



Massive immigration balances high anthropogenic mortality in a stable eagle owl population: Lessons for conservation

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ABSTRACT

The modern anthropized landscape is a major source of hazards for large animals such as raptors. Collisions with cables, vehicles and trains, as well as electrocution cause casualties, which may negatively impact populations. Yet, demographic studies of that impact remain scarce, which is an impediment to evidence-based conservation action. We studied the dynamics of an eagle owl (*Bubo bubo*) population in the northwestern Alps (Switzerland). We estimated, firstly, its demographic parameters using a Bayesian integrated population model; secondly, the frequency of different types of casualty through radio-tracking. Thirdly, we investigated the effects of reductions of human-related mortality on population trends. The breeding population was small but remained fairly stable during 20 years, suggesting that it was apparently in a good shape. However, survival probabilities of all age classes were very low (≤ 0.61), productivity fairly good (0.93), and immigration very high (1.6 females per pair and year), indicating that the population operated as a sink. Half of the mortality was caused by infrastructure, with electrocution accounting for 24% of all fatalities. The elimination of electrocution would result in a strong population increase (17% annually). Under that scenario, immigration rate could decline by 60% and the population would still remain stable. Given that the supply of recruits from elsewhere is likely to continue, we can expect a rapid local population recovery if dangerous electric pylons are mitigated systematically. Our study demonstrates that detailed demographic analyses are necessary to diagnose problems occurring in populations and to identify efficient conservation actions.

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1. Introduction

Small populations face a higher extinction risk than large populations (Lande, 1993). Even populations that remain stable during a long time may have a high risk of extinction. They may function as sinks, being able to maintain an apparent stable demography although this is only due to recurrent immigration. Thus, their continued existence depends on other populations. To diagnose such latent vulnerability of small, non-declining populations we need a specific analytical framework, essentially because targeted conservation options may substantially differ depending on the underlying demographic status and structure of a population. This calls for sophisticated analytical demographic tools such as integrated population modelling (Besbeas et al., 2002; Brooks et al., 2004; Schaub et al., 2007).

The modern landscape is characterized by dense infrastructure networks such as railways, motorways, electric power lines or wind turbines, to mention but a few. Infrastructure not only impacts landscapes, it also represents a source of danger for many animal species. Collisions with vehicles and aerial cables, and electrocution on dangerous pylons are major causes of casualties among animals (Schaub and Pradel, 2004). Such human-related mortality may actually have a considerable impact on populations, yet empirical studies remain scarce (Sergio et al., 2004). Understanding the relative impact of these sources of mortality on population dynamics requires unbiased estimates of the frequency of the mortality causes (Schaub, 2009), an assessment of whether the mortality cause considered is fully additive to the remaining mortality (Schaub and Lebreton, 2004), as well as the construction of a demographic model to evaluate whether a reduction in a focal mortality cause may improve the demography of the study population.

The eagle owl (*Bubo bubo*) is a nocturnal bird of prey that is widespread in Europe. In Western Europe, a marked decline took place until the 1980s, but several areas have been progressively

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re-colonised afterwards, which is due either to massive release programmes (e.g. Germany, Bergerhausen et al., 1981) or natural re-colonisation from core distribution areas (e.g. Rhône valley in France, Cochet, 2006). The Swiss population of eagle owls has also decreased strongly over the past decades, but there have been signs indicating slight recoveries in many areas recently. Yet, a major characteristic of the Swiss and other nearby eagle owl populations seems to be a highly intermittent occupancy of traditional breeding sites with frequent disappearance of territorial adults which are replaced only slowly (Sergio et al., 2004; Cochet, 2006; Ortego, 2007). This turn-over is unusual for a long-lived species and seems to coincide with local casualties: adult eagle owls are often victims of electrocution and traffic accidents in the close vicinity of breeding sites which are then temporarily abandoned (Sergio et al., 2004). Delgado and Penteriani (2005) have shown that an insufficient number of individuals in the floater segment of a population may destabilize species population dynamics and site occupancy, affecting overall reproductive performance. However, the impact on eagle owl demography of the mortality induced by the artificialization of the landscape through infrastructure networks remains unclear.

We investigated the population dynamics of a small eagle owl population inhabiting a large Alpine valley in southwestern Switzerland (Arlettaz, 1988). This population is demographically open although the valley is enclosed within very high mountain ranges (Aebischer et al., 2010). We first estimate demographic rates (age-specific survival, fecundity, immigration) from different types of data (radio-tracking, population surveys, number of fledglings, age-at-death ratio). We base our population diagnosis on a single coherent Bayesian integrated population model (Besbeas et al., 2002; Brooks et al., 2004; Schaub et al., 2007). This powerful framework allows determining whether a local population is a sink (population growth rate < 1 in the absence of immigration) or a source. Secondly, we estimate the relative importance of various mortality sources with respect to age classes using a sample of locally radio-tagged owls. Finally, we use our population model to investigate what-if scenarios to gauge the demographic response of the population if human-related mortality could be completely or partially removed. Our study provides the necessary strategic guidance for developing efficient and yet pragmatic conservation policies for eagle owl populations and other large raptors facing similar threats in the modern landscape.

