\delta_t$ is number of fledglings per breeding pair in year t, i.e. fecundity. Finally, w_t is the net dispersal rate, i.e. the difference between immigration and emigration, in year t. Immigration and emigration rates are pooled since no explicit data are available to estimate these parameters separately. Note that IPMs are often parameterized with immigration only because the emigration rate is usually confounded with survival (apparent survival) (Schaub and Fletcher 2015). However, in our case we estimated true survival and consequently the remaining parameter is net dispersal which combines both immigration and emigration. We defined the net dispersal rate as the number of net dispersing individuals in year $t+1$ per individual present in year t. We assumed that dispersing individuals are all one year old, thus that only natal, but not breeding dispersal to and from our study area has occurred (Greenwood 1980).

For the capture–recapture–recovery data, we formulated a multistate mark–recapture model (Brownie et al. 1993). We used six states to control for age (two age classes), mark type (aluminum ring or aluminum and color ring) and to include recovery information. Due to lack of data we were not able to control for sex and thus we assumed equal survival between sexes. Generally raptors show few difference in survival between sexes (Newton et al. 2016). The details of this model are given in Supplementary material Appendix 1. The data are summarized in an m-array table (Lebreton et al. 1992), whose numbers ($\boldsymbol{m}$) follow a multinomial distribution with cell probabilities that are a function of age-specific survival ($\boldsymbol{S}$), recapture ($\boldsymbol{p}$) and recovery probabilities ($\boldsymbol{r}$). All these parameters were modeled with random time effects. The formulation of the likelihood of this model is $L_{CR}(\boldsymbol{m}|\boldsymbol{S}_1, \boldsymbol{S}_2, \boldsymbol{p}_{alu}, \boldsymbol{p}_{col}, \boldsymbol{r})$.

Two types of reproductive data were available: first, for a subset of broods, it was known whether a brood had been successful given that a clutch was laid (breeding success). Second, the number of nestlings that reached the ringing age was recorded for all successful broods (productivity given success). Our estimate of productivity should be very close to the number of fledglings since most of chick mortality occurs before the ringing age (Cavé 1968). To model the annual breeding success we used a binomial model: $BS_t \sim B(M_t, \gamma_t)$ where BS_t is the number of successful broods in year t, M_t is the number of monitored broods in year t and γ_t is the estimated breeding success in year t. Productivity of successful broods was modeled using a normal distribution: $PR_{i,t} \sim N(\delta_t, \sigma^2_{PR})$ where $PR_{i,t}$ is the productivity of pair i in year t, δ_t is the average productivity in year t and σ^2_{PR} is the residual variance. Fecundity is the product of breeding success and productivity of successful broods. The likelihood is therefore the product of the likelihood of the two underlying models $L_f = L_{BS}(BS, M \mid \boldsymbol{\gamma}) \times L_{PR}(PR \mid \boldsymbol{\delta}, \sigma^2_{PR})$.

To model the population index, we used a state-space model (de Valpine and Hastings 2002). The state process described the dynamics of the population which is given in eq. 1. Owing to the large size of the modelled population (several hundreds of pairs) we did not include demographic stochasticity (Lande et al. 2003). For the observation process that links the population counts with the population sizes, we distinguished two error sources. First, we considered a normally distributed error for the estimation of the population index, i.e. $y_t \sim N(\hat{y}_t, \sigma^2_{obs,t})$, where y_t is the estimated annual population index and $\sigma^2_{obs,t}$ is the standard deviation of the population index. Both were obtained from a Poisson regression model on the annual number of territories found in the monitored quadrats. Then we included an additional error (σ^2_{fit}) due to possible lack of fit of the population model, i.e. $\hat{y}_t \sim N(N_{1,t} + N_{2,t}, \sigma^2_{fit})$. The likelihood of the state-space model (L_{SS}) for the population index is the product of the likelihood of the process (L_{SY}) and the observation equations (L_{OB})

$$L_{SS} = L_{SY}\left(N \mid \boldsymbol{\alpha}, S_1, S_2, \boldsymbol{\gamma}, \boldsymbol{\delta}, w\right) \times L_{OB}(y, \sigma^2_{obs,t} \mid N, \sigma^2_{fit})$$

