



Original Research Article

Age, sex, and climate factors show different effects on survival of three different bat species in a woodland bat community



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ABSTRACT

1. Bats are the second largest mammalian Order and important providers of ecosystem services including insect pest control, pollination and seed dispersal. Yet, the lack of basic information on their demographic rates hampers detecting changes in population trends, and thus conservation efforts.

2. The elusive life-styles, that leads to imperfect and biased detection, limits the quantity of individually based information as well as the extent to which information can be utilised to assess accurate and unbiased demographic rates.

3. We overcome the problem of imperfect and biased detection using a multilevel capture-mark-recapture framework to produce robust estimates of survival during hibernation period, and to evaluate the effect of age, sex, social group, and external weather factors on survival and capture heterogeneity in three vespertilionid species (*Myotis daubentonii*, *M. nattereri*, and *Plecotus auritus*) from the same woodland community.

4. While controlling for emigration and for the species-specific roosting group structure, we show that females survive better than males in two species, and that adults survive better than juveniles in all species - these survival differences being species-specific. Only one external environmental factor (average summer temperature) explained a substantial proportion of the between-year variation in *M. daubentonii* survival.

5. Our study provides, for the first time, a robust estimate of annual survival in bats. We advocate careful attention to possible sources of biases when studying survival rates in the wild, considering species-specific life-history and population-specific features. Considering these factors that influence wider community responses to environmental conditions is important for the effective conservation management of an area.

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1. Introduction

Bats (Order Chiroptera) are the second largest mammalian order after rodents (Order Rodentia) with over 1300 species (Simmons, 2005). Bats are important providers of ecosystem services, including insect pest control, pollination and seed dispersal (Kunz et al., 2011). The majority of bat species are listed as of conservation concern (endangered, threatened, near threatened, or vulnerable) or as data deficient (Hutson et al., 2001). A fundamental requirement for accurate prediction of population level responses to threats such as habitat loss and fragmentation, disease, and climate change is an understanding

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of basic demography. Yet, there is a paucity of data on survival rates in bats (O'Shea et al., 2004) that would provide a baseline for impact assessments (e.g. quantification of increased mortality risk at wind farms, or roost loss through exclusion or development, Zeale et al., 2014). This is partly caused by the elusive life-style and longevity (Brunet-Rossinni and Austad, 2004), that pose significant challenges to obtaining accurate and unbiased long-term data. Previous survival estimates have often been restricted to a particular sex, usually females (Lentini et al., 2015) and were often obtained from a single roost site which may or may not be representative of the wider population (Sendor and Simon, 2003; Frick et al., 2010).

Because survival is shaped by complex interactions among life history, habitat quality, climatic conditions, and individual traits, ecologically similar species can respond differently to the same external factors (Lintott et al., 2016). These differences in responses of species within the same community can provide valuable insights into the relative importance of environmental (e.g. weather), biological factors (e.g. social organisation, diet) and their interaction effects (e.g. phenology) on survival. Few previous studies of survival in bats have considered the role of climate, but warmer spring temperatures and earlier parturition have been associated with increased survival and recruitment (Tuttle 1976; Ransome, 1995; Frick et al., 2010). Analyses that evaluate the relative sensitivities of multiple species within a community can also guide selection of representative bio-indicator taxa and identification of particularly vulnerable species for targeted conservation efforts. Furthermore, effective conservation monitoring of environmental health and population management plans should ideally be based on the demographic rates of the wider community of species inhabiting the area.

Because of capture heterogeneity (systematic variation in detectability between individuals) imperfect (i.e. less than 100%) recapture rates, and temporal emigration (Gimenez et al., 2012) survival in the wild is challenging to estimate. Furthermore, observed differences in population dynamics between species could in fact be the result of species-specific recapture rates, and not reflect true population trends. Similarly, heterogeneity in detection rates in relation to sex or age can affect inferences about life-stage or sex related selective forces (Cubaynes et al., 2010; Fletcher et al., 2012). Finally, some individuals could be temporarily unobservable, for example if they are not using places where they can be observed/captured. In this case, an apparent population crash might reflect this temporal non-detectability, rather than mortality (Peron et al., 2010). To study and understand survival rates from the perspectives of both evolutionary ecology and population dynamics, a unified approach is needed that considers multiple influences on survival while accounting for sources of bias in the survival estimates.

In this study we use a statistical framework that controls for several possible sources of observation bias that may arise in studies of elusive species. We apply this framework to eight years of individually based data on three bat species Daubenton's bat, *Myotis daubentonii*, Natterer's bat, *M. nattereri*, and Brown long-eared bat, *Plecotus auritus* to: (i) obtain robust survival estimates; (ii) test hypotheses on age and sex specific survival in accordance to life-history and social organisation of different species and between sexes; (iii) evaluate the extent to which climatic conditions influence survival; and (iv) evaluate the extent of the difference to which ecologically similar species react to fluctuating environmental factors.