2. Methods

2.1. Data collection

The study was conducted in the upper bottom of the Rhone valley in the southwestern Swiss Alps (Canton of Valais: 46.1–46.4°N; 6.8–8.9°E) from 1988 to 2008. The study area was 1–6 km wide and about 105 km long. It is flanked by high mountain ridges above 3000–4000 m altitude. The plain is characterized by intensive agriculture and dense human settlement. Numerous roads, railways, channelized rivers and powerlines cross the plain. Eagle owls mostly breed in cliffs adjacent to the valley bottom where they hunt preferably (Nyffeler, 2004).

We collected three different types of data from Valais eagle owls. Firstly, the study area was prospected annually to count the number of breeding pairs. This was done mostly by visiting formerly occupied breeding sites and potentially suitable sites during the courtship period, either at dusk or dawn, to locate singing adults (Arlettaz, 1988). Secondly, we counted annually the number of fledglings which were located through their characteristic begging calls and/or with the use of telescopes, binoculars, spotlights or night devices. Thirdly, we radio-equipped 41 young eagle owls

at nest of which 28 were tracked after they left their parents in 2002–2008 (Aebischer et al., 2010). Twenty-one of these young were equipped with 30 g, battery-powered satellite transmitters (lifespan: 6.5–8.5 months) and 20 young with 15 g VHF-tags (lifespan: 32 months) (for information about suppliers, see Aebischer et al., 2010). However, young equipped with satellite tags also wore a conventional VHF-tag. All VHF-tags were fitted with an activity sensor. The young stemmed from 23 different broods at 10 sites. We checked tagged birds at least once every fortnight within an area of about 11,000 km² covering Valais and some adjacent regions.

Another data set consisted of all eagle owls found dead throughout Switzerland from 1988 to 2008. A questionnaire was sent to most Swiss cantonal hunting and fishery services, bird rescue centres and museums of natural history. We inquired about the number of eagle owls found dead by any given institution, about date and location of finding. For 102 individuals (skins and stuffed birds) age-at-death could be determined based on plumage pattern, whilst cause of death could be assessed from 117 eagle owls. The sample was restricted to free-ranging, wild birds. Captive-reared eagle owls that were released in the course of reintroduction programmes, and were systematically ringed, were not considered as their mortality pattern may differ substantially from that of wild-born birds (Bezzel and Schöpf, 1986).

2.2. Estimation of demographic parameters

We used an integrated population model (Besbeas et al., 2002; Brooks et al., 2004; Schaub et al., 2007) to estimate survival, immigration, fecundity and population size from the above described different sources of demographic data (population surveys, number of fledglings, radio-tracked young, age-at-death data). A major advantage of an integrated population model is that all data sets are analysed within a single model simultaneously, which allows to estimate demographic parameters for which no explicit data are sampled (immigration in our case) and to get more precise parameter estimates (Abadi et al., 2010a). We fitted the integrated model in the Bayesian framework as it provides more flexibility than the frequentist framework (Brooks et al., 2004; Schaub et al., 2007) and exact measures of parameter uncertainty (Link and Barker, 2010). Next we describe the likelihoods of the demographic data and then show how they are integrated into a single model.

2.3. Likelihood for radio-tracking data

We considered the tracking data (T) obtained from the 28 tagged young after they had left their parents to estimate apparent survival during the first year of life (see Aebischer et al. (2010) for details on data sampling). Although all tagged individuals were checked at least once every second week, some could not be located at a given occasion although it was *a posteriori* clear that they were still alive in the study area. We had thus to use capture-recapture methods (Lebreton et al., 1992) to estimate survival corrected for detection. When the tag batteries failed before the owls reached 1 year of age, the corresponding birds were treated as censored at last encounter. That is, only the period of their life history between tagging and battery exhaustion was considered for the estimation of survival. Some tagged owls died before reaching 1 year of age and they might have been retrieved. We assumed that the probability to reencounter an individual alive in the survey area was higher when that individual had already been detected at the preceding occasion (trap-happiness effect). Based on these data, we constructed a multistate capture-recapture model with the three stages (“alive and encountered”, “alive but not encountered” and “dead”) to estimate apparent juvenile survival (ϕ_{juv} :

probability to survive and not emigrate permanently from the survey area from one occasion to the next, i.e. during 14 days), re-encounter rates (p_{ss} : probability to encounter an individual that is alive and in the study area at a given occasion and that was encountered already at the preceding occasion; p_{ns} : probability to encounter an individual that is alive and in the study area at an occasion but that was not encountered at the preceding occasion), and recovery rate (r : probability that an individual that has recently died is found). The likelihood of this submodel is multinomial conditional on the number of released individuals and we used a state-space parameterization to implement the model (Gimenez et al., 2007). We assumed constancy of all parameters across time. Based on the estimate of apparent juvenile survival that considers a 14 day period, we calculated annual apparent survival of juveniles as $S_{juv} = (\phi_{juv})^{26}$. The likelihood of the telemetry data is $L_T = (T|S_{juv}, p_{ns}, p_{ss}, r)$.