Once the likelihoods of the three datasets were defined, we created the joint likelihood, i.e. the likelihood of the integrated population model. Given that the population index and the demographic data are independent, the joint likelihood becomes the product of the component likelihoods:

$$\begin{aligned} L_{IPM}&(m, BS, M, PR, y \mid S_1, S_2, p_{alu}, p_{col}, r, w, \sigma^2_{PR}, N, \sigma^2_{obs}, \sigma^2_{fit}) \\ &= L_{CR}(m \mid S_1, S_2, p_{alu}, p_{col}, r) \times L_{BS}(BS, M \mid \boldsymbol{\gamma}) \times L_{PR}(PR \mid \boldsymbol{\delta}, \sigma^2_{PR}) \\ &\times L_{SY}(N \mid \boldsymbol{\alpha}, S_1, S_2, \boldsymbol{\gamma}, \boldsymbol{\delta}, w) \times L_{OB}(y \mid N, \sigma^2_{obs,t}, \sigma^2_{fit}) \end{aligned}$$

We used the Bayesian approach for inference and Markov chain Monte Carlo (MCMC) simulation for parameter

estimation. We specified vague priors for all estimated parameters. Details for the specification of the prior are available with the JAGS code of the model in the Supplementary material Appendix 2. The analysis was conducted in JAGS (Plummer 2003) via the R package jagsUI (Kellner 2016). Posterior summaries from three Markov chain Monte Carlo (MCMC) chains were based on 100 000 iterations after a burn-in of 40 000 and a thinning rate of 1/10. We confirmed parameter convergence using the Gelman–Rubin statistic. All the R-hat values were below 1.02 supporting convergence. We generally report the posterior means and the 95% credible intervals (here after CRI). There is no omnibus test available to assess the goodness-of-fit (GOF) of an IPM (Besbeas and Morgan 2014). Hence, we performed GOFs separately for each model component (details and results in Supplementary material Appendix 3).

Transient life table response experiments

We applied a transient life table response experiment (transient LTRE) to estimate the contribution of the variability of each demographic rate and of population structure to the variability of the realized population growth rate (Koons et al. 2016, 2017). We used the following equation to estimate the contribution of the temporal variability of each vital rate θ_i and of population structure (here N_1 and N_2) to the temporal variance of λ_t

$$\text{Contribution}_{\theta_i}^{\text{var}(\lambda_t)} \approx \sum_j \text{cov}\left(\theta_{i,t}, \theta_{j,t}\right) \frac{\partial \lambda_t}{\partial \theta_{i,t}} \left. \frac{\partial \lambda_t}{\partial \theta_{j,t}} \right|_{\bar{\theta}}$$

Here, $\partial \lambda_t / \partial \theta_{i,t}$ is the sensitivity of the population growth rate with respect to θ_i and i and j are indices for vital rates and population structure. Thus the contributions are estimated by the sum of the products of the pair-wise covariance between the demographic parameters with the sensitivity matrices. The results obtained are dimensionless values that can be scaled to sum to 1 for easier comparison. More details about transient LTRE and their applications using results from IPMs are presented in Koons et al. (2016, 2017).

Sensitivity analysis and the effects of nest types on fecundity

Breeding probabilities of one year-old (i.e. recruitment probability) and adult individuals could not be estimated from our dataset. We used values from the literature and ran a sensitivity analysis to check whether uncertainty regarding these parameters did affect our conclusion (see Supplementary material Appendix 4 for details). To assess the role of nest boxes on population dynamics, we first conducted a review to get the effect of nest type on fecundity distinguishing nest boxes, natural cavities and open nests (Supplementary material Appendix 5). Secondly, we used these effect sizes in our population model to predict the kestrel net dispersal rate under the assumption that all nesting sites had been natural cavities or open nests.

Data deposition

Results

The average recovery probability was 0.03 (CRI = [0.02, 0.04]) and the average recapture probabilities were 0.01 (CRI = [0.01, 0.02]) and 0.08 (CRI = [0.02, 0.27]) according to the mark type, aluminum ring or aluminum and color ring respectively. The average annual survival probabilities were estimated to be 0.72 (CRI = [0.69, 0.76]) for adults and 0.49 (CRI = [0.45, 0.54]) for juveniles (Table 1, Fig. 2). Both breeding success and productivity given success showed substantial annual variation with averages of 0.88 (CRI = [0.87, 0.90]) and 4.20 (CRI = [3.99, 4.41]), respectively. The net dispersal rate was negative and the 95% credible interval did not overlap 0 (Table 1), thus there was more emigration than immigration. Given that this population had increased with an average annual growth rate of 1.07 (CRI = [1.05, 1.08]), this result suggests that our kestrel population breeding in nest boxes was a source. The result is qualitatively the same for all the values of adult breeding probability considered (Fig. 3). We found that the 95% CRI of the net dispersal rate overlaps with 0 only when the adult breeding probability is equal or lower than 0.50 and does not overlap 0 whatever the yearling breeding probability. These results show that the inference about the source–sink status of our study population is very robust.