2. Material and methods

2.1. Study species and data collection

Between April and October of 2007–2014, a total of 639 *M. daubentonii* day roosts (containing 1 to 45 individuals/roost), 552 *M. nattereri* day roosts (1–39 individuals/roost) and 210 *P. auritus* day roosts (1–30 individuals/roost) were found within 677 of the 1265 woodcrete boxes (Schwegler™ 2 M or 1B) distributed across the approximately 385 ha of woodland that comprises Wytham Woods (51° 77' N, 1° 33' W).

All three study species are long-lived, with longevity records of 20–30 years having been recorded in the wild (Wilkinson and South, 2002) and show differences in feeding-niche and social organisation. *M. daubentonii* forage primarily over water (Jones and Rayner, 1988), whilst *M. nattereri* and *P. auritus* specialise in gleaned prey within cluttered habitats (Shiel et al. 1991). The two *Myotis* species exhibit sexual segregation during the summer maternity period, with adult females and juveniles roosting in maternity groups. Male *M. daubentonii* are gregarious and roost in bachelor groups, while male *M. nattereri* are typically solitary. *P. auritus* adults of both sexes are found in mixed roosts throughout the summer. All three species have summer weights between 7 and 10 g and adult females typically give birth to a single juvenile each summer (Wilkinson and South, 2002). Juveniles become fully grown and can reach sexual maturity by autumn in the year of their birth. Detectability within our study populations varies with species, sex, age, and social group, but recapture rates are generally high (over 50% of all individuals ringed have been recaptured, with a between encounters interval of less than two years for 95% of recaptures) (DML, unpublished data).

Bats were ringed upon first encounter under a project licence from English Nature/Natural England (2014/SCI/0399 and preceding licences). The age at first capture (juvenile or adult) was determined by examination of the metacarpal epiphyses (Racey, 1974). Bats with unfused epiphyseal joints were classed as juveniles (i.e. born in the current year). Secondary characteristics such as grey colouration of thin pelage, the condition of wing membranes, the presence of a 'chinspot' (Richardson, 1994), weight, nulliparous nipple in females or dark tunica vaginalis and unfilled epididymides (Racey, 1988) in males were also used to identify probable juveniles later in the season when epiphyses were ossified. Adult bats were often distinguishable by their reproductive condition, especially pregnant or parous females. A minority of bats could not be reliably aged and were classified as 'unknown age' at first capture.

2.2. Modelling approach

To obtain robust estimates of winter survival rates, and to test for biological (sex and age) and environmental (weather conditions) factors that might influence survival, while at the same time dealing with capture heterogeneity and problems that arise when bats do not roost in boxes (and are thus in an unobservable state), we used a multi-event mark-recapture modelling approach (Pradel, 2005). In this approach, observations of individuals (called events) are related to the true (but unobservable, or partly observable) state of the individuals thought a series of conditional probabilities. The capture-mark-recapture dataset consisted of capture histories of 1751 *M. daubentonii* (681 females, 1070 males), 795 *M. nattereri* (471 females, 324 males), and 600 *P. auritus* (392 females, 208 males). Data are available online (please see Research Data Availability). Observations, which form a capture history of an individual, were coded as '0' (individual not captured in the season) and '1' (individual captured in the season).

We used a simple survival model and a model with an unobservable ('hidden') state 'Alive but unobservable' (Peron et al., 2010). The second modelling structure allows for the possibility that bats do not use boxes in some years (and thus are not susceptible to capture). The parameters of this model were the probability of survival followed by the emigration to unobservable state (or emigration back to observable state) and detection (only possible when the animal is in the observable state).

We conducted the analysis in four main steps. First, we tested for the presence of capture heterogeneity and identified which factors need to be taken into account for any further model selection to ensure the model fit. Next, we identified the main structural model that describes age, sex, and between-year variation in survival and detection rates. We used this main structural model to test for the influence of weather factors on survival rates. Finally, we tested whether there is any indication that bats migrate to an 'unobservable' state, and, if so, what factors influence the probability of transition to/from the unobservable state.

We tested for different factors that might influence variation in survival, recapture and transition to/from unobservable state by comparing the performance of models with different combinations of age-, social group, sex- and year-effects on each of the parameters of interest. To compare the support for models with different parameter variation we used the Akaike information criterion (Burnham and Anderson, 2002) corrected for the small sample size (QAICc), with the commonly applied cut-off value of 2AICc. We used the normalised QAICc weights to calculate the relative support for each model in the set of considered models. We fitted the models in the software E-SURGE (Choquet et al., 2009a,b). Because of the differences in social organisation, species biology and ecology, and resulting issues with detectability of different species we conducted model selection on each species separately. We report the parameter estimates as obtained by the best model as mean value with the 95% CI.

2.3. Detecting social groups

The studied species have intra-specific non-overlapping roost home ranges per colony (August et al., 2014). Thus, the social group membership could influence detection probability and transition to/from an unobservable state (either because of the specific social group behaviour itself, or because of the structural features of the spatial area a group inhabits). We identified social groups using walktrap community detection and edge betweenness community detection algorithms in R package *igraph* (Csárdi and Nepusz, 2006) according to shared membership of day roosts. We identified six social groups of *M. daubentonii*, seven social groups of *M. nattereri*, and 12 social groups of *P. auritus*.

