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Comparing survival among species with imperfect detection using multilevel analysis of mark–recapture data: a case study on bats

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For comparative demography studies, 2 prerequisites are usually needed: 1) using typical parameter values for species, 2) correctly accounting for the uncertainty in the species specific estimates. However, although within-species variability may be essential, it is typically not considered in analytical procedures, resulting in parameter estimates that may not be representative of the species. Further, data are analysed in 2 steps, first separately for each species, then estimates are compared among species. Accounting for the uncertainty in the species specific estimates is then difficult. Here we propose the application of multilevel Bayesian models on mark–recapture (MR) data for comparative studies on survival probabilities that solves these problems. Our models account for within-species variability in space and time in the form of random effects. Models reflecting different biological predictions related to the species' ecology and life-history traits may further be contrasted. To illustrate our approach, we used long-term data from 5 temperate tree-roosting bat species and compared their survival probabilities. Results suggest that species foraging in open space, high reproductive output and short longevity records have lower survival than species foraging at short distances, with low reproductive output and high longevity records. Multilevel models provided relatively precise estimates, away from the edges of the parameter space, even for species with low encounter rates and short study duration. This is particularly valuable for less studied taxa such as bats for which available data are often more sparse. Our approach can be easily extended to include additional groups or levels of interest and effects at the individual level (e.g. sex or age). Different hypotheses regarding differences or similarities in parameters among species can be tested through the application of different models. Overall, it offers a flexible tool to ecologists, and population and evolutionary biologists for comparative studies, explicitly accounting for multilevel structures often encountered in MR data.

Ecological data are often complex and hierarchically structured. Hierarchical/multilevel statistical models (Gelman and Hill 2007) provide a flexible framework for their analysis (Clark and Gelfand 2006b, Royle and Dorazio 2008, Link and Barker 2010, Kéry and Schaub 2011). Recent advances in computational methods, software, and computer power have allowed the rapid expansion of such modelling applications in ecological studies over the last decade (Ecol. Appl. 2009, 19: 551–596). Hierarchical/multilevel models are often fitted in a Bayesian framework because classical approaches using maximum likelihood (ML) techniques may become rapidly intractable when model complexity increases (Clark and Gelfand 2006a, but see de Valpine 2004 and Lele et al. 2007). Bayesian applications in ecology became feasible with the use of Markov chain Monte Carlo (MCMC) algorithms (Ellison 2004, Clark 2005) along with the development of freely available software such as BUGS (Lunn et al. 2000). In contrast to the ML approach, this method provides posterior distributions of the parameters, which describe the ranges of their possible values, provided the data and prior information for the parameters (see McCarthy 2007 for an introduction).

Hierarchical/multilevel models are extensions of classical regression models in which data are structured and variables measured at multiple levels or groups (Gelman and Hill 2007). Note that the term hierarchical induces confusion as it may sound as referring exclusively to nested designs. Therefore, throughout this paper, we use the term multilevel. Multilevel models are a compromise between complete pooling (excluding categorical predictors from analysis) and no-pooling analysis (separate models within each level of categorical predictors), by taking into account variation between levels of analysis without over-fitting the data (partial pooling; Gelman and Hill 2007). In these models, coefficients may vary by level and error terms account for heterogeneity at the different levels in the data (Gelman et al. 2004, Gelman and Hill 2007). Both coefficients and error terms are derived by common probability distributions across levels. Sources of variability are therefore treated as random effects, which specify probability distributions and provide information about their magnitude and uncertainty.

In ecology, multilevel models have been applied widely, for instance for modelling species diversity and distribution (Gelfand et al. 2005, 2006), estimating nest survival accounting for heterogeneity (Natarajan and McCulloch 1999, Rotella et al. 2007, Schmidt et al. 2010), predicting animal abundance in space and time (Link and Sauer 2002, Wikle 2003, Link et al. 2006, Royle and Dorazio 2008), and investigating population dynamics (Buckland et al. 2004, Newman et al. 2006). Multilevel models were initially fitted to mark–recapture (MR) data to estimate population abundance and density (George and Robert 1992, Rivot and Prevost 2002, Royle and Young 2008) but are increasingly used for other parameters (e.g. survival: Zheng et al. 2007, birth, death, and immigration rates: O'Hara et al. 2009). MR models are a fundamental tool for the study of wildlife populations, allowing reliable estimation of demographic parameters. However, parameter estimates may be biased, if spatial, temporal or individual heterogeneity is ignored. Accounting for heterogeneity by fitting parameters to subdivisions of a population (e.g. sex, age, location) independently may result in overfitted models with uninformative estimates, i.e. highly imprecise or near the boundaries of the parameter space. This occurs particularly in data sets with small sample size, low capture probabilities, and/or short study duration, which are common to MR studies (Rivot and Prevost 2002, Clark 2003) and in particular to taxa that have relatively recently started to be more intensively studied such as bats compared for instance to birds. Moreover, factors affecting parameters are often not known. Multilevel models provide a solution by naturally accommodating variability in a flexible and scientifically rigorous manner through the use of random effects.