We could use 25 studies reporting breeding parameters of 35 populations (here defined both by the location and the nest-type used) to quantify the effect of nest type on fecundity in kestrels (Supplementary material Appendix 8 Table A1). There was a clear relationship between nest type and the average number of fledglings per breeding attempt (Fig. 4, Supplementary material Appendix 8 Fig. A1). Fecundity was highest in nest boxes (3.9 fledgings per reproduction, CRI = [3.3, 4.4]), moderate in natural cavities (3.1, CRI = [2.6, 3.6]) and lowest in open nests (2.5, CRI = [2.0, 3.0]). The differences primarily originated from higher hatching success and chick survival in nest boxes rather than from an increase in clutch size (Supplementary material Appendix 8 Fig. A2).

Table 1. Posterior means and temporal variance (σ^2) with 95% credible intervals in parentheses of demographic rates obtained from the integrated population model for kestrels breeding in nest boxes in Switzerland (2002–2016).

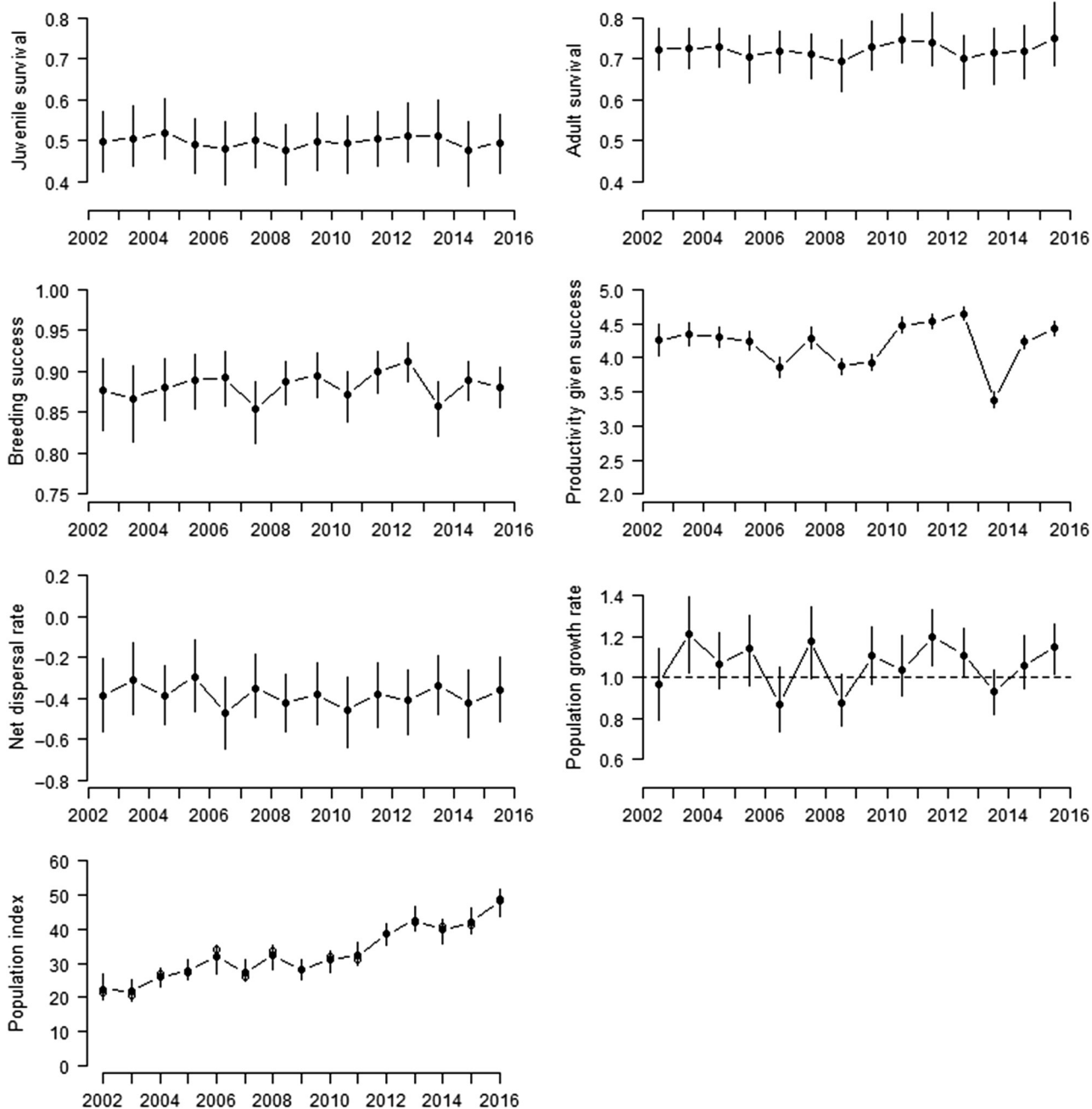| Demographic rates	Mean	σ^2
Adult survival	0.72 (0.69, 0.76)	0.03 (0.00, 0.15)
Juvenile survival	0.49 (0.45, 0.54)	0.02 (0.00, 0.11)
Breeding success	0.88 (0.87, 0.90)	0.06 (0.01, 0.20)
Productivity given success	4.20 (3.99, 4.41)	0.15 (0.06, 0.34)
Net dispersal rate	−0.38 (−0.49, −0.27)	0.01 (0.00, 0.03)
Population growth rate	1.07 (1.05, 1.08)	–