2.4. Detecting heterogeneity in the capture-recapture dataset – GOF test

To detect the presence of capture heterogeneity (CH) we performed the Goodness-of-fit (GOF) test (Fletcher, 2012) in program U-CARE (Choquet et al., 2005), focusing on the Test 2.CT and Test 3.SR (Pradel et al., 2005; Fletcher, 2012). Test 2.CT tests the hypothesis that there is no 'trap response': all individuals alive at t and $t+1$ have the same probability of being recaptured at $t+1$, regardless of whether or not they were captured at t . Test 3.SR tests the hypothesis that there is no 'transience effect': all individuals captured in year t have the same probability of being recaptured later, regardless of their previous capture history.

Given our study system and the main mechanisms leading to CH (see Appendix S1 in Fletcher et al., 2012), we expected several possible reasons for CH: observation bias, social group, and higher mortality or emigration rates of juveniles. To determine which of these are the most likely cause for CH in our system (if any), we conducted GOF tests on the i) full dataset; ii) each social group; iii) dataset that exclude the first encounter of individuals that were first captured as juveniles; and iv) dataset that exclude the first year of capture for all individuals. If social groups cause CH, we expect group-specific GOF to be non-significant. If juvenile individuals have higher mortality, or higher permanent emigration rates, any transience-effect (if previously present) should disappear when the first capture of juvenile individuals is excluded. If transient individuals are present in the system the transience-effect (if previously present) should disappear when the first capture of all individuals is excluded.

2.5. The main structural model: influence of age, sex, and year on survival and recapture rates

Following our main hypothesis and considering the possible sources of capture bias, we constructed a set of candidate models that incorporated different combinations of the main effects on survival and recapture. Given species-specific results

of the GOF test, and species-specific roosting group composition, we constrained the variation in some of the parameters or their combinations.

To model recapture rates, we considered the possible influence of year, social group, and sex, separately and in different combinations. We considered the social group effect depending on the species-specific social structure. Because *M. daubentonii* and *M. nattereri* exhibit sexual segregation we included social group as a factor that acted independently on adult males and females. *P. auritus* forms mixed roosting groups, thus we kept the effect of social group equal between sexes. After selecting the best recapture structure, we selected the best survival model, by including the influence of year, age (juvenile vs adult), and sex in different combinations.

2.6. Environmental covariates

Four candidate weather covariates were selected that might influence survival during the hibernation period: April to October average temperature, cumulative rainfall (mm) and number of dusks with rain (3 h after sunset), and the average temperature over January and February. Weather conditions experienced during April to October (non-hibernation period) when feeding and breeding occurs can influence survival over the following winter through their effect on body condition before hibernation (Ransome 1995). Temperature and cumulative rainfall are likely to influence the abundance of prey (Anthony et al. 1981; Racey et al. 1987), while the number of wet dusks determines the time available for optimal foraging. Because the average April to October temperature showed a very strong correlation with cumulative rainfall (correlation coefficient -0.90) we excluded cumulative rainfall. We added the three weather covariates (average summer temperature, number of rainy dusks, average winter temperature) to the best final models (or set of models) from the preceding analysis and used this to evaluate the influence of external climatic factors on winter survival probability of juvenile and adult individuals of both sexes, for each species separately. Following Grosbois et al. (2008), we considered the influence of weather covariates on survival rates to be supported if the AICc value of the model with the covariate was a) 2 or more AICc units lower than the AICc of the model with constant survival ($AICc[Scov]-AICc[Sct] < -2$), and b) maximum 2 units higher than the AICc of the model with the full time variation in survival ($AICc[Scov]-AICc[St] < 2$).

2.7. Unobservable state

To test for the possibility that bats might not roost in nest boxes in some years (and thus not be susceptible to capture) we used models with the hidden state 'Alive but unobservable' (Peron et al., 2010). We first tested if there is any support for the model that includes an unobservable state by comparing the AICc of a model allowing for, and not allowing for the presence of the unobservable state. If the model with the unobservable state was supported, we further tested what factors influence the transition to/from the unobservable state: year and weather conditions (average breeding season temperature), previous state (observable or unobservable), social group, age, and sex. Survival and recapture were kept in accordance to the best structural model, however without any between-year variation in these parameters due to common identifiability issues.

3. Results

3.1. Goodness-of-fit test

The results of the GOF tests on the *M. daubentonii* female and male datasets (Table A.1&2, Appendix A) indicated the presence of transient individuals and that part of the capture heterogeneity is caused by social group (Table 1). Thus, in all models for both sexes we included age since first capture (newly and previously captured individuals) as an effect on survival rates (a common procedure to control for transience, Pradel et al. 1997), and included social group as an effect for recapture

Table 1

Summary of significance (Yes = test significant, No = not significant) of the GOF tests components for *M. daubentonