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Michael Schaub[1,2], Olivier Gimenez[3], Antoine Sierro[2,4], & Raphaël Arlettaz[1,2,4]

1. Zoological Institute – Conservation Biology, University of Bern, Baltzerstrasse 6, CH–3012 Bern, Switzerland

2. Swiss Ornithological Institute, CH–6204 Sempach, Switzerland

3. Centre for Research into Ecological and Environmental Modelling, University of St Andrews, St Andrews, The Observatory, Buchanan Gardens, KY16 9LZ, Scotland

4. Valais Bat Conservation Group, Nature Centre, CH–3970 Salgesch, Switzerland

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Correspondence author: Michael Schaub

Zoological Institute – Conservation Biology University of Bern

Baltzerstrasse 6

CH–3012 Bern

Switzerland

Fax: +41 31 631 31 63 E-mail: michael.schaub@nat.unibe.ch

Abstract

Demographic data of rare and endangered species are often too sparse to estimate vital rates with sufficient precision for understanding population growth and decline. Yet, the combination of different sources of demographic data into one statistical model holds promise. We applied Bayesian integrated population modeling to demographic data from a colony of the endangered greater horseshoe bats (*Rhinolophus ferrumequinum*). Available data were the number of subadults and adults emerging from the colony roost at dusk, the number newborns from 1991 to 2005, as well as recapture data of subadults and adults from 2004 and 2005. Survival rates did not differ between sexes and demographic rates remained constant across time. The greater horseshoe bat is a long-lived species with high survival rates (first year: 0.49 [SD: 0.06], adults: 0.91 [SD: 0.02]) and low fecundity (0.74 [SD: 0.12]). The yearly average population growth was 4.4%. Had we analyzed each data set separately, we would not have been able to estimate fecundity, the estimates of survival would have been less precise and the estimate of population growth biased. Our results demonstrate that integrated models are suitable for obtaining crucial demographic information from limited data.

Key words: Bats, demography, monitoring, *Rhinolophus ferrumequinum*, species conservation, state-space model, integrated population modeling.

Introduction

In the face of the rapid global biodiversity loss, the declining population paradigm has become central in conservation biology (Caughley 1994). It aims to identify the reasons for the decline of a specific population. There are several possible approaches to identify causes of population declines, the most popular being demographic analysis (Norris 2004). Central to demographic analysis is the estimation of demographic parameters (survival, reproduction, immigration, emigration) and the exploration of the relationship between variation of these parameters and population growth rate. This approach requires that the strength of impact of a particular demographic parameter on the population growth rate be assessed with a sensitivity analysis (van Groenendael et al. 1988). The final step is to identify environmental- and density-related factors that affect those demographic parameters that are most relevant to variation of population growth rate.

Although a demographic analysis is a powerful tool, it is difficult to apply for many species because the necessary, detailed demographic data are often not available and because inferences based on demographic analyses with insufficient data can be flawed (Doak et al. 2005). Even worse, data are frequently insufficient for declining or rare species (Beissinger 2002). Data of endangered species can be scarce because species' sample size is naturally low and researchers hesitate to catch and mark individuals, a prerequisite to obtain most demographic data. Typically, population size is usually well documented, whereas few longitudinal data on individuals (demographic data) are available. In such a situation, it is crucial to make most efficient use of all available data.

Recently developed integrated population models (Besbeas et al. 2002; Buckland et al. 2004; Brooks et al. 2004; Besbeas et al. 2005) are likely to prove useful for detailed demographic analyses. Once again, Buckland et al. 2004 do not deal with integrated population modeling. . This ref. should be deleted. These models combine population counts and

demographic data in a single model, which thus allows the estimation of demographic parameters and the prediction of population trajectories. Because the population counts also contain information about all demographic parameters of the population under study, the estimates of the demographic parameters become considerably more precise and otherwise inestimable demographic parameters can become estimable (Besbeas et al. 2002). Thus, one might hope that such models could be used to estimate vital parameters even if few demographic data were available. So far, these models have been applied mainly by statisticians to species without deficiency of demographic data. We applied this modeling approach to a small data set on a rare species and evaluated its usefulness for demographic analysis.

We will use data from a bat as a case study. Bats are declining globally (Mickleburgh et al. 2002), but few detailed demographic analyses have been performed so far. Even single demographic parameters have been poorly studied, as exemplified by the few estimates of survival rates obtained with reliable statistical methods (Boyd & Stebbings 1989; Gerell & Lundberg 1990; Hoyle et al. 2001; Sendor & Simon 2003; O'Shea et al. 2004; Pryde et al. 2005). Population dynamics of bats is difficult to study for three reasons. First, the most popular methods to assess whether a bat population is changing is counting individuals at nursery colonies (Warren & Witter 2002). Such colonies mostly consist of reproducing females, with some nonreproducing subadult females and males (Ransome 1990; Neuweiler 2000). Because sexing and ageing of bats is impossible unless they are captured, the fraction of reproducing females remains unknown. If this fraction changes over time, annual counts at nursery colonies will not reflect population changes accurately. Second, estimation of fecundity (number of offspring a mature female is producing in a year) is difficult. In many bat species females give birth to a single offspring per year, but little is known about regularity of breeding from year to year in individual females (Racey 1982). Because females that skip a breeding event are usually not at the nursery colonies (R. Arlettaz, unpublished data on mouse-eared bats), the ratio of the

number of newborn to the number of mature females present at the colony appears to be an unreliable estimate of fecundity. Third, catching and marking bats is not considered ethical anymore because catching may disturb them and rings may affect foraging performance (Norman et al. 1999) or cause injury (Baker et al. 2001). Therefore, good individual longitudinal data are not available for many bat species, which precludes the estimation of survival probabilities. Because basic demographic information is lacking for many bat species, it is difficult to devise conservation actions for them.