2.4. Likelihood of age-at-death data

Based on the progress of moult (Martinez et al., 2002), the 102 dead eagle owls inspected could be allocated to four age classes: 1 year old: 44 individuals; 2 years old: 26; 3 years old: 11; older than 3 years: 21. Using a multinomial likelihood, survival of birds from this age-at-death sample (D) can be estimated provided that the age distribution is stable, that the growth rate of the population (λ) is known and that the finding probabilities of dead owls is independent of age (Udevitz and Ballachey, 1998). Here we assumed that the age distribution was stable and that the finding probabilities were independent of age. Finding probabilities are likely to be age-dependent if the reasons for death differ between age classes (Schaub and Pradel, 2004). However, this was not the case in our data (see below). The population growth rate is a function of the parameters of the integrated population model, and its estimate can therefore be used for the age-at-death likelihood (see Fig. 1). Since the data are from Switzerland as a whole, survival probability

estimates are hardly affected by permanent emigration. This may be a drawback for our model of the Valais population since this is a geographically open population whose dynamics is greatly affected by immigration and emigration (Aebischer et al., 2010). However, dispersal over large distances is restricted to young individuals (natal dispersal) in eagle owls (Dalbeck et al., 1998; Aebischer et al., 2010) as in most birds (Greenwood and Harvey, 1982). We therefore considered the estimated survival of immatures (S_{imm}) and of adults (S_{ad}) from the age-at-death data, but discarded the estimated juvenile survival (S_{juv}^*) for the local population model. The likelihood of the age-at-death data is $L_D = (D, \lambda | S_{juv}^*, S_{imm}, S_{ad})$.

2.5. Likelihood for productivity data

We monitored the number of fledglings (J) from a total of 111 broods (B). We assumed that the number of fledglings follows a Poisson distribution where the mean productivity (f) is the Poisson parameter. The likelihood is thus $L_F = (J, B | f)$. Note that productivity includes males and females, but for the local population model, which is female based, we only consider the female fledglings. Since the sex of the fledglings was unknown, it requires the assumption of an even sex ratio.

2.6. Likelihood for population survey

Because the annual counts did not result from a constant effort during the course of time (1988–2008), we split the survey data in 3-year periods and considered the maximal number of annually occupied territories within these 3 years periods to be indicative of our breeding population size. To model the survey data (C) we used a state-space model. This model consists of two sets of equations, the first describes the true but unknown development of the population, and the second the observation conditioned on the true population size.

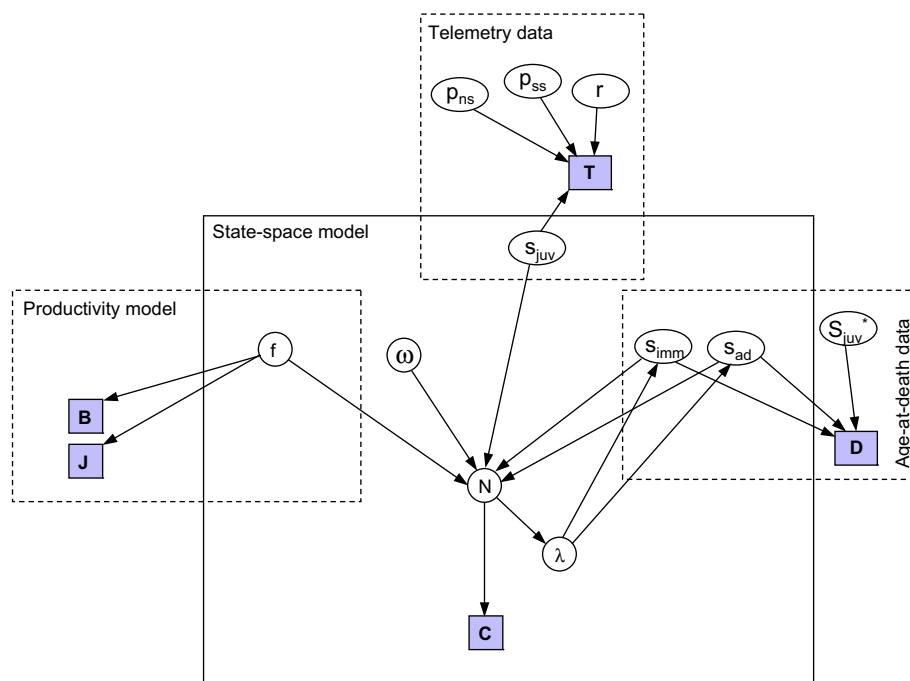


Fig. 1. Directed acyclic graph of the integrated population model used to estimate demographic parameters of eagle owls. Data are symbolized by grey rectangles, parameters by ellipses, the relationship between them by arrows and sub-models by open rectangles. Notation: T: telemetry data; D: age-at-death data; C: population survey; B: number of surveyed broods for assessing reproductive success; J: annual number of fledglings; S_{juv} : apparent juvenile survival; S_{imm} : immature survival; S_{ad} : adult survival; S_{juv}^* : juvenile survival; ω : immigration rate; f : productivity; N : population size; λ : population growth rate; p_{ns} : reencounter rate after preceding encounter failure; p_{ss} : reencounter rate after preceding encounter; r : probability to find a freshly dead individual. Note that the priors are excluded from this graph to increase visibility.