In this paper, we propose the application of multilevel models on MR data for comparative demographic studies. Specifically, we compare annual survival probabilities between animal species with contrasting ecologies and life-history traits using a Bayesian approach through MCMC algorithms. Our data are structured in 3 levels, with species at the highest level, different sites (or populations) nested within species, and time intervals nested within sites. Within-species variability in survival that cannot be assigned to specific sources is thus accommodated by the models in the form of random effects; it is structured in space and time and is explicitly quantified along with estimation errors. Accounting for within-species variability may be essential when estimating inter-specific differences in population parameters (Dochtermann and Peacock 2010). However, in comparative studies, it is typically not accommodated by the models and MR data are analysed in 2 steps: first separately for each species, then inference is obtained by comparing estimates between species or groups of species (Johnston et al. 1997, Peach et al. 2001, but see Lahoz-Monfort et al. 2010). We perform comparisons at 1 step, integrating within-species variability in estimates and we compare different models representing alternative hypotheses related to the species' ecology and life-history traits. Our method is illustrated using long-term data from individually marked adult female bats from 5 temperate tree-roosting species. We present 2 reference models: all species have different survival and survival probabilities do not differ among species. The first reference model is equivalent to analysing each species separately. We also present a model testing a specific biological prediction as an example. In particular, we predict that more opportunistic species that cover long distances to forage in open space will have different survival probabilities than species that hunt close to substrates and fly slowly over relatively short distances, because of differences in exposure to mortality risks. According to life history theory, we further predict that species with high reproductive output and short longevity records will have lower survival than species with low reproductive output and high longevity records.

Material and methods

Study species

We selected 5 European tree-roosting bat species: the Bechstein's bat *Myotis bechsteinii*, the brown long-eared bat *Plecotus auritus*, the Daubenton's bat *M. daubentonii*, the Leisler's bat *Nyctalus leisleri*, and the greater noctule *N. lasiopterus* (Table 1). *Nyctalus leisleri* and *N. lasiopterus* hunt flying insects in open space (aerial insectivores) and, therefore, usually fly fast over long distances during foraging. In contrast, *M. bechsteinii, P. auritus* (gleaners), and *M. daubentonii* (water-surface forager) hunt close to a substrate, usually fly slowly over relatively short distances, and are more restricted to certain habitat types (Dietz et al. 2009).

We used long-term data from individually marked adult females from maternity colonies roosting in forests either in artificial bat boxes or in tree cavities (Table 1). These colonies typically last from spring to late summer or early autumn, having dispersed by late autumn for subsequent hibernation apart from the summer habitat. We used data from a colony of *N. leisleri* previously studied by Schorcht et al. (2009). We selected only locally born individuals, because foreign individuals were less frequently present and had a much stronger dispersal, affecting survival estimates (Schorcht et al. 2009). We used data from 4 and 2 different colonies from *M. bechsteinii* and *P. auritus* respectively, whereas 1 colony was used from the other 3 species (Table 1). Long-term studies of the Bechstein's colonies, combining genetic and behavioural data, have shown that females form closed social units and that there is no switching of colonies (Kerth et al. 2002). While the 4 Bechstein's bat colonies live close to each other (<10 km apart, Kerth et al. 2002) the 2 brown long-eared bat colonies are found in different locations of Germany (ca 400 km distance). Again previous genetic and behavioural studies have shown that brown long-eared bats are faithful to their natal colonies (Burland et al. 2001). Female philopatry is a feature of temperate

Table 1. Summary data of 5 European tree-roosting bat species used in multilevel analysis.

Species	Colony	Study period (number of yr)	Number of individuals marked	Number of individuals recaptured (% of the total marked)
Myotis bechsteinii	Blutsee (BS1), Germany	1996–2009 (14)	53	37 (77%)
M. bechsteinii	Guttenberg (GB), Germany	1996–2009 (14)	105	79 (80%)
M. bechsteinii	Höchberg (HB), Germany	1996–2009 (14)	85	54 (69%)
M. bechsteinii	Unteraltertheim (UH), Germany	1996–2009 (14)	58	38 (72%)
Plecotus auritus	Blutsee (BS2), Germany	2002–2009 (8)	98	52 (53%)
P. auritus	Krangen (KR), Germany	1986–2008 (23)	188	127 (68%)
Myotis daubentonii	Neuhaus (NH), Germany	1987–1995 (9)	1608	795 (49%)
Nyctalus leisleri	Wasungen (WS), Germany	1989–2008 (20)	181	109 (60%)
N. lasiopterus	Parque de María Luisa (PML), Spain	1999–2007 (9)	204	33 (16%)

These are data from adult females. Four separate sites (colonies) were used for *Myotis bechsteinii* and 2 for *Plecotus auritus,* whereas only 1 site (colony) was used for each of the rest of the study species.

bats in general (Burland and Worthington Wilmer 2001, Kerth 2008) and of forest bats in particular (Burland et al. 2001, Kerth et al. 2002, Popa-Lisseanu et al. 2008). Movements between colonies were thus not considered and each colony corresponds to a different site in modelling procedures.

Field techniques

Bats were captured up to 3 times a year from late spring to early autumn, either directly from roosts or mist-netted near their roosts following emergence at dusk. *Myotis daubentonii*, *P. auritus* in the colony in Krangen (Table 1), and *N. leisleri* were all fitted with uniquely numbered aluminium alloy rings (various types), whereas *M. bechsteinii* were marked with a subcutaneously implanted microchip (transponder) with a unique code that can be identified with a mobile reading device (trovan, Euro ID Usling, maximal reading distance 15 cm) (Kerth and König 1999). Most *N. lasiopterus* were both ringed and marked with a transponder. Each bat was assessed for sex, age, and reproductive condition and biometric data were recorded. All bats were released shortly after handling.