We sought to demonstrate the flexibility and power of integrated population models to estimate demographic parameters from sparse data, with a relictual colony of greater horseshoe bats (*Rhinolophus ferrumequinum*). We tested whether demographic parameters changed over time and estimated the rate of change of the study population. This allowed us to identify roughly whether a gradual change of a demographic parameter resulted in a population change and to evaluate the current state of the population. Finally, we compared the rate of population change obtained from the counts alone with the estimate from the population model and considered the general benefits of an integrated population model and how it could be used in demographic monitoring.

Data and methods

Study species

The greater horseshoe bat is one of the most threatened bat species of Central and Western Europe (Stebbings 1988). In Switzerland it is listed as endangered (Duelli 1994), and there are only two known nursery colonies, one in eastern Switzerland (Grisons) and one in southwestern Switzerland (Valais). Results of studies of populations at the northern margin of the species distribution range in Great Britain show that females start reproducing at 2 or 3 years, that survival rate during the first year of life is 53%, that survival of adult females is in the range of

67-91%, and that the breeding probability (probability of an adult female reproducing in a given year) is about 0.9 (Ransome 1990, 1995). Moreover, population dynamics are driven mainly by the variation of offspring production (Ransome 1989), which itself is related to weather conditions in spring (Ransome & McOwat 1994). Yet, the results of these studies rely on the untested assumption that the fate of each bat is known with certainty.

Data collection

We studied a greater horseshoe bat colony in the attics of a twelfth-century chapel in Vex, Valais, Switzerland (46°13'N, 7°24'E). This colony was isolated from the other known Swiss population and from the Italian and French populations by high mountain ridges (Arlettaz et al. 1997). This population was discovered in 1986, just prior to the renovation of the building (1987-1988), which was planned in compliance with the requirements for the colony's preservation (Arlettaz et al. 1997).

With the exception of 2 years, we counted from 1987 onwards in every year the number of individuals emerging from the roost at dusk, prior to the onset of parturition. Since 1991, during the first weeks after parturition, we visited the attics after the emergence of subadult and adult bats – when young were left unattended – and counted and ringed most newborns (260 out of 285 newborns ringed in total). This way, adults were never disturbed at the colony roost. In 2004 and 2005, shortly before parturition, which corresponded to the period when the census was carried out and when the population peaked (R. Arlettaz and A. Sierro, unpublished data), we blocked the main entrance and captured, in 1 day at daylight, the entire population. Ring number and sex of the bats ($n_{2004} = 54$, $n_{2005} = 52$) were recorded. This massive capture did not affect the number of bats that returned to the roost on the following days nor reproduction. Indeed, 2004 and 2005 yielded an unequalled number of offspring. Because we only began

ringing newborn bats in 1991 only, we considered for our analysis the period from 1991 to 2005, although in the year 1991 no population count was carried out.

Integrated population model

We used an integrated population model, which integrated different kinds of data into a common model, to study the population dynamics of the greater horseshoe bat (Besbeas et al. 2002). We describe the development of the population size with two linked processes, namely the state and the observation process. The state process describes the true, but unknown, size of the population at different times, and the observation process links the size of the population to the observed part of the population during the surveys. The state process is described by different demographic parameters (survival, fecundity), which were estimated each with separate probabilistic models. To allow for maximal flexibility regarding the model assumptions, we used Markov chain Monte Carlo (MCMC) methods within a Bayesian framework to fit the model (Brooks et al. 2004; Maunder 2004).

Because most greater horseshoe bats do not start to reproduce in their first year of life (Ransome 1990; R.A. unpublished data: only 2 out of 14 females were pregnant in their first year of life), we considered for each sex two age classes in our model: individuals aged 1 year (subadults) and individuals older than 1 year (adults). To describe the model, we start with the likelihoods for the different demographic parameters and the population sizes and then we show how they were linked and how they were estimated in the integrated population model.

Likelihood for estimation of local survival rates

To estimate local survival probabilities ($\phi_{x,t}^{k}$, probability to survive and not to emigrate permanently from the population between year t and year t+1 of individuals of sex k and age class x) from individual capture-recapture data, we used the Cormack-Jolly-Seber (CJS) model

(Lebreton et al. 1992). The frequency of individual encounter histories followed a multinomial distribution with cells that were functions of the two parameters local survival ($\phi_{x,t}^{k}$) and recapture ($p_{x,t}^{k}$) probabilities (notation as above). The formulation of the likelihood of this model was straightforward and is described in many papers (e.g., Lebreton et al. 1992). Because we only had recaptures from the last 2 years, we set the recapture probabilities for all but the last 2 years equal to zero.

Likelihood for estimation of fecundity

We derived fecundity from the yearly counts of the newborn. The fecundity rate (f_t) was defined as the number of offspring produced per mature female in year *t*. We assumed that the number of newborns at time *t* (J_t) followed a Poisson distribution and depended on the number of adult females ($N_{a,t}^{f}$) and the fecundity rate (f_t), thus $J_t \sim \text{Po}(N_{a,t}^{f} f_t)$.

Likelihood of the estimation of population sizes

Our population count of horseshoe bats emerging from the nursery colony at dusk consisted of subadults and adults from both sexes. We knew that all reproducing females and a varying fraction of males and subadult, nonreproducing females are present at nursery colonies (Gaisler 1966). However, flying bats cannot be aged or sexed. To include these counts in a state-space model, we needed to know the proportion of the four sex and age classes. We estimated these parameters as follows. First, we noted that the recapture probability estimated with the CJS model was composed of two parts, the probability that a bat would be recaptured given presence in the colony and the probability it would be present in the colony. This partition is strictly true if the probability of being present is random (Burnham 1993; Schaub et al. 2004). Because we captured all bats that were in the colony at time of capture, the true recapture probability was 1.

Assuming that the probability of being present at the colony was random, the estimated recapture rate (from the CJS model) was equal to the probability to be in the colony. Because we only had such estimates for each sex and age class from the last 2 years, we calculated the geometric mean of the 2 values and considered these mean values the same over the duration of the study. Specifically, the probability that an individual of age *x* and sex *k* was present in the colony was calculated as $\tau_x^k = \sqrt{p_{x,2004}^k p_{x,2005}^k}$. The population count in year *t* (y_t) was then related to the actual population sizes with a normal distribution as

$$y_t \sim N(\tau_1^f N_{1,t}^f + \tau_a^f N_{a,t}^f + \tau_1^m N_{1,t}^m + \tau_a^m N_{a,t}^m, \sigma_y^2),$$

where $N_{x,t}^k$ is the number of individuals of sex *k* in age class *x* in year *t* and the variance σ_y^2 quantifies the counting error. Superscripts *m* and *f* denote male and female, respectively, subscript 1 denotes the subadult age class and subscript *a* the adult age class.

Linking demography and population size

The next step was to link the demographic parameters with the number of individuals in each sex and age class. We used a Leslie matrix that described the transition probabilities between sex and age classes from one year to the next and that was parameterized with the survival rates and fecundity. We assumed that annual survival rate during the first year of life was different from annual survival later on and that the latter did not change further with age. Furthermore, we assumed that all females began to reproduce when they were 2 years old and that the sex ratio of the newborn was even. The latter assumption was supported by the sex ratio of the newborn with known sex (52.5% females, $n = 260$). To account for demographic stochasticity, we described the change of each population segment with Poisson and binomial distributions. Specifically, we modeled the number of subadults in year t+1 according to a Poisson distribution:

$$N_{1,t+1}^f \sim \text{Po}\left(N_{a,t}^f \frac{1}{2} f_t \phi_{1,t}^f\right) \text{ for females and}$$

$$N_{1,t+1}^{m} \sim \text{Po}\left(N_{a,t}^{f} \frac{1}{2} f_t \phi_{1,t}^{m} \right) \text{ for males.}$$

The number of adults in year t+1 was distributed as binomial:

$$N_{a,t+1}^{f} \sim \text{Bin}\left(N_{a,t}^{f} + N_{1,t}^{f}, \phi_{a,t}^{f}\right) \text{ for females and}$$

$$N_{a,t+1}^{m} \sim \text{Bin}\left(N_{a,t}^{m} + N_{1,t}^{m}, \phi_{a,t}^{m}\right) \text{ for males.}$$

The integrated model

The joint likelihood of the integrated model was the product of the likelihoods of each part. The different likelihoods (survival, fecundity, and population size) had parameters in common, as illustrated graphically by the directed acyclic graph (Fig. 1).

The frequentist approach to estimate the unknown parameters would require maximizing the joint likelihood, which involves a high dimensional integral corresponding to the state-space model (Buckland et al. 2004) that could be handled by using Kalman filtering (Besbeas et al. 2002, 2003). This approach requires strong assumptions such as linearity and normality in the state process equations (Besbeas et al. 2002, 2003). The Bayesian approach combines the joint likelihood with prior probability distributions of the parameters to obtain the posterior distribution of the parameters of interest based on Bayes' theorem. We used Markov chain Monte Carlo (MCMC) methods to simulate observations from the posterior distributions. This allowed us to cope with complex integrals that are involved in this likelihood when the linear and/or normal assumptions have to be relaxed (Brooks et al. 2004). This part reads much better than before! The MCMC sampling scheme simulates values for the unknown quantities of interest following a Markov chain in which the stationary distribution is the needed posterior distribution (e.g., Brooks 1998). A burn-in period ensures that the Markov chain has reached its stationary distribution. Inference is then based on the remaining simulated values by computing numerical summaries such as empirical means and confidence intervals for the quantities of interest.

Candidate models, prior distributions and derived parameters

We were interested in whether survival and/or fecundity rates changed gradually over time. Thus, we considered linear relationships

$$\text{logit}\left(\phi_{x,t}^{k}\right) = \alpha_x^k + \beta_x^k year \text{ and}$$

$$\log\left(f_t^k\right) = \gamma^k + \delta^k year,$$

where year is a continuous variable. Furthermore, we included models in which survival was not sex specific, and we applied models where these demographic rates were constant (β_x^k and/or δ^k set equal to 0). We used different combinations that resulted in a set of 15 candidate models. We also included a more general model with time-dependent parameters. We used the deviance information criterion (DIC; Spiegelhalter et al. 2002) to rank these models according to their support by the data. The DIC quantifies the trade-off between quality of fit and model complexity and takes prior information into account. It is calculated as,

$$DIC = -2\log L(data \mid \theta) - 2p_D,$$

where $\log L(data \mid \theta)$ is the deviance and p_D is the effective number of parameters. In the case of uninformative priors the DIC is approximately equal to the well known Akaike information criterion (Burnham & Anderson 1998). The model with the smallest DIC is selected as the best.

For the complete specification of the Bayesian model, prior distributions for all parameters need to be chosen. Because a priori knowledge about demographic parameters in the greater horseshoe bat is limited, we choose uninformative priors for all parameters we intended to estimate. Specifically, we used vague normal priors (N(0,1000)) for the regression parameters (α, β, γ, δ), vague beta priors (β(1,1) equivalent to a uniform distribution between 0 and 1) for the recapture rates, and vague normal priors truncated to positive values for the initial state-specific population sizes (N(10,10000) for $N_{1,1}^k$, and N(20,10000) for $N_{a,1}^k$).

To calculate the posterior distributions of the parameters of interest, we used MCMC simulations implemented in program WinBUGS (Spiegelhalter et al. 2004) that we executed from R (R Development Core Team 2004) with package R2WinBUGS (Sturtz et al. 2005). (See Supplementary Material for information on the code for fitting the model.) Initial trials showed that convergence occurred quickly (after about 5000 iterations) as evidenced by the Brooks – Rubin – Gelman diagnostic (Brooks & Gelman 1998). Therefore, for the main analysis we ran the MCMC algorithm for 1,100,000 iterations, discarded the first 100,000 iterations as burn in, and thinned the remainder to 1 in every 10 iteration.