For the underlying population model we assumed that half of the eagle owls start to reproduce when 3 years old and all reproduce at age 4, which are typical ages of first reproduction in eagle owl populations from northern and alpine regions (Radler, 1991; Olsson, 1997). The annual number of fledged young (Y_t) follows a Poisson process:

$$Y_t \sim \text{Pois}\left(\left[\frac{1}{2}N_{3,t} + N_{4,t}\right] \frac{f}{2}\right), \quad (1)$$

where $N_{3,t}$ and $N_{4,t}$ are the number of individuals that are 3 years old and older than 3 years in year t , respectively. The number of 1-year old local recruits (R_{t+1}) given Y_t follows a binomial process:

$$R_{t+1} \sim \text{Bin}(Y_t, S_{juv}). \quad (2)$$

The number of immigrants (I_{t+1}) follows again a Poisson process with:

$$I_{t+1} \sim \text{Pois}\left(\left[\frac{1}{2}N_{3,t} + N_{4,t}\right] \omega\right), \quad (3)$$

where ω is the immigration rate (defined as the number of 1-year old immigrated females per breeding pair in the previous year). Finally, the number of 1-year old individuals in year $t+1$ ($N_{1,t+1}$) is the sum of locally recruited individuals plus immigrants:

$$N_{1,t+1} = R_{t+1} + I_{t+1}. \quad (4)$$

The numbers of 2–3 years old and older individuals are modelled with binomial distributions as:

$$\begin{aligned} N_{2,t+1} &\sim \text{Bin}(N_{1,t}, S_{imm}) \\ N_{3,t+1} &\sim \text{Bin}(N_{2,t}, S_{ad}) \\ N_{4+,t+1} &\sim \text{Bin}(N_{3,t} + N_{4+,t}, S_{ad}). \end{aligned} \quad (5)$$

We assumed a Poisson distribution for the observation equation (Abadi et al., 2010b), because the normal approximation for the observation error does not work well when the population size is small. Thus the number of counted breeding pairs (C_t) in year t is:

$$C_t \sim \text{Pois}\left(\frac{1}{2}N_{3,t} + N_{4+,t}\right). \quad (6)$$

The likelihood of the population survey data is $L_C = (C|f, S_{juv}, S_{imm}, S_{ad}, \omega, N, \lambda)$ and that of the complete integrated model is the product of the likelihood of its different parts ($L = L_T \times L_D \times L_F \times L_C$). The model requires the assumption that the different likelihoods are independent. Because the population is small some individuals are likely to occur in different data sets, violating this assumption. However, a simulation study based on census, capture-recapture and fecundity data has shown that the violation of this assumption does not have a severe impact on the estimated parameters (Abadi et al., 2010a). We assumed the same for our model although the structure of Abadi's and our data sets slightly differs.

We used the Bayesian approach to estimate the parameters. That is, we based inference on the posterior distribution, which is proportional to the likelihood and the prior distribution, and sampled the posterior using Markov Chain Monte Carlo (MCMC). For all demographic parameters we used uninformative priors, i.e. $U(0,1)$ for all probabilities, $N(0,100)$ truncated to values smaller than 2 for the logarithm of productivity and $U(0,10)$ for immigration rate (see Supporting information Appendix A). For the initial population sizes we used weakly informative priors. We have chosen normal distributions truncated to positive values with wide variance and mean values reflecting the population size and a stable age distribution. We used WinBUGS (Lunn et al., 2000) called from R (R Development Core Team, 2004) to fit our integrated model (code available in Supporting information Appendix A). We ran 1000,000 iterations of which we discarded the first

500,000 iterations to eliminate effects of initial conditions, and retained every 20th MCMC sample. We ran two chains and checked the convergence using the Brooks-Gelman-Rubin criterion (Brooks and Gelman, 1998), which indicated convergence ($\hat{R} < 1.005$ for all parameters of interest).

2.7. Assessing mortality causes from radio-tracking data

All tagged owls were radio-tracked until battery exhaustion, death or emigration from the survey area. Mortality cause was assessed for 21 individuals found dead, if necessary through in-depth necropsy by veterinarians (Institute of Pathology, University of Bern). Our sample of radio-tracked eagle owls allows a proper assessment of the actual frequency of different mortality causes because the probability of retrieving a carcass does not depend on the type of mortality. This unbiased sample was then compared with the frequency of mortality causes of the 117 dead eagle owls found dead across Switzerland to evaluate whether the frequency of mortality causes obtained from casual findings is biased.

2.8. Modelling the effect of mortality reduction

We were interested to see how the Valais eagle owl population would react to reduction or elimination of all anthropogenic mortality by mitigation measures. We thus simulated the demography of a population where anthropogenic mortality is removed, all other things being equal. We had to assume that human-induced mortality was additive to any other mortality, since testing for additive or compensatory mortality requires much better data than available here (Burnham and Anderson, 1984; Schaub and Pradel, 2004; Schaub and Lebreton, 2004). Yet, compensation is usually weak in long-lived species (Lebreton, 2005) such as the eagle owl (Radler, 1991; Olsson, 1997), thus justifying our approach.