Figure 2. Estimates of annual demographic parameters, population growth rate and population index obtained from the integrated population model along with 95% credible intervals for kestrels breeding in nest boxes in Switzerland (2002–2016). Open circles in the graph of the population index show population counts.

When the advantage of nest boxes is removed, the net dispersal rate would decrease by 37–50% if all broods had been conducted in a natural cavity and by 68–92% if all broods were in an open nest depending on the value of adult breeding probability. The 95% credible intervals of the latter case overlap 0 (Fig. 3), suggesting that, other things being equal, the population might not have operated as a source when no nest boxes had been available and all kestrels had to breed in open nests. A similar conclusion is obtained with the scenario where 80% of broods occur in open nests and 20% in natural cavities (Supplementary material Appendix 5, 8 Fig. A3).

Elasticities were highest for adult survival and fecundity indicating that proportional changes in these two parameters would result in the strongest change of the population growth rate. Net dispersal rate and population structure had markedly smaller elasticities. Retrospectively, temporal variation of the population growth rate was mostly explained
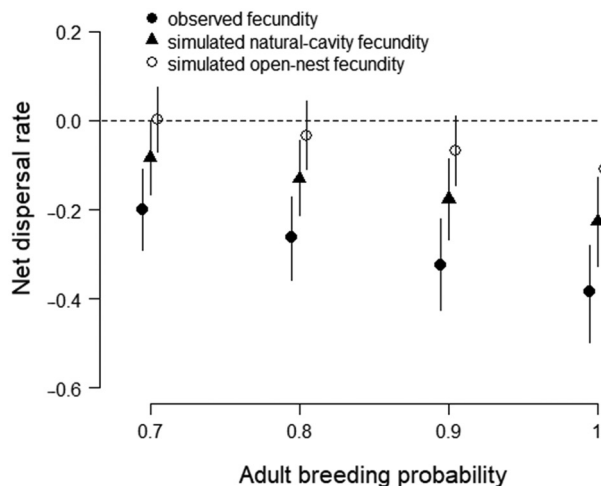
Figure 3. Posterior means with 95% credible intervals of the average net dispersal rate over the study period (2002–2016) obtained from the integrated population model according to different values of adult breeding probability. Results are given considering the fecundity estimate from our studied population breeding in nest boxes (closed dots) and with simulated fecundities assuming that all kestrels either breed in natural cavities (closed triangles) or in open nests (open dots) (Supplementary material Appendix 5).