We calculated some derived parameters to characterize the population. The annual growth rate λ_t was calculated as the ratio of the number of females in year *t* to the number of females in year *t*+1. The averaged population growth rate over the study period was calculated as the geometric mean of all year-specific values. The size of the complete population prior to birth was the sum of the members from all sex and age classes in that year. We calculated the probability that subadult males and females would be differentially present at the nursery colony as the quotient of the number of times the difference between these quantities was larger than zero in the MCMC samples and of the total number of MCMC samples. These quantities were easily obtained as by-products of the MCMC iterations.

Results

The number of individuals we counted each year increased over time from 27 in the year 1992 to 59 in the year 2005, and the number of newborns increased from 11 in year 1991 to 33 in year 2005 (Fig. 2).

Model selection revealed that the simplest model with constant survival and fecundity rates and no sex dependence had the strongest support (Table 1). However, the difference in DIC to the next-best candidate models was small, and thus there remained considerable uncertainty

about the structure of the best model. The models that were closest to the most parsimonious contained sex effects on survival and a linear trend in fecundity.

The estimated demographic rates showed that the greater horseshoe bat is a long-lived species with average adult survival of 0.91 (Table 2). The fecundity rate was rather low with about 74% of all adult females that reproduce in a year. As expected, the probability for an individual would be present at the roost was lowest in adult males (0.28) and highest in adult females (0.92). The probability that subadult males would be present at the colony tended to be lower (0.68) than that of subadult females (0.82), but this difference was not significant (difference: 0.14, SD: 0.17, probability that the difference was different from zero: 0.20; Table 2).

All estimated demographic parameters for males had larger standard deviations than the corresponding parameters for females (Table 2). This was also apparent for the sex-specific juvenile survival rates from the second-best model: the standard deviation for the males (0.142) was twice as large as the standard deviation of the females (0.071), although the means were almost identical (males, 0.506; females, 0.496).

The estimated population sizes of females and subadult males were increasing over time (Fig. 3). The estimates for 1991, in particular those of the subadults were not reliable, and the estimates of the adult males were generally imprecise. The size of the complete population (sum of both age classes and sexes) increased from 70 individuals (SD 21) in the year 1992 to 96 individuals (SD 12) in the year 2005. Because the estimation of the males was less reliable than that of the females, we considered that the total population size was twice the total number of females. This can reasonably be assumed given the even sex ratio at birth and no sex-specific differences in local survival probabilities. Under this assumption, the model estimated that the entire population had increased from 51 (SD 9) to 92 (SD 10) individuals between 1992 and 2005.

The mean annual population growth rate calculated as the geometric mean of the year-specific population growth rates of the adult females indicated positive population growth (1.044, SD: 0.014, 95% credible interval: 1.018 – 1.073; range: 0.979 [SD: 0.077] – 1.085 [SD: 0.073]). The mean population growth rate obtained by the counts was higher (1.062), and the variation between years was larger (Fig. 4).

To assess the impact of model selection uncertainty on our conclusions, we considered the estimates of each demographic parameter across all models with $\Delta DIC < 2$ and calculated the difference between the maximum and the minimum value. These differences were small for all parameters (survival rates: < 0.04; fecundity: < 0.06, population sizes: < 3.5; population growth rate: 0.018) indicating that our conclusions were robust despite considerable model selection uncertainty. OK, neat idea ;-)

Discussion

The combination of different sources of information in a Bayesian framework through the product of three different likelihoods applied to a sparse data set of an endangered bat species was helpful for estimating demographic rates and population size. In addition we could test hypotheses regarding the variation of demographic rates. We found that the greater horseshoe bat colony at Vex has increased by 4.4% each year, that the species is long-lived with survival rates of about 50% in the first year and of about 90% when adult, and that females reproduced successfully in about 3 out of 4 years.

Our estimated survival rates for juvenile greater horseshoe bat (0.49) were similar to those of Ransome (1990). In contrast, our estimates for the adults (0.91) were higher on average than Ransome's (1990) (0.66 – 0.91). This discrepancy is likely a consequence of calculating return instead of local survival rate; the former is unreliable when trappability is not 100% (Martin et al. 1995). Reliable estimates of survival rates from other bat species are scarce. In all

species studied so far adult survival is lower than 0.9 (Boyd & Stebbings 1989; Gerell & Lundberg 1990; Hoyle et al. 2001; Sendor & Simon 2003; O'Shea et al. 2004; Pryde et al. 2005). Among bats, different life histories are likely to exist with a cline from short-lived species that are relatively more productive to relatively longer-lived species that are less productive, as found in other groups of vertebrates (Saether & Bakke 2000). Although basic demographic information of many other bat species must be known to make strong conclusions, there is evidence that the greater horseshoe bat is at the long-lived end of this continuum (Gaisler 1989).

Comparison of fecundity with other bat species is difficult because such estimates are largely lacking. As regards greater horseshoe bats, Ransome's (1995) fecundity estimate of 0.9 is likely an overestimation given that the ratio of females that showed signs of reproduction to all adult females captured in a given year was used. If nonreproducing females do not use the nursery roost where captures are carried out, for instance because they skip reproduction during certain years (this study), then this estimate of fecundity is biased high. The combination of a high survival rate (0.9) and high fecundity (Ransome's 0.9) would have lead to an unrealistic doubling of the British population of greater horseshoe bats within ~5 years assuming that all individuals started to reproduce only at 3 years of age. In contrast, our model actually accounted for temporary absence from the colony.

We can only speculate at this stage about why the population in Vex has increased. Because there is no strong evidence that the demographic parameters have changed over time, it is likely that good conditions already prevailed because of the bat-friendly restoration of the building in 1989 when we started to monitor the colony. This conservation measure may have been crucial for the colony's increase. However, a model in which fecundity gradually increased was not very far from the best model (Table 1). Thus, there remains uncertainty about whether the population increase was supported by (it might not be clear what you mean by supported by) increasing fecundity. With sparse data, subtle patterns are difficult to recognize.

If the population increases further, we can expect that density-dependent mechanisms may start to operate. These may affect all demographic parameters, yet we expect that they will become evident first in emigration. This is because, historically, the greater horseshoe bat was widespread in Valais, and there is some potential for recolonization of abandoned colonies if local foraging habitat is still suitable. If emigration were to become stronger, this would be evident in a decrease of juvenile local survival.