We used a deterministic Leslie matrix population model (as defined in Eqs. (1)–(5), but using expected values) to assess the effect of a potential reduction of mortality on population growth. We were particularly interested in knowing whether our population may function as a source after mitigating anthropogenic mortality. This question arises from the observation that the Valais population is part of a system of spatially structured populations with numerous exchanges of individuals across the Western European Alps (Aebischer et al., 2010).

The proportion of human-related mortality causes among all mortality causes is α (see below for estimation of α), the overall survival rate of age class z is S_z , and then the survival rate of age class z in the absence of any human-related mortality is:

$$S_{alt,z} = 1 - (1 - \alpha)(1 - S_z). \quad (7)$$

Since there is no closed form solution to the population model that we used, we applied a trial and error method to assess the impact of declining mortality on immigration for different levels of population growth. For different levels of reduction of mortality and different immigration rates (from 0 to 1.5 with steps of 0.05), we identified the immigration rate with which population growth rate was closest to a specified value. In order to incorporate the uncertainty due to parameter estimation, we used 1000 samples from their posterior distribution.

This simulation uses a constant immigration rate, rather than a constant number of immigrants. As long as the population is not self-sustainable without immigrants, the latter would have resulted in population growth rates of 1 in the long run, but at different equilibrium population sizes depending on the scenarios considered. The qualitative conclusions about the effect of the different scenarios on eagle owl population would, however, remain the same.

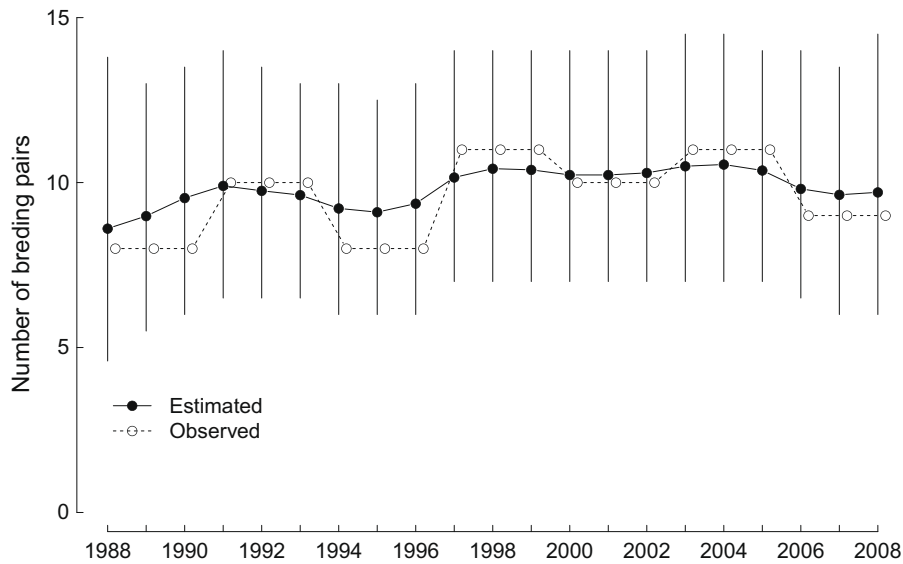


Fig. 2. Estimated (posterior mean and 95% credible intervals) and observed population sizes of the eagle owl population in Valais, southwestern Swiss Alps.

We performed two further calculations in order to evaluate how much reproduction or survival had to increase to obtain a population growth rate of 1 with neither immigration nor emigration occurring. This is of interest since the main conservation goal is to obtain a self-sustainable population. Following Aebischer et al. (2010) we assumed that the emigration rate of the surviving young is about 0.5, i.e. only half of the young remained in the study area. To simulate a scenario of no emigration, we doubled the estimated apparent juvenile survival probability. We used again the Leslie matrix projection model and the trial and error method as described above to compute the values of the unknown parameters.

3. Results

The Valais eagle owl population stayed fairly stable over the 20 years of the study (Fig. 2, Table 1), with an average population size of about 10 breeding pairs. The mean demographic rates are presented in Table 1 (for the posterior distributions see Supporting information Appendix B). Demography of eagle owls was characterized by low annual survival rates in all age classes (≤ 0.61) and high immigration (1.6 females per breeding pair and year). Apart from immigration, all demographic rates are estimated quite precisely, despite the relatively small sample size.

Based on the radio-tracking data, we could infer the mortality causes of 21 individuals that did not emigrate from the study area (Fig. 3). Ten dead retrieved owls (48%) were extremely lean and

had starved to death according to necropsy. The second cause of death was electrocution with five cases (24%), which represented 50% of anthropogenic mortality. Collisions with car or train ($n = 3$, 30% of anthropogenic mortality) were the third cause of mortality, whereas collisions with aerial cables came in the fourth and last position ($n = 2$, 20% of anthropogenic mortality). One individual did not find the exit from a church tower anymore where it was hunting pigeons.