Data analysis

Model likelihood

Data consisted of individual encounter histories constructed from MR data for each site (colony) within species (Table 1). In encounter histories, 1s represent capture or sighting events and 0s show that individuals were not encountered at a particular capture occasion. Encounter histories were summarised in the form of first recaptures arrays (Lebreton et al. 1992, Gimenez et al. 2009) for each species × site combination. The likelihood for each site within species was then written as a product of multinomial probability distributions for which cells probabilities were expressed as species- and site-specific functions of survival and encounter probabilities (see Gimenez et al. 2009 for more details). In *N. lasiopterus,* encounter probabilities were fixed to zero for 2002 when captures did not take place, and survival for the intervals immediately before and after this year were set equal to ensure parameter identifiability and interpretability.

Goodness-of-fit

Survival or recapture heterogeneity may induce bias in survival estimates. To check for survival or recapture heterogeneity prior to multilevel modelling, we assessed the fit of the general time-dependent model (φ_t, p_t) (Pradel et al. 2005) for each site within species, where φ_t, and p_t, are time-dependent survival and recapture probabilities respectively. To perform the tests we used program U-CARE (Choquet et al. 2009).

Multilevel model for survival

We considered annual survival for each species, with species treated as a fixed effect at the highest level. At the following level, sites (among-site variation) nested within species, and time (temporal variation) nested within sites at the lowest level (Fig. 1) were treated as random effects. Species-specific survival φ was then considered as a realisation of the 2 random processes of space and time (Fig. 1). This model admitted parameter variability assuming that each set of parameters (e.g. time intervals for a given site or sites for a given species) were derived from the same distribution. This model is not restricted to balanced designs, which means that numbers of sites per species and/or time intervals per site need not be equal (Fig. 1). Its mathematical expression (model 1) is:

$$\operatorname{logit}(\varphi_{sgt}) = \mu_s + \eta_{sg} + \varepsilon_{sgt} \qquad (1)$$

$$\eta_{sg} \sim N(0, \sigma^2_s)$$

$$\varepsilon_{sgt} \sim N(0, \tau^2_{sg})$$

where φ_{sgt} is the probability that an individual of species s and site g survives to occasion $t+1$ given that it is alive at time t, μ_s is the mean survival probability of species s, η_{sg} is drawn from a normal distribution with mean 0 and species-specific among-site variances σ^2_s, and ε_{sgt} is drawn from a normal distribution with mean 0 and species- and site-specific temporal variances τ^2_{sg}. Mean survival probability μ_s, and variances σ^2_s and τ^2_{sg} are estimated on the logit scale, which was used to ensure that survival estimates would lie within the interval [0, 1]. Annual survival per species was calculated as the inverse logit of μ_s:

$$S_s = \frac{1}{1+e^{-\mu_s}} \qquad (2)$$

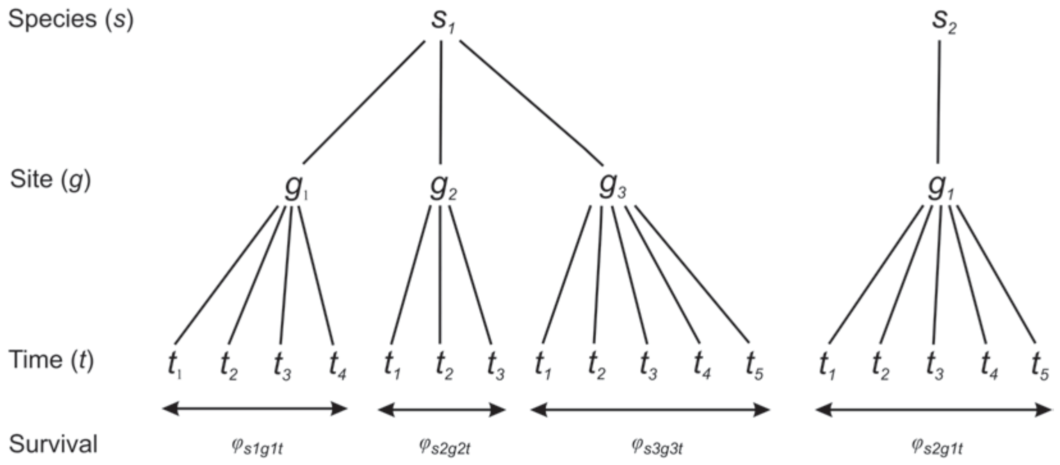

Figure 1. A graphical representation of the multilevel model applied to estimate and compare annual survival among different species (model 1). Mean survival probability μ_s of species *s* corresponds to the top level, the random effect of site (*g*) η_{sg} drawn from a normal distribution with mean 0 and species-specific among-site variances σ^2_s, corresponds to the second level and the random effect of time (*t*) ε_{sgt} drawn from a normal distribution with mean 0 and species- and site-specific temporal variances τ^2_{sg} corresponds to the third level. Survival φ is estimated for each time interval *t,* within each site *g* and species *s*; for example, φ_{s1g1t} corresponds to survival for time interval *t* in site 1 of species 1.