The population sizes for 1991 were not estimated reliably, probably because there was no census carried out in this year. More generally, the fact that obviously no information is available prior to the beginning of the study may explain why the estimate from the first year is less reliable than those of later years. Technically, it is indeed very difficult to provide initial values that are required to start the fitting algorithm close enough to the true population sizes. I MUST CONFESS THAT THIS POINT IS NOT CLEAR TO ME EITHER. I KNOW THAT PANAGIOTIS (BESBEAS) IS WORKING ON DIFFERENT TECHNIQUES TO PROVIDE GOOD GUESS FOR THOSE INITIAL VALUES IN ORDER TO BURN AS LESS AS POSSIBLE THE INFORMATION IN THE BEGINING OF THE STUDY (THIS IS PROBABLY WHAT HAPPENS HERE).

Our model was based on a number of assumptions and simplifications. These had to be realistic; otherwise, the model would not be useful and the parameter estimates would be biased. The assumption that temporary emigration was random (i.e., the probability of a bat being present at the colony depended on whether it was present one year before) was necessary so that we could use the recapture probabilities as estimates of the probability of presence of the different sex and age classes. Because nonreproducing females are often not present at the colony (this study) and reproduction is costly for female bats (Kurta et al. 1989; Kunz et al. 1995; Korine et al. 2004), it is possible that temporary absence from the colony depends on the reproductive success in the previous year and is thus a first-order Markov process.

We assumed that the age at first reproduction was 2 years, even though some individuals of this species may reproduce for the first time only when they are 3 or more years old (Ransome 1995). We constructed a modified model in which we assumed that all individuals start to reproduce when they are three years old only, but this model was clearly worse than the best one (ΔDIC = 26.70).

We also assumed that immigration was nonexistent. Although we included all losses due to mortality and permanent emigration in our model, we only included gains through local recruitment. Immigration into the studied population was unlikely because the next colony of greater horseshoe bats was several hundreds of kilometers away in bat flight distance due to the high mountain ridges around the Rhône valley where our study colony was situated. Finally, our model was fairly simple in regards to the age structure of survival and fecundity rates.

These assumptions and simplifications were necessary to produce basic demographic information about this endangered bat species from sparse data. However, if the assumptions and simplifications have to be relaxed, or if finer patterns of the life history are detected, more data, in particular more years with recapture data, will be required. If more data were available, the integrated population model could easily be adapted to include nonrandom temporary emigration, probabilistic instead of deterministic age at first reproduction, and finer age structures in survival and fecundity. Clearly, a richer data set would also allow one to test for possible sex differences and temporal trends of vital rates with more power or to estimate temporal variation of the vital rates (hierarchical modeling with hyperparameters, e.g., Barry et al. 2003). Relaxing the assumption of no immigration can be achieved by specifying the model differentially. Because the immigrants are included in the counts, no additional data would be required to estimate immigration rate.

Potential of integrated modeling

Integrated population models are flexible tools that can be adapted to a variety of sampling situations. The strength of the integrated population model is that each model fragment borrows information from other model fragments, resulting in higher precision of parameter estimates and enabling estimation of parameters that could not be estimated otherwise (Besbeas et al. 2002). A further advantage of this framework is that it allows modeling of biologically plausible population processes and estimation of key biological parameters, while explicitly recognizing the uncertainties involved in the data collection (Besbeas et al. 2002; Buckland et al. 2004; Brooks et al. 2004; Besbeas et al. 2005). Once again, Buckland et al. 2004 do not deal with integrated population modeling. This ref. should be deleted. It is critical that the biological processes are well captured in the integrated model and that the count and the demographic data sets are independent. As demonstrated here, integrated population models allow one to estimate basic demographic parameters (fecundity in our example) that could otherwise not be estimated and its application resulted in much more accurate estimates of population growth and survival.

The level of confidence that one should give to each source of data is automatically handled with in the integrated population model. For example, the precision of survival rate is much poorer if estimated from count data alone compared to when capture-recapture data are used alone. The precision increases further, if both data types are used in conjunction to estimate survival, yet compared to the precision of survival from capture-recapture data alone the improvement is not so large. Thus, both types of data contain information about survival, but the quality is higher in the capture-recapture data than in the count data. Overall, the combination makes the sample size larger and hence increases precision and improves inference. This issue is explored in details in Brooks et al. (2004). OK, excellent!

In many monitoring systems the number of newborns and adults are recorded annually. Unless only reproducing females are included in the counts (which is rarely achieved in bats), these data would not be sufficient to estimate demographic parameters from an integrated

population model. If, however, longitudinal data on marked individuals are available, estimation of demographic parameters is possible, as demonstrated in our example. It is not necessary to mark all young each year, and recapturing of adults does not necessarily have to be done on a yearly basis. In our example, the demographic parameters could have been estimated with one recapture event (i.e., without the data from year 2005), although parameter estimates would have been less precise. Not having to catch adults each year is appealing, especially if disturbance of the animals is a concern.

An important advantage of the integrated population models to monitoring is that a reliable estimate of fecundity can be obtained, which is particularly difficult in bats (Tuttle & Stevenson 1982). The estimation requires, however, that the proportion of females present in a breeding population (e.g. a colony) be estimated. In most situations it will be impossible to capture all the adults in a population; therefore, the estimation of temporary emigration cannot be done as we did it. A possible solution is to perform at least two capture events in a year and to incorporate the robust design model (Kendall et al. 1997) into the integrated model. Another solution is to include a multistate model with an unobservable state (Schaub et al. 2004), but this requires that temporary emigration be nonrandom.

With an increasing number of species and populations at risk, an understanding of the ultimate causes of negative population trends in endangered organisms is needed. Carefully conducted demographic analyses have the potential to isolate the vital rates responsible for demographic variation. Targeted ecological, behavioral, or genetic investigations can then be performed to determine the proximate factors that effect (AFFECT?) the most crucial demographic parameters. This in turn will lead to accurate guidelines for the implementation of tailored conservation action plans. Given its potentially high resolution power, despite the scarcity of demographic data, integrated population models should become an essential tool of the modern conservation biologist.