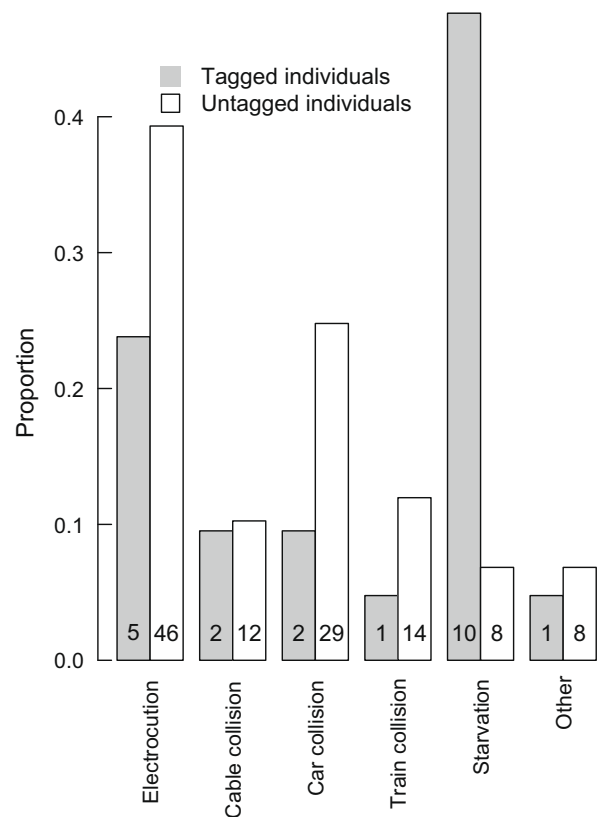


Fig. 3. Proportion of mortality causes of 21 tagged and 117 untagged (incidentally found) eagle owls. Starvation refers to natural mortality, with all other mortality causes being anthropogenic. The figures at bar foot indicate sample size.

Table 1

Posterior mean, 95% credible intervals and standard deviations of the annual demographic parameters of eagle owls from Valais estimated with the integrated population model.

Parameter	Mean	Credible interval	Standard deviation
Apparent juvenile survival (S_{juv})	0.086	0.023–0.197	0.046
Immature survival (S_{imm})	0.538	0.414–0.658	0.063
Adult survival (S_{ad})	0.606	0.462–0.742	0.072
Productivity (f)	0.932	0.755–1.127	0.095
Immigration rate (ω)	1.591	0.541–3.196	0.664
Population growth rate (λ)	1.006	0.984–1.029	0.012
Resighting probability (p_{ss})	0.859	0.801–0.909	0.028
Resighting probability (p_{ns})	0.389	0.264–0.523	0.066
Recovery probability (r)	0.523	0.323–0.718	0.102

In contrast, the frequency of mortality causes derived from 117 untagged, free-ranging wild individuals showed a very small proportion of starved individuals ($n = 8$, 7%) and a large proportion ($n = 109$, 93%) of individuals dying from anthropogenic causes (Fig. 3). Among anthropogenic factors, electrocution was the first cause of mortality (46%), followed by collision with vehicle (43%, with 29% for car and 14% for train) and collision against cable (12%) (Fig. 3). The frequency of mortality causes of this sample did not differ significantly between young (up to 1 year of age) and adult individuals ($\chi^2_4 = 4.7$, $P = 0.3$). Because it is unlikely that mortality-specific finding probabilities varied with respect to age, we can infer that mortality causes do not change with age and thus used a common proportion of human-related mortality (α) for all age classes in the simulations.

Assuming an additive anthropogenic mortality, we modelled the population growth rate under different levels of immigration rate (Fig. 4). If the immigration rate would stay at its current high level and if the entire anthropogenic mortality could be completely eliminated, the population would increase annually by 31.4%. Growth rate would still be 16.7% if only electrocution could be eliminated totally. Conversely, if the entire anthropogenic mortality or just electrocution could be eliminated, immigration rate could decrease to 0.14 or 0.63, respectively, and the population

would still remain stable. These figures are, respectively, 11.8 and 2.5 times lower than current values. However, due to the uncertainty of the parameter involved in this exercise, the confidence intervals are wide (Fig. 4).

The population growth rate under the current conditions but not accounting for immigration and emigration equals only 0.66, clearly indicating that the population functions as a sink. The yearly average reproductive output per breeding pair would need to increase to a biologically impossible 17.4 fledglings to achieve a population growth rate of 1 under the current survival probabilities in the absence of immigration and emigration. Likewise, the mortality would need to decline by 55% under the current reproductive success, again in the absence of immigration and emigration, to obtain a stable population. Compared to all current survival probabilities ≤ 0.61 , this would correspondingly require dramatic increases in juvenile (0.63), immature (0.79) and adult survival (0.82).