For species for which data on only 1 site were available, the site random effect was excluded. In model 1 (Eq. 1), survival differs among all species examined. On the other extreme, considering that all species have equal survival, we constrained $\mu_s \equiv \mu$ for all species (model 2) where μ is the mean survival probability, equal among species; all other variables are as applied in model 1. Models 1 and 2 are not based on specific biological predictions but are rather used as a reference. Models reflecting specific biological hypotheses are variations of these reference models. Based on the ecological similarities and differences between our study species, we applied a third model (model 3) predicting that mean annual female adult survival probabilities will be different between 2 groups of species, namely group A comprising *M. bechsteinii*, *P. auritus*, and *M. daubentonii*, and group B comprising *N. lasiopterus* and *N. leisleri.* We further predicted that species in group A will have higher survival probabilities than species in group B. A trade-off between survival and reproduction has been well documented in wild animals with larger litter sizes inducing lower survival of females (Koivula et al. 2003). *Nyctalus* species generally exhibit higher reproductive rates by usually giving birth to twins, while the other species typically have a single offspring per year. In addition, their lower longevity records (up to 12 yr vs 21–30 yr for the other 3 species, Dietz et al. 2009) suggest a shorter life span. Our prediction corresponded to the following equation:

$$\text{logit}(\varphi_{sgt}) = \mu A + \eta_{sg} + \varepsilon_{sgt},\quad \text{if species } s = \textit{M. bechsteinii, P. auritus} \text{ or } \textit{M. daubentonii}$$

$$\text{logit}(\varphi_{sgt}) = \mu B + \eta_{sg} + \varepsilon_{sgt},\quad \text{if species } s = \textit{N. lasiopterus} \text{ or } \textit{N. leisleri} \qquad (3)$$

$$\eta_{sg} \sim N(0, \sigma^2_s)$$

$$\varepsilon_{sgt} \sim N(0, \tau^2_{sg})$$

where μA and μB are mean logit survival probabilities for groups A and B respectively. In this model, survival is equal between species within groups. All other variables are as defined in model 1.

We treated recapture probabilities as fixed effects and we constrained them to be different among sites and species. Separate analyses for each site within species were run prior to multilevel models to select between models with time-dependent and constant recapture probabilities (p_t vs p respectively). We did so to avoid running many multilevel models which take much longer to run. Here, survival for each site was modelled using the equation:

$$\text{logit}(\varphi_t) = \mu + \varepsilon_t$$

$$\varepsilon_t \sim N(0, \sigma^2)$$

where φ_t is the probability that an individual survives to occasion $t+1$ given that it is alive at time t, μ is the mean survival probability for the site, and ε_t, is the temporal variation in survival treated as a random effect following a normal distribution with mean 0 and variance σ^2. The selected recapture probabilities (time-dependent or constant) were subsequently incorporated in multilevel models.

Bayesian model fitting and selection using MCMC methods

We fitted models in a Bayesian framework using OpenBUGS, the most recent and developed version of the freely available software BUGS (<www.openbugs.info>) by calling it from program R through the package R2WinBUGS (Sturtz et al. 2005). This is a convenient tool for model formulation and MCMC analysis using Gibbs sampling and other procedures. OpenBUGS was used to specify priors and likelihoods while R for setting initial values, avoid specifying parameters in each run, and post-processing the results (Gimenez et al. 2009). As a by-product of the MCMC procedure, we obtained the posterior distribution of annual survival per species S_s by applying Eq. 2 to the sampled values from the posterior distribution of μ_s. To calculate posterior distributions we ran 2 different Markov chains starting at dispersed initial values over the parameter space.

Convergence of chains to stationary distributions was evaluated using the Brooks–Gelman–Rubin criterion (*R-hat*, Brooks and Gelman 1998), included in BUGS. We applied vague prior distributions for unknown variables, namely a normal prior distribution $N(0, 1000)$ for mean survival probabilities, a uniform prior on [0, 5] for the standard deviations, and a uniform prior on [0, 1] for the detection probabilities. We provide BUGS codes in Supplementary material Appendix 1. To select between models with time-dependent and constant recapture probabilities (model p_t vs p respectively) in separate analyses and between different multilevel models, we used the deviance information criterion (DIC, Spiegelhalter et al. 2002):

$$\mathrm{DIC} = \overline{\mathrm{D}(\theta)} + p_{\mathrm{D}} \qquad (4)$$

where $\overline{\mathrm{D}(\theta)}$ is the posterior mean of the model deviance and p_{D} is the effective number of parameters in the model (Spiegelhalter et al. 2002). DIC can be considered as the Bayesian counterpart to the Akaike information criterion (AIC) used as a model selection criterion in the maximum-likelihood approach (Burnham and Anderson 2002). The model with the lowest DIC value is selected for inference, because it is the most parsimonious, which means that it explains better the variation observed in the data while containing the smallest number of parameters. DIC is readily available in OpenBUGS through program R following model fit. We acknowledge that the use of DIC for model selection with multilevel models is somehow controversial (King et al. 2009). However, the DIC was easily accessible in OpenBUGS, while implementing alternative methods like posterior model probabilities was beyond the scope of this paper.

Results

The CJS model fitted the data adequately for all species (Table 2). Separate analyses for each species showed that recapture probabilities were time-dependent in 4 and constant in 5 out of 9 colonies (Table 3).

Approximate convergence of the 2 chains (*R-hat* < 1.2 for all parameters) was achieved after 500 000 iterations with a burn-in of 100 000 iterations in all 3 models. Model 3 (Eq. 3) had the lowest DIC and was thus best supported by the data, and it was followed by model 1 (Eq. 1) (Table 4). The complete lack of difference in survival among all study species expressed by model 2 was not supported by the data (Table 4). The difference in DIC between model 3 that expressed a difference in survival between the 2 groups of species and model 1 that expressed a complete difference in survival among all study species was small ($\Delta\mathrm{DIC} < 2$). Point estimates of survival posterior distributions of species in group A were higher than those of species in group B (Table 5), in agreement with our prediction. However, the 95% credibility intervals (CI) estimated for the 2 groups overlapped (group A: $S = 0.79$ [0.64; 0.86] vs group B: $S = 0.74$ [0.66; 0.81]).