Acknowledgements

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Supplementary Material

The WinBUGS code for the integrated population model, the demographic data of greater horseshoe bats from Vex (1991-2005), and the starting values to fit the most parsimonious model $\phi_1(.), \phi_a(.), f(.)$ for reproducing the results are provided in conjunction with the online version of this paper at http:// xxx (I'll fill this in).

In your cover letter to Dr. Meffe, justify the inclusion of this supplementary material with the online version. Such material needs to be useful to researchers well into the future.

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Table 1. Modeling results of different integrated population models of greater horseshoe bats from the Vex colony (1991-2005).*

Model	Deviance	pD	ΔDIC
$\phi_1(.), \phi_a(.), f(.)$	261.69	28.07	0.00
$\phi_1(s), \phi_a(.), f(.)$	262.21	28.38	0.83
$\phi_1(.), \phi_a(s), f(.)$	262.16	28.81	1.22
$\phi_1(.), \phi_a(.), f(T)$	262.43	28.59	1.27
$\phi_1(.), \phi_a(T), f(.)$	262.54	28.59	1.37
$\phi_1(.), \phi_a(T), f(T)$	263.33	28.96	2.53
$\phi_1(s), \phi_a(s), f(.)$	263.06	29.71	3.01
$\phi_1(s), \phi_a(.), f(T)$	263.26	29.65	3.15
$\phi_1(T), \phi_a(.), f(.)$	262.29	30.66	3.19
$\phi_1(.), \phi_a(s), f(T)$	263.18	29.91	3.33
$\phi_1(s), \phi_a(s), f(T)$	264.01	30.82	5.07
$\phi_1(T), \phi_a(.), f(T)$	263.25	31.89	5.38
$\phi_1(T), \phi_a(T), f(T)$	264.12	32.82	7.18
$\phi_1(T), \phi_a(T), f(.)$	263.22	34.58	8.04
$\phi_1(t), \phi_a(t), f(t)$	215.35	728.38	653.97

** The model parameters are the age-specific survival rates (ϕ_1: juveniles, ϕ_a: adults) and fecundity rate (f). The other parameters in the models, the population sizes and the recapture*

rates, were in all models time-, sex- and age-specific. The notation (T) refers to a linear time trend of the specific parameter, (t) indicates year-specific rates, (s) refers to sex specific rates, and (.) denotes constancy. The model deviance, model complexity (pD), and difference of the deviance information criterion between the best and the current model (ΔDIC) are provided. Models are ranked according to their support of the data; the best supported model is at the top.

Table 2. Estimated demographic parameters of greater horseshoe bats from the Vex colony (1991-2005).*

	Mean	SD	Lower	Upper
Juvenile survival (ϕ_1)	0.489	0.064	0.371	0.619
Adult survival (ϕ_a)	0.906	0.020	0.865	0.943
Fecundity (f)	0.743	0.115	0.562	1.008
Presence of subadult females (τ_1^f)	0.821	0.105	0.575	0.974
Presence of adult females (τ_a^f)	0.919	0.042	0.821	0.981
Presence of subadult males (τ_1^m)	0.675	0.140	0.393	0.927
Presence of adult males (τ_a^m)	0.282	0.093	0.131	0.494
Census variance (σ_y^2)	22.41	14.41	6.44	59.33

** Given are the posterior mean, standard deviation (SD) and limits of the 95% credible intervals (lower, upper) of demographic parameters estimated with the most parsimonious model ($\phi_1(.), \phi_a(.), f(.)$).*