4. Discussion

Integrated population modelling allowed us a detailed analysis of the demography and diagnosis of the source-sink dynamics of a small and fragile eagle owl population in the Alps. Although the population remained stable over the past 20 years, it has functioned as an extreme sink with a massive immigration necessary to balance the high mortality in all age classes. Actually, the turn-over in the population was very high, with regular disappearances of territorial adults and a slow replacement rate of dead mates (on average 30 weeks, $n = 12$; R. Arlettaz and N. Jordan, unpublished observations). Half of the eagle owls in Valais were victims of infrastructure networks such as dangerous electric pylons, cars, trains and aerial cables. Mitigating these sources of anthropogenic mortality would result in a rapid population increase. However, the Valais population, which also sends numerous individuals to nearby populations (Aebischer et al., 2010), would still remain dependent on immigration to achieve demographic stability.

The demography of eagle owl populations is generally very poorly known. Some estimates of survival probabilities exist (Glutz von Blotzheim and Bauer, 1980; Radler, 1991), but mostly were obtained using unreliable methods that do not consider imperfect detection. The single exception is Olsson (1997) who estimated survival from Swedish ring-recoveries. Annual survival probability in the first year was 0.66 ± 0.03 (SE), in the second year 0.79 ± 0.03 and in the following years 0.89 ± 0.02 . These estimates are much higher than those we obtained from the Valais population (0.18 [assuming that emigration probability is 0.5], 0.54 and 0.61, respectively), and better match expectations about survival of such a large-sized bird. The comparison between the Swiss and the Swedish populations suggests that the high mortality in Valais is unusual and results from an adverse, heavily humanized environment.

It seems clear that survival but not productivity is a problem for the Valais eagle owl population: as shown by our simple simulation, productivity would need to increase to biologically impossible values (17.4 young per pair and year!) for compensating the current mortality. Actually, an eagle owl pair can produce up to four, exceptionally five young a year (Glutz von Blotzheim and Bauer, 1980). Compared to other Alpine populations (except maybe at high altitude, less anthropized areas such as Grisons; Supporting information Appendix C), productivity in the Valais is relatively high (0.93), which further supports the view that the main demographic problem of the Valais eagle owls is the low survival of all age classes. Hence, even a substantial increase in productivity would not suffice to achieve demographic stability in the absence of immigration.

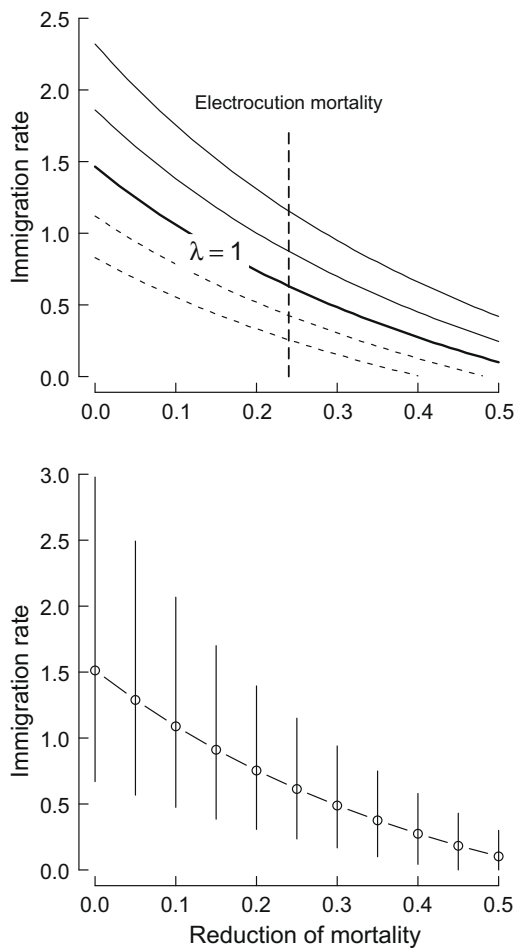


Fig. 4. Relationship between proportional reduction of mortality, immigration rate and population growth rate. Upper panel: the two solid lines represent positive population growth (upper: $\lambda = 1.10$, lower: $\lambda = 1.05$), two broken lines negative population growth (upper: $\lambda = 0.95$, lower: $\lambda = 0.90$), and the bold line population stability ($\lambda = 1$). Lower panel: 95% credible intervals of the population growth when it equals 1.

Immigration into the Valais population is massive. With a population estimated at around 10 breeding pairs, an immigration rate of 1.6 means that each year 16 1-year old females immigrate. These same 10 breeding pairs will produce on average about 10 fledglings a year, i.e. five females. Due to the low apparent juvenile survival, only about 10% will still be present in Valais at 1 year of age, i.e. 0.5 female. These figures illustrate that the Valais population is almost completely dependent on immigrants, with local recruitment being almost negligible despite a good reproductive success.

Yet, the Valais population also exports a few individuals to other nearby populations. According to Aebischer et al. (2010), about 50% of the individuals that survived the first year emigrated, settling down at distances of up to 100 km in adjacent regions of France and Italy. Even in the unlikely situation where natal dispersal would stop, a strong dependence on immigrants would remain. Valais eagle owls thus represent an extreme example of a sink population (Pulliam, 1988): any slight decrease in immigration would cause a population decline.