Table 2. Results of goodness-of-fit tests of the CJS model on mark–recapture data from 5 temperate tree-roosting species of bat. The simultaneous MR study of colonies of *Myotis bechsteinii* allowed us to test the goodness of fit on all 4 colonies simultaneously, whereas this was not the case for the 2 colonies of *Plecotus auritus*. For colony abbreviations see Table 1.

Species	χ^2	DF	p
Myotis bechsteinii (4 colonies)	25.25	49	1.00
Plecotus auritus (BS2)	8.62	10	0.57
P. auritus (KR)	19.77	27	0.84
Myotis daubentonii (NH)	23.10	35	0.94
Nyctalus leisleri (WS)	41.38	49	0.77
N. lasiopterus (PML)	13.68	9	0.13

Table 3. Selection between models with time dependent p_t and constant p recapture probabilities run for each colony prior to multilevel modelling. We report differences in DIC values (ΔDIC) between these models. Where ΔDIC is negative, recapture models with time dependent probabilities were selected.

		Model		
Species	Colony	p_t	p	ΔDIC
Myotis bechsteinii	BS1	75.3	68.9	6.4
M. bechsteinii	GB	101.9	110.2	–8.3
M. bechsteinii	HB	86.8	75.9	11.0
M. bechsteinii	UH	88.2	79.4	8.8
Plecotus auritus	BS2	64.9	147.6	–82.7
P. auritus	KR	148.6	244.8	–96.2
Myotis daubentonii	NH	181.2	225.7	–44.5
Nyctalus leisleri	WS	200.9	193.6	7.3
N. lasiopterus	PML	85.6	76.8	8.8

Discussion

We fitted multilevel Bayesian models to MR data to estimate and compare annual survival among bat species, accounting for within-species variation. Survival estimates obtained were generally comparable to estimates for other bat species (O'Shea et al. 2004). Estimates for *Nyctalus* species (Table 5) were similar to those obtained by Schorcht et al. (2009)

Table 4. Models fitted to mark–recapture data from 5 temperate tree-roosting species of bat.

Model	Deviance (SD)	DIC	pD	ΔDIC
Model 1 (all species have different survival; Eq. 1):	899.31 (18.48)	988.90	88.69	1.40
Model 2 (survival probabilities do not defer among species):	902.36 (19.14)	990.00	88.20	2.50
Model 3 (survival differs between 2 groups of species; Eq. 3):	**901.68** **(18.48)**	**987.50**	**85.66**	0

Deviance is the mean posterior deviance (standard deviation); DIC is the deviance information criterion; *p*D is the number of effective parameters; ΔDIC is the difference between the DIC of a model and the DIC for the minimum DIC model. Detection probabilities were time dependent (p_t) for both *Plecotus auritus* colonies and 3 out of 4 colonies of *Myotis bechstenii* and constant (*p*) for *Nyctalus leisleri, N. lasiopterus* and 1 colony of *M. bechsteinii*. The most parsimonious model, i.e. the model with the lowest DIC, is shown in bold. Posteriors were calculated using 500 000 iterations with a burn-in of 100 000 iterations.

Table 5. Posterior medians [95% credible intervals] for parameters of model 3 (Eq. 3) applied to data sets from 5 European tree-roosting species of bat. Mean survival probability estimate is constrained to be the same for *Myotis bechsteinii*, *Plecotus auritus* and *M. daubentonii* (group A) and the same for *Nyctalus leisleri* and *N. lasiopterus* (group B).

	Myotis bechsteinii				*Plecotus auritus*		*Myotis daubentonii*	*Nyctalus leisleri*	*Nyctalus lasiopterus*
	(A)				(A)		(A)	(B)	(B)
Parameter	BS1	GB	HB	UH	BS2	KR	NH	WS	PML
S	0.79 [0.64; 0.86]							0.74 [0.66; 0.81]	
σ^2_s	0.19 [0.00; 4.81]				0.57 [0.00; 16.63]		–	–	–
τ^2_{sg}	0.07 [0.00; 0.81]	0.60 [0.13; 2.37]	0.29 [0.01; 1.42]	0.30 [0.00; 1.85]	2.57 [0.23; 18.30]	1.07 [0.34; 3.17]	0.75 [0.08; 5.69]	0.36 [0.08; 1.37]	3.66 [0.12; 19.33]
p	0.97 [0.94; 0.99]	**0.92** **[0.88; 0.94]**	0.97 [0.94; 0.99]	0.96 [0.92; 0.99]	**0.70** **[0.64; 0.75]**	**0.81** **[0.77; 0.84]**	**0.37** **[0.34; 0.43]**	0.75 [0.69; 0.80]	0.22 [0.13; 0.36]

Parameters are: S, mean survival probability (see Eq. 2 and section 'Bayesian model fitting and selection using MCMC methods'); σ^2_s, inter-colony variance; τ^2_{sg}, site-specific temporal process variance; p, encounter probability. Inter-colony variance was estimated for *M. bechsteinii* (4 colonies: BS1, GB, HB, UH) and *P. auritus* (2 colonies: BS2, KR). Colony abbreviations are explained in detail in Table 1. For colonies or species where encounter probabilities were time dependent, arithmetic means of the year-specific estimates were computed and these are shown in bold; otherwise constant encounter probabilities are reported.