by temporal variability of fecundity (34%, CRI = [0.11, 0.74]). Variability in net dispersal rate accounted almost as much (30%, CRI = [0, 0.64]), followed by temporal variability of population structure (18%, CRI = [0.02, 0.35])), juvenile survival (11%, CRI = [0, 0.45]) and adult survival (6%, CRI = [0, 0.26]), and (Table 2).
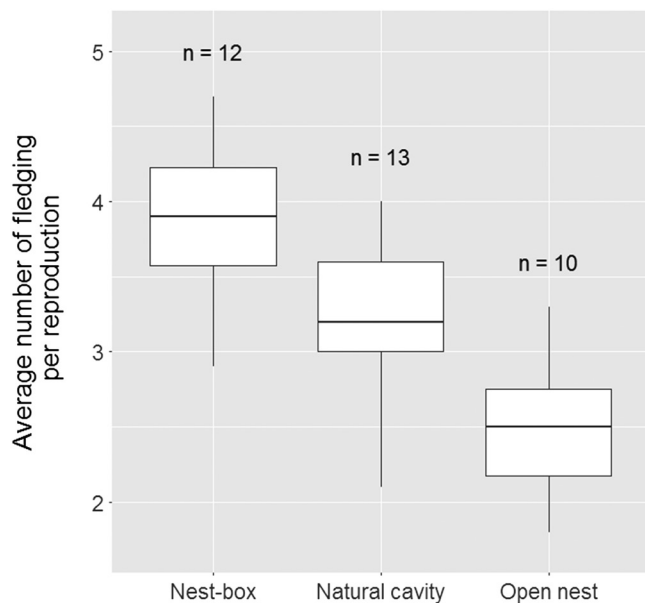

Figure 4. Fecundity according to nest type in the kestrel *Falco tinnunculus*. Estimates are obtained from the meta-analysis on the studies presented in the Supplementary material Appendix 8 Table A1. The sample size, i.e. the number of populations monitored for each nest type is provided by n.

Discussion

Using an integrated population model, we estimated the relevant demographic rates to properly assess the sink–source status of a large kestrel population that breeds in nest boxes. Results indicate that the population operated as a source over the 15 study years and that nest boxes likely have contributed to the growth of the population and its ability to export individuals. Our study showed that nest box deployment, which is a regularly applied management action, can impact local population dynamics and may affect population dynamics at larger spatial scales by providing surplus individuals.

Demographic rates and population dynamics of the kestrel population

Obtaining estimates of demographic rates as required to assess the source–sink status of a population is highly challenging (Runge et al. 2006, Furrer and Pasinelli 2016). Using an integrated population model we estimated simultaneously population growth rates as well as juvenile and adult survival, fecundity and the net dispersal rate. The model relied on simplifying assumptions. Potential effects of their violations have been assessed by sensitivity analyses or are discussed (Supplementary material Appendix 6). The estimated demographic rates are consistent with those provided by the literature. Fecundity was 3.71 (CRI = [3.65, 3.76]) fledglings per breeding attempt which is typical for kestrels breeding in nest boxes (Fig. 4). Our estimates of juvenile (0.49, CRI = [0.44, 0.54]) and adult survival (0.72, CRI = [0.68, 0.76]) were slightly higher than previous estimates ranging between 0.32 and 0.45 for juveniles and between 0.65 and 0.70 for adults (Schifferli 1964, Noer and Secher 1983, Wallin et al. 1983, Dijkstra et al. 1990, Village 1990). All these estimates are based on relatively old datasets where kestrels were still subject to human persecution (Newton et al. 1999) and originated from different habitats. We believe that our survival estimates are representative for a population experiencing virtually no direct human persecution and living in good environmental conditions. Our estimate of adult survival is consistent with the allometric equation regarding survival in diurnal raptors (Newton et al. 2016). Given an average body mass of 225 g (Village 1990) the expected survival of adult kestrels is 0.719.

The transient LTRE suggests that the population dynamics was mainly affected by fecundity (34%) and marginally by adult survival (6%). This result contrasts with another study on kestrels showing that population dynamics was mostly driven by the variation in adult survival and not by the variation in fecundity (Robinson et al. 2014). However, this study differs with respect to the spatial scale and the overall population trend and thus we cannot expect to find the same demographic drivers of population dynamics (Newton 1998, Coulson et al. 2005). We found that the contribution of the net dispersal rate was also substantial (30%). However, the interpretation of this result is tricky because net dispersal rate was estimated without explicit data, i.e. estimated as the missing parameter in a balance equation

Table 2. Estimated sensitivities of realized population growth rate to changes in underlying vital rates and stage-specific proportions of abundance, corresponding elasticities (proportional sensitivities) and transient life table response experiment (LTRE) contributions to past variation in realized population growth rates for kestrels breeding in nest boxes in Switzerland (2002–2016). Given are posterior means and the 95% credible intervals (parentheses).