Half of the mortality was due to natural causes (starvation) and half was due to infrastructure. One of the originalities of this study is to provide assessments of the actual frequencies of different sources of mortality, which contrasts with previous studies which were based exclusively on casual findings (Rubolini et al., 2001; Marchesi et al., 2002; Sergio et al., 2004). Not surprisingly, the relative importance of anthropogenic mortality was lower in our radio-tracked birds than in other studies using indirect evidence. This is because birds dying from natural causes such as starvation are much less likely to be retrieved than birds dying close to transport and electricity networks where most human activities concentrate. Our small, but unbiased sample establishes that starvation may greatly affect the demography of eagle owl populations. In our case, there may be a direct link between risk of starvation and degraded habitats typical of highly artificialized landscapes offering poor prey supplies.

Power lines have been reported to be the most important anthropogenic mortality factor for Alpine eagle owls (Rubolini et al., 2001; Marchesi et al., 2002; Sergio et al., 2004). Valais eagle owls appear to pay a heavy toll to them, with 33% of total mortality. Interestingly, this proportion is nearly identical to that of Swiss white storks (*Ciconia ciconia*, Schaub and Pradel, 2004), another large bird species inhabiting anthropized Swiss lowlands. However, contrary to Schaub and Pradel (2004), our current study distinguishes between fatalities due to collision with electric cables (20% of anthropogenic mortality) and electrocution on dangerous pylons (50%). This distinction is essential when it comes to recommend sound conservation strategies. Aerial cables constitute a tangle of linear obstacles all over the place in Alpine regions, while dangerous pylons represent single isolated pixels on a map. Within a radius of 4 km around a Valais eagle owl breeding site we measured that 61.5 km of only medium-tension powerlines face with 135 dangerous pylons (E. Revaz and R. Arlettaz, unpublished). Mitigating dangerous pylons would hence not only be the first conservation priority, but it would certainly be the best cost-effective action to take. Measures to mitigate dangerous pylons are nowadays well established (Haas and Schürenberg, 2008). Our simulations show that by the complete elimination of electrocution (24% reduction of total mortality) the local population would grow annually by 17%.

There is increasing empirical evidence that many local populations need immigrants, basically because a significant part of the locally produced young disperse (Baillie et al., 2000; Murphy, 2001; Schaub et al., 2006). A system of such spatially structured populations is referred to as an open recruitment system (Franklin et al., 2004). As this system seems to be frequent, we cannot expect the Valais eagle owl population to become independent from immigrants, even if local food supplies existed *ad libitum*. Aebi-

sch et al. (2010) have recently shown that young eagle owls disperse on a wide range. The crucial question remains yet, which immigration rate would be necessary under natural circumstances, i.e. in the absence of infrastructure obstacles and in presence of excellent food supplies? The estimated immigration rate of 0.63 in the absence of electrocution hazards still seems a bit high. Similarly, removing electrocution still results in survival lower than in the Swedish population, possibly pointing towards additional problems. The fact that starvation was the most important natural mortality cause suggests that food resources may not be sufficient locally.

This study shows that detailed demographic analyses are necessary to diagnose problems occurring in a population. Had we relied entirely on the population survey, which is typical in most monitoring programs, we would have concluded that the population is stable, and hence apparently in a good shape. To get detailed information about demography, integrated population models are very powerful and particularly suited when available information is limited (Schaub et al., 2007). The ease with which different sources of information can be combined into a common model is very compelling. Here, we used for the first time age-at-death data in an integrated population model. Age-at-death data are often considered as not particularly useful to estimate survival, because the analysis requires relatively strong assumptions (Conn et al., 2005). Yet, using the integrated model, we could relax one of those, namely that the population size must remain constant over time. This was possible because the actual population growth rate is estimated using survey data and was therefore known for the age-at-death analysis. Other assumptions like stable age distribution or age-independent finding probabilities still remain, but are likely to have no serious impact in our case. The population did not fluctuate much over time, which is indicative of a fairly stable age distribution. Further, the mortality factors did not vary between age classes, as probably also recovery rates. Another big advantage of the integrated model is the possibility to estimate immigration, a parameter that is notoriously difficult to evaluate. However, the precision of the immigration rate remains relatively weak, which seems to be typical when immigration into populations of small size is estimated with integrated population models (Abadi et al., 2010b).

Following the above reasoning, two pragmatic options can be envisioned for restoring the Valais eagle owl population. First, dangerous pylons need to be mitigated to annihilate any risks of electrocution. This would also benefit other large-sized birds which face similar risks (Schaub and Pradel, 2004). If productivity and immigration stayed at their current level, this should result in a rapid population increase. Second, source populations should be identified and protected in order to guarantee the persistence of a functional system of spatially structured populations across the Alps. Locally implemented policies to mitigate the electrocution hazards must thus be accompanied by trans-national conservation strategies as described by Aebischer et al. (2010). It is likely that other eagle owl populations inhabiting anthropized landscapes suffer from the same symptoms as our Valais population. These recommendations therefore should apply beyond the local context, if not to other large-sized birds trying to survive in heavily humanized areas.

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Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.04.047.

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