who used the same colony of *N. leisleri* (0.76 ± 0.04 SE). Multilevel models generally provided reasonable survival estimates, i.e. relatively precise and away from the edges of the parameter space, even for species with low encounter rates and comparatively short study duration (<10 yr) (Supplementary material Appendix 2). These models were less prone to boundary estimates even for high (real) values of parameters, because information from all data was shared among levels of the hierarchy by assuming that parameters arose from common distributions across levels (among-site variability per species and temporal variability per site). Treating sources of variation as random effects from common probability distributions across levels further decreased the number of parameters (e.g. variances and means for survival instead of separate coefficients governing survival and encounter probabilities for each site and time interval). This is particularly useful for bats and other taxa that have been less studied compared for instance to birds, and for which available data are often more sparse. In the comparative framework, however, potential differences among species may still be masked by the relatively low precision of estimates yielded by samples combining small size, low encounter rates, and short study duration (Table 1, Supplementary material Appendix 2). Systematic long-term field protocols should therefore be preferred, especially if capture rates are low. Further, estimates from single sites may not be representative (e.g. a single population may be particularly exposed to high risks of mortality), and the large 95% CI including '0' for colony variances may be due to the fact that these were estimated based on only 2 and 4 sample sites for *P. auritus* and *M. bechsteinii* respectively. Hence the use of more sites per species or other level of interest is strongly recommended, although the exact number will depend on species, the degree of spatial heterogeneity, the size of the targeted populations, and accumulated experience from many species and geographical areas in future (Papadatou et al. 2011).

The multi-species multi-level models that we propose not only do they fit well with animal species for which available MR data are sparse such as bats, but also with numerous broad scale MR protocols such as constant effort site (CES) ringing programs (Robinson et al. 2009). These programs are now operating in many countries providing detailed demographic data on bird species at large spatial scales. Our approach could raise interest to compare different populations or different species at the broad spatial scales where they operate. In fact, Robinson et al. (2009) mention that hierarchical modelling techniques appear to be well suited for analysis of MR data from CES schemes, and that their development and implementation is a key priority for future analytical work, since they better reflect the structure of CE data. This would increase data utility for understanding population processes. It would also allow explicit estimation of spatial variation in demographic parameters (Robinson et al. 2009), which is included in our models.

Our approach is flexible, as models applied can naturally be extended to include new data by adding new groups within levels (e.g. more sites) and/or levels (e.g. habitat types or countries). Other hypotheses regarding differences or similarities in parameters among species or other groups of interest can be tested through the application of a number of different models. Because biological process variance is estimated separately from sampling variance by treating sources of variation as random effects, comparisons may further be extended to include temporal variance in parameters, under systematic field protocols whereby data are collected in parallel across levels of interest (time overlap of capture events across e.g. sites and species). In this way, testing and comparing potentially different effects of environmental factors on parameters across levels may be possible, as it has been applied at multi-population scales (Grosbois et al. 2009). Additional effects can generally be incorporated in the form of covariates inserted at any level of the hierarchy. Models then include regression coefficients of these covariates (intercepts and slopes) with group and level indicators; coefficients are derived from common distributions across levels and interactions between covariates at different levels may be added in this case (Gelman and Hill 2007). In model 3 we added covariates at the species level by grouping species in 2 groups. Provided the data, we could further add covariates at the site and/or time levels, if we have effects of interest acting on survival at any of these levels (e.g. some known environmental factor). Finally, covariates may be added to include effects at the individual level, e.g. sex or age effects. For instance, we assumed no senescence effect in adult survival, because it is not known in bats. However, if senescence affects adult survival (Festa-Bianchet et al. 2003), it can be accommodated in the model through a covariate.

In practice, model extensions can be achieved by adjusting BUGS codes used for model specification (Supplementary material Appendix 1). Increasing model complexity resulting from model extensions can be flexibly dealt via MCMC algorithms. Although computationally intensive, the rapid development of statistical software such as BUGS and the increase in computer power allows their relatively easy application. However, model specification is not straightforward for users without programming skills. Solutions may be provided by making BUGS codes publicly available (Supplementary material Appendix 1, Kéry and Schaub 2011, Papadatou et al. 2011), collaborations between statisticians and ecologists, and training on hierarchical Bayesian modelling (Gimenez 2008, Ogle et al. 2009).

From a biological point of view, our results may provide a first indication that bats hunting flying insects in open space covering long distances, with generally higher reproductive output and shorter longevity records (*Nyctalus leisleri* and *N. lasiopterus*) have lower survival probabilities than bat species hunting insects primarily from substrates in cluttered space at shorter distances, with more restricted foraging requirements, lower reproductive output and higher longevity records (*Myotis daubentonii, M. bechsteinii,* and *Plecotus auritus*). Our finding is in accordance with the pattern generally observed in wild animals with regards to the trade-off between survival and reproduction (Stearns 1992). In a comparative study of 64 species of bat, Wilkinson and South (2002) reported that life span significantly decreased with reproductive rate. However, using a less rigorous approach for MR data analysis, Hitchcock et al. (1984) reported that 2 species of insectivorous temperate bats, *Myotis leibii* and *Eptesicus fuscus* had similar survival probabilities, although their productivity differed (one and two pups per year, respectively). Safi and Kerth (2004) compared the extinction risk among 35 temperate species of bat with contrasting ecological features. They reported that bats with a higher degree of specialisation in foraging strategies and habitats such as *Plecotus auritus* and *Myotis bechsteinii* were more vulnerable to extinction, in accordance with the results of a similar study (Jones et al. 2003). We found that these species had higher survival probabilities compared to less specialised aerial insectivores which were generally classified with lower extinction risk. This contrasts to findings of a comparative study on birds, where species with a slower life history experienced lower extinction risks than species with a fast life history (Saether et al. 2005). Further studies are needed to link extinction risk in bats with their life history, and multilevel models, as presented here, could provide sound estimates (mean as well as temporal and spatial variability of survival) to parameterize population models.