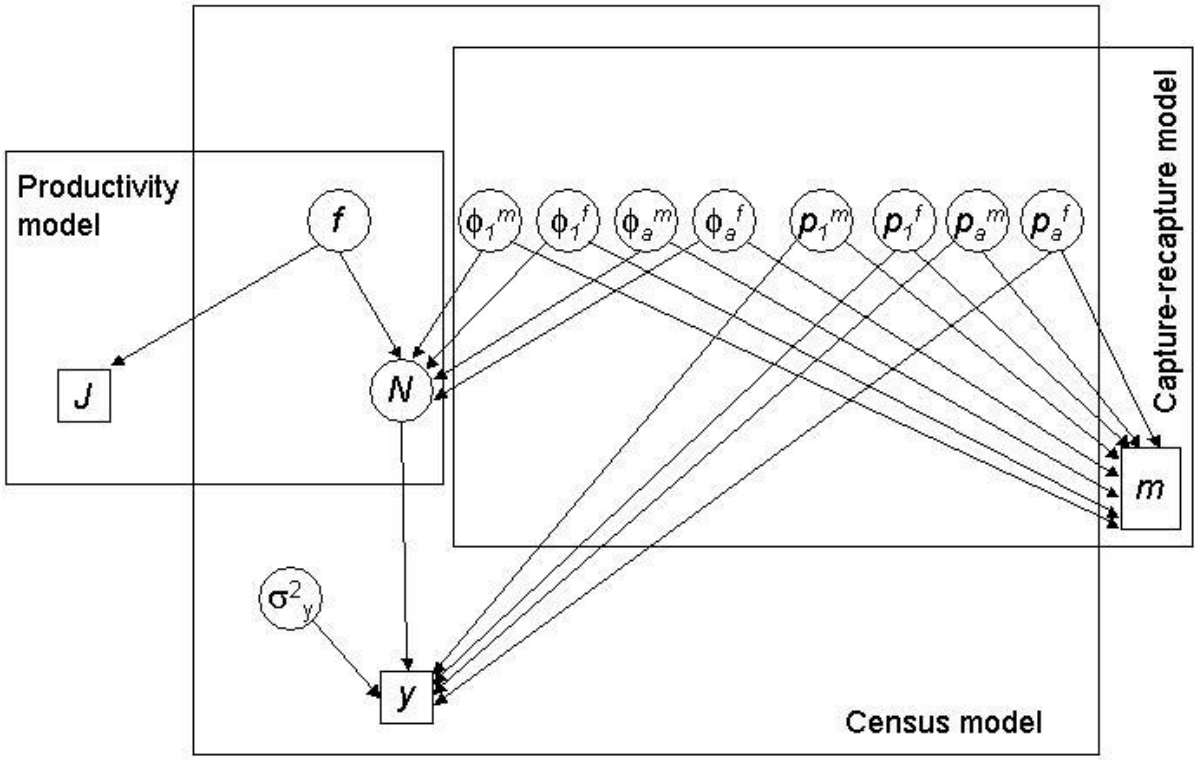
Figure captions

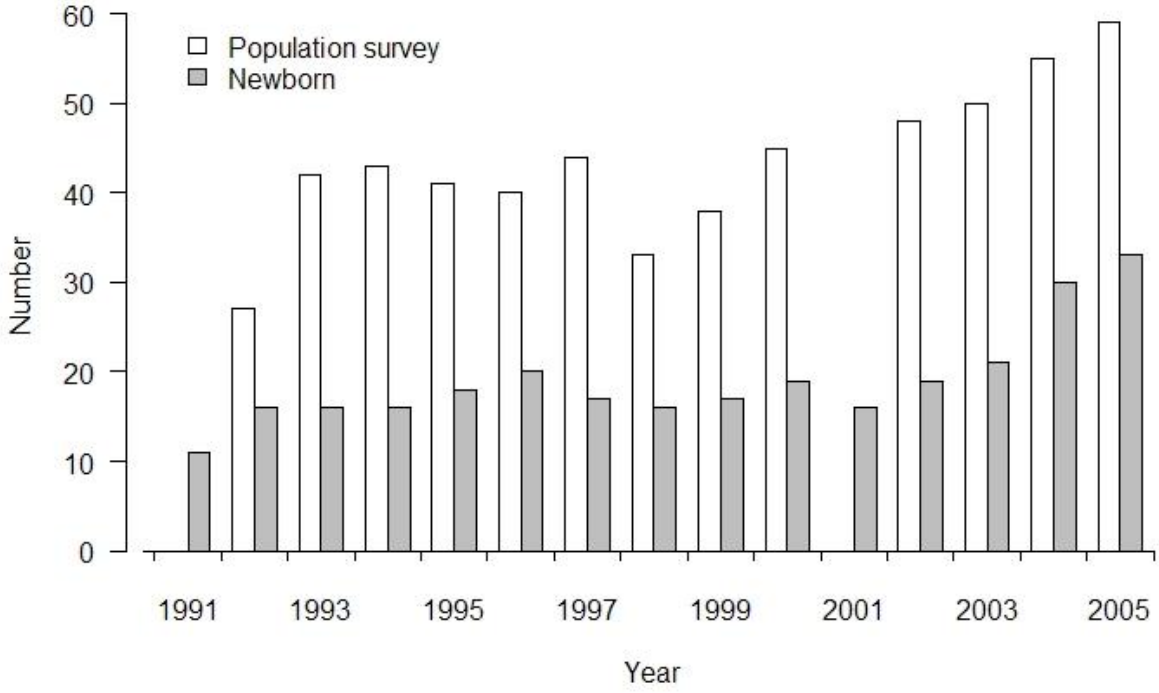
Figure 1. Directed acyclic graph (DAG) of the integrated population model for greater horseshoe bats in the Vex colony. Estimated parameters are represented by circles, and the data are represented by rectangles. Arrows represent dependences between nodes. To simplify the graph, the different sex and age classes are represented by one node *N*. Node notations: *m*, capture-recapture data; *y*: count data, *J*: number of newborns; *f*: fecundity rate; ϕ_x^k: local survival rate of bats in age class *x* with sex *k* (where 1, first year; ad, adult; m, male; f, female); p_x^k: recapture rate of bats in age class *x* with sex *k* (where 1, first year; ad, adult; m, male; f, female); *N*: population size; σ_y^2: variance of the count.

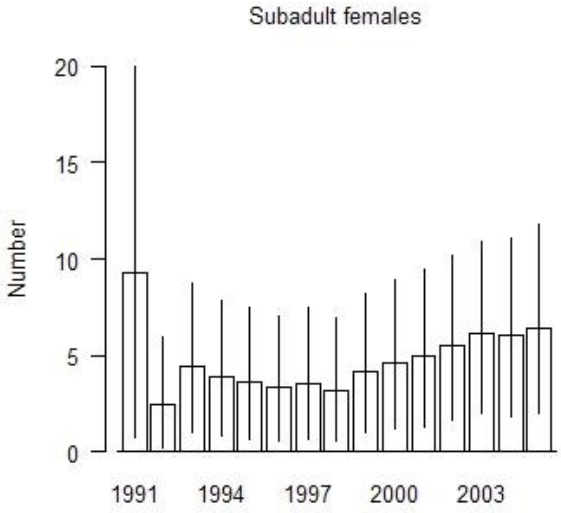
Figure 2. Annual population surveys (counts) of greater horseshoe bats at emergence of the roost in Vex (no survey was carried out in 1991 and 2001) and the annual number of newborn greater horseshoe bats in Vex.

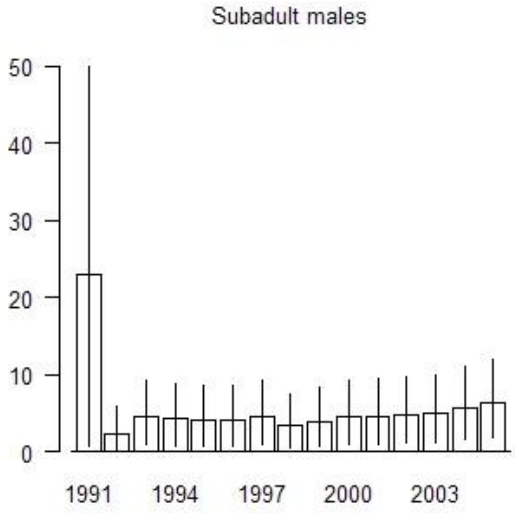
Figure 3. Estimated population size of greater horseshoe bat colony in Vex stratified according to sexes and age classes based on the most parsimonious model ($\phi_1(.), \phi_a(.), f(.)$). Bars are the posterior mean, and the vertical lines represent the limits of the 95% credible intervals.

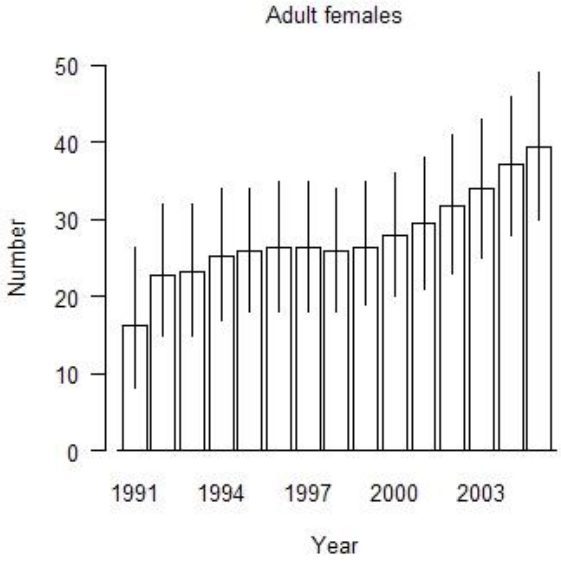
Figure 4. Annual population growth rates of greater horseshoe bats in Vex estimated based on the raw counts (population surveys) and on the integrated population model (IP model). The closed dots from the IP model are posterior means based on the most parsimonious model ($\phi_1(.), \phi_a(.), f(.)$); the vertical lines show the limits of the 95% credible interval.

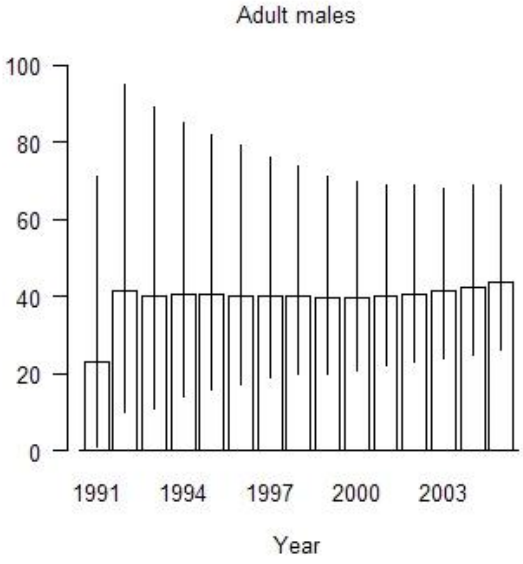

Productivity model
f
J
N
ϕ_1^m
ϕ_1^f
ϕ_a^m
ϕ_a^f
p_1^m
p_1^f
p_a^m
p_a^f
Capture-recapture model
m
σ^2_y
y
Census model

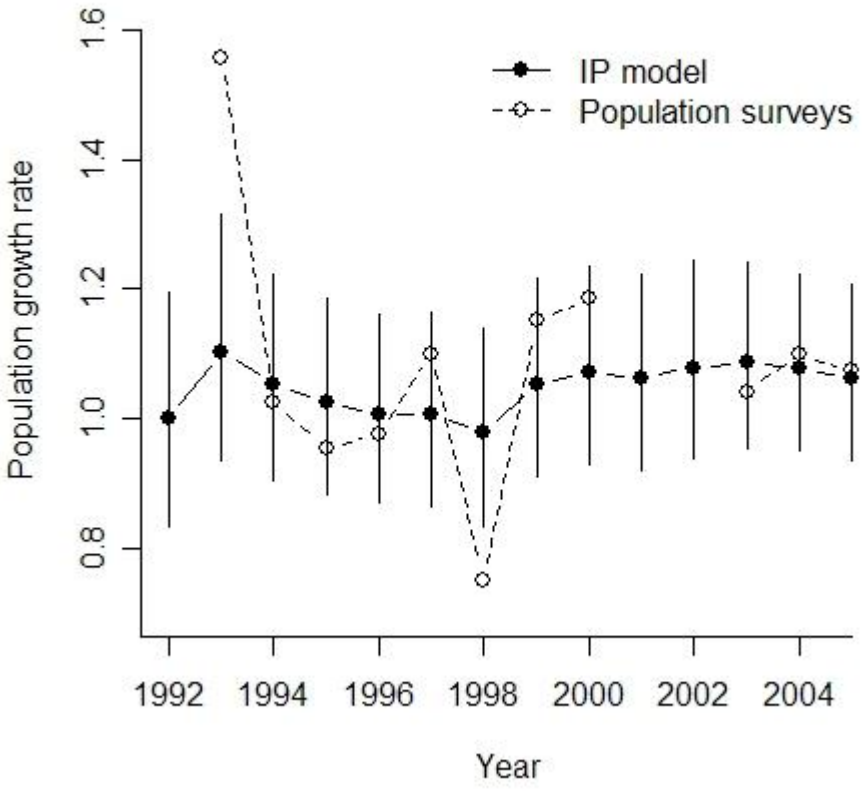

Population survey
Newborn
Number
Year
0
10
20
30
40
50
60
1991
1993
1995
1997
1999
2001
2003
2005


Subadult females
Number
0
5
10
15
20
1991
1994
1997
2000
2003


Subadult males
0
10
20
30
40
50
1991
1994
1997
2000
2003


Adult females
Number
0
10
20
30
40
50
1991
1994
1997
2000
2003
Year


Adult males
0
20
40
60
80
100
1991
1994
1997
2000
2003
Year


IP model
Population surveys
Population growth rate
0.8
1.0
1.2
1.4
1.6
1992
1994
1996
1998
2000
2002
2004
Year