Parameter	Sensitivity	Elasticity	LTRE contribution
Juvenile survival	1.59 (1.51, 1.59)	0.72 (0.65, 0.79)	0.0019 (−0.0009, 0.0083)
Adult survival	1 (1, 1)	0.68 (0.65, 0.71)	0.0010 (−0.0008, 0.0041)
Fecundity	0.21 (0.19, 0.22)	0.72 (0.66, 0.77)	0.0049 (0.0024, 0.0077)
Net dispersal rate	1 (1, 1)	−0.39 (−0.32, −0.47)	0.0067 (−0.0004, 0.0205)
Juvenile population component	−0.31 (−0.34, −0.28)	−0.09 (−0.10, −0.09)	0.0024 (0.0001, 0.0058)
Adult population component	0.15 (0.13, 0.17)	0.09 (0.09, 0.10)	0.0012 (0.0000, 0.0028)

(Schaub and Fletcher 2015). Therefore, it also includes other demographic processes such as recruitment and adult breeding probability. Indeed, while we have included a mean value of these processes in the integrated population model, this is not true for their temporal variability. Thus, we can conclude that the temporal variability of different demographic processes (i.e. net dispersal, recruitment and adult breeding probability) have contributed strongly to the observed population dynamics. Further studies that collect more detailed data such that recruitment and adult breeding probability can be estimated separately would be necessary to shed more lights on the relative importance of these processes for population dynamics.

Could the nest box population have contributed to large-scale dynamics?

A source population produces surplus individuals that disperse to surrounding populations whose dynamics are thereby affected (Pulliam 1988). The surplus individuals may either recruit into the breeding pool of surrounding populations immediately, or they may become floaters that are ready to recruit should the number of established breeders decline. As long as the flow of surplus individuals continues, the extinction risk of the surrounding populations is null ('rescue' effect). Generally, emigrants are expected to have a positive effect on populations by buffering their dynamics (Hanski et al. 1997). Our results showed that the kestrels breeding in nest boxes operated as a source producing surplus individuals. About 40% of the ringed nestlings from the study population that were found dead during a later breeding period originated from outside the study area (Supplementary material Appendix 8 Fig. A5). This finding shows that locally born individuals emigrated to neighboring populations where they were likely to be recruited. Further, results show that our study population produced a large number of surplus individuals. For example in year 2015 about 1400 nest boxes were occupied by a kestrel pair. Using the estimated demographic parameters we can infer that about 5200 fledglings were produced totally, of which about 2540 were still alive after one year when they became mature. About half of them were recruited into the local population to maintain the local dynamics and consequently the remaining, about 1270 individuals, were surplus. This quantitative approach shows that the number of emigrants is substantial suggesting that the kestrel population breeding in nest boxes may support other populations outside the managed area.

Nest boxes as a conservation tool

Nest boxes are expected to be advantageous for bird populations for two reasons: first they can relax the constraint related to nesting sites availability (Newton 1994) and second, they can increase breeding performance compared to natural nesting sites which are often more vulnerable to predation, parasite infection and adverse weather events (Møller 1989, Bolton et al. 2004, Catry et al. 2009, Sutherland et al. 2014). The Swiss kestrel population has benefited from the nest boxes probably through both mechanisms (Jeanmonod and Broch 2001). The fecundity of a pair breeding in a nest box is on average 56% higher compared to a natural open nest (Fig. 4). Furthermore, nest-site availability could be locally limiting for kestrels in Switzerland (Schimd 1990), a situation which is fairly common for this species (Cavé 1968, Village 1990, Fargallo et al. 2001). Nest box deployment has been regularly applied as a conservation measure for populations limited by nest-site availability or quality. Such management has been used for seabirds (Libois et al. 2012), raptors (Catry et al. 2009), passerines (Brazill-Boast et al. 2013), ducks (Savard and Robert 2007), parrots (White et al. 2005), hoopoes (Arlettaz et al. 2010) and even mammals (Harley 2006). Following the installation of nest boxes, populations have usually rapidly increased (Bolton et al. 2004, Catry et al. 2009, Libois et al. 2012, Sutherland et al. 2014). Massive local recruitment and immigration are the main drivers of the rapid increase observed in the first couple of years (Bolton et al. 2004, Catry et al. 2009, Arlettaz et al. 2010, Sutherland et al. 2014), while the improvement of fecundity contributes more to the lasting population growth (Catry et al. 2009, Altwegg et al. 2014). Our study implies that nest boxes may not only impact local, but also large-scale population dynamics. We suggested that nest box deployment can create source populations providing emigrants for populations outside the managed area. Because the positive effect of such a management measure on reproduction is pervasive (Møller 1989, Bolton et al. 2004, Catry et al. 2009, Sutherland et al. 2014 but see Bragin et al. 2017), it could be fairly common that birds breeding in nest boxes operate as source population. However, a requirement is that other key resources for the population are not restricted.

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