Although the data of the proposed multilevel model must not necessarily be balanced, an ideal comparative demographic analysis would consist of data from several species each sampled at several sites (colonies) and over long time. We only used a single colony of both *Nyctalus* species, and therefore colony and species characteristics are confounded. More species and sites per species ideally from a variety of geographical areas (Papadatou et al. 2011) would help clarify our finding in future analyses. Further, closely related species may show similarities in life history traits because of recent common ancestry, and not independent responses to evolutionary and ecological processes (Bennett and Owens 2002). Our model could be further developed to account for phylogeny, for example by including evolutionary independent species or by incorporating elements of phylogenetic comparative methods in the models (Martins and Hansen 1997, Freckleton et al. 2002). This is ongoing work.

In conclusion, our approach offers an effective, flexible and promising statistical tool to ecologists, and population and evolutionary biologists for comparative analyses of demographic parameters estimated from MR data. We provide a model framework for comparative studies that explicitly accounts for multilevel structures often encountered in MR studies and that may be particularly useful for species for which data may generally be sparse such as bats.

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References

Bennett, P. M. and Owens, I. P. F. 2002. Evolutionary ecology of birds life histories, mating systems and extinction. – Oxford Univ. Press.

Brooks, S. P. and Gelman, A. 1998. General methods for monitoring convergence of iterative simulations. – J. Comput. Graph. Stat. 7: 434–455.

Buckland, S. T. et al. 2004. State-space models for the dynamics of wild animal populations. – Ecol. Model. 171: 157–175.

Burland, T. M. and Worthington Wilmer, J. W. 2001. Seeing in the dark: molecular approaches to the study of bat populations. – Biol. Rev. 76: 389–409.

Burland, T. M. et al. 2001. Mating patterns, relatedness and the basis of natal philopatry in the brown long-eared bat, *Plecotus auritus*. – Mol. Ecol. 10: 1309–1321.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information – theoretic approach, 3rd ed. – Springer.

Choquet, R. et al. 2009. U-CARE: utilities for performing goodness of fit tests and manipulating CApture–REcapture data. – Ecography 32: 1071–1074.

Clark, J. S. 2003. Uncertainty and variability in demography and population growth: a hierarchical approach. – Ecology 84: 1370–1381.

Clark, J. S. 2005. Why environmental scientists are becoming Bayesians. – Ecol. Lett. 8: 2–14.

Clark, J. S. and Gelfand, A. E. 2006a. A future for models and data in environmental science. – Trends Ecol. Evol. 21: 375–380.

Clark, J. S. and Gelfand, A. E. (eds) 2006b. Hierarchical modelling for the environmental sciences: statistical methods and applications. – Oxford Univ. Press.

de Valpine, P. 2004. Monte Carlo state-space likelihoods by weighted posterior kernel density estimation. – J. Am. Stat. Assoc. 99: 523–536.

Dietz, C. et al. 2009. Bats of Britain, Europe and northwest Africa. – A and C Black.

Dochtermann, N. A. and Peacock, M. M. 2010. Differences in population size variability among populations and species of the family Salmonidae. – J. Anim. Ecol. 79: 888–896.

Ellison, A. M. 2004. Bayesian inference in ecology. – Ecol. Lett. 7: 509–520.

Festa-Bianchet, M. et al. 2003. Variable age structure and apparent density dependence in survival of adult ungulates. – J. Anim. Ecol. 72: 640–649.

Freckelton, R. P. et al. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. – Am. Nat. 160: 712–726.

Gelfand, A. E. et al. 2005. Modelling species diversity through species level hierarchical modelling. – J. R. Stat. Soc. C 54: 1–20.

Gelfand, A. E. et al. 2006. Explaining species distribution patterns through hierarchical modelling. – Bayesian Analysis 1: 41–91.

Gelman, A. and Hill, J. 2007. Data analysis using regression and multilevel/hierarchical models. – Cambridge Univ. Press.

Gelman, A. et al. 2004. Bayesian data analysis, 3rd ed. – Chapman and Hall/CRC.

George, E. I. and Robert, C. P. 1992. Capture–recapture estimation via Gibbs sampling. – Biometrika 79: 677–683.

Gimenez, O. 2008. Discussion: towards a Bayesian analysis template? – Can. J. Stat. 36: 21–24.

Gimenez, O. et al. 2009. WinBUGS for population ecologists: Bayesian modeling using Markov chain Monte Carlo methods. – In: Thomson, D. L. et al. (eds), Modeling demographic processes in marked populations. Springer, pp. 883–897.

Grosbois, V. et al. 2009. Modeling survival at multi-population scales using mark–recapture data. – Ecology 90: 2922–2932.

Hitchcock, H. B. et al. 1984. Survival rates of *Myotis leibii* and *Eptesicus fuscus* in southeastern Ontario. – J. Mammal. 65: 126–130.

Johnston, J. P. et al. 1997. Survival rates of tropical and temperate passerines: a Trinidadian perspective. – Am. Nat. 150: 771–789.

Jones, K. E. et al. 2003. Biological correlates of extinction risk in bats. – Am. Nat. 161: 601–614.

Kerth, G. 2008. Causes and consequences of sociality in bats. – BioScience 58: 737–755.

Kerth, G. and König, B. 1999. Fission, fusion and nonrandom associations in female Bechstein's bats (*Myotis bechsteinii*). – Behaviour 136: 1187–1202.

Kerth, G. et al. 2002. Mean colony relatedness is a poor predictor of colony structure and female philopatry in the communally breeding Bechstein's bat (*Myotis bechsteinii*). – Behav. Ecol. Sociobiol. 52: 203–210.

Kéry, M. and Schaub, M. 2011. Bayesian population analysis using WinBUGS – a hierarchical perspective. – Academic Press.

King, R. et al. 2009. Bayesian analysis for population ecology. – Chapman and Hall.

Koivula, M. et al. 2003. Cost of reproduction in the wild: manipulation of reproductive effort in the bank vole. – Ecology 84: 398–405.

Lahoz-Monfort, J. J. et al. 2010. A capture–recapture model for exploring multi-species synchrony in survival. – Methods Ecol. Evol. 2: 116–124.

Lebreton, J.-D. et al. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. – Ecol. Monogr. 62: 67–118.

Lele, S. R. et al. 2007. Data cloning: easy maximum likelihood estimation for complex ecological models using Bayesian Markov chain Monte Carlo methods. – Ecol. Lett. 10: 551–563.

Link, W. A. and Sauer, J. R. 2002. A hierarchical analysis of population change with application to Cerulean warblers. – Ecology 83: 2832–2840.

Link, W. A. and Barker, R. J. 2010. Bayesian inference with ecological applications. – Academic Press.

Link, W. A. et al. 2006. A hierarchical model for regional analysis of population change using Christmas Bird Count data, with application to the American black duck. – Condor 108: 13–24.

Lunn, D. J. et al. 2000. WinBUGS – a Bayesian modelling framework: concepts, structure, and extensibility. – Stat. Comput. 10: 325–337.

Martins, E. P. and Hansen, T. F. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. – Am. Nat. 149: 646–667.

McCarthy, M. A. 2007. Bayesian methods for ecology. – Cambridge Univ. Press.

Natarajan, R. and McCulloch, C. E. 1999. Modeling heterogeneity in nest survival data. – Biometrics 55: 553–559.

Newman, K. B. et al. 2006. Hidden process models for animal population dynamics. – Ecol. Appl. 16: 74–86.

Ogle, K. et al. 2009. Hierarchical statistical modeling of xylem vulnerability to cavitation. – New Phytol. 182: 541–554.

O'Hara, R. B. et al. 2009. Estimation of rates of births, deaths, and immigration from mark–recapture data. – Biometrics 65: 275–281.

O'Shea, T. J. et al. 2004. Survival estimation in bats: historical overview, critical appraisal, and suggestions for new approaches. – In: Thompson, W. L. (ed.), Sampling rare or elusive species: concepts, designs, and techniques for estimating population parameters. Island Press, pp. 297–336.

Papadatou, E. et al. 2011. Assessing survival in a multi-population system: a case study on bat populations. – Oecologia 165: 925–933.

Peach, W. J. et al. 2001. Do southern African songbirds live longer than their European counterparts? – Oikos 93: 235–249.

Popa-Lisseanu, A. G. et al. 2008. Highly structured fission-fusion societies in an aerial-hawking, carnivorous bat. – Anim. Behav. 75: 471–482.

Pradel, R. et al. 2005. Principles and interest of GOF tests for multistate capture–recapture models. – Anim. Biodivers. Conserv. 28: 189–204.

Rivot, E. and Prevost, E. 2002. Hierarchical Bayesian analysis of capture–mark-recapture data. – Can. J. Fish. Aquat. Sci. 59: 1768–1784.

Robinson, R. A. et al. 2009. Constant effort: studying avian population processes using standardised ringing. – Ringing Migr. 24: 199–204.

Rotella, J. J. et al. 2007. Extending methods for modeling heterogeneity in nest-survival data using generalized mixed models. – Stud. Avian Biol. 34: 34–44.

Royle, J. A. and Dorazio, R. M. 2008. Hierarchical modelling and inference in ecology. – Academic Press.

Royle, J. A. and Young, K. V. 2008. A hierarchical model for spatial capture–recapture data. – Ecology 89: 2281–2289.

Saether, B. E. et al. 2005. Time to extinction of bird populations. – Ecology 86: 693–700.

Safi, K. and Kerth, G. 2004. A comparative analysis of specialization and extinction risk in temperate-zone bats. – Conserv. Biol. 18: 1293–1303.

Schmidt, J. H. et al. 2010. A general Bayesian hierarchical model for estimating survival of nests and young. – Auk 127: 379–386.

Schorcht, W. et al. 2009. Variation of adult survival drives population dynamics in a migrating forest bat. – J. Anim. Ecol. 78: 1182–1190.

Spiegelhalter, D. J. et al. 2002. Bayesian measures of model complexity and fit. – J. R. Stat. Soc. B 64: 583–616.

Stearns, S. C. 1992. The evolution of life histories. – Oxford Univ. Press.

Sturtz, S. et al. 2005. R2WinBUGS: a package for running WinBUGS from R. – J. Stat. Softw. 12: 1–16.

Wikle, C. K. 2003. Hierarchical Bayesian models for predicting the spread of ecological processes. – Ecology 84: 1382–1394.

Wilkinson, G. S. and South, J. M. 2002. Life history, ecology and longevity in bats. – Aging Cell 1: 124–131.

Zheng, C. Z. et al. 2007. Age-dependent survival analyzed with Bayesian models of mark–recapture data. – Ecology 88: 1970–1976.

Supplementary material (Appendix E7084 at <www.oikosoffice.lu.se/appendix>). Appendix 1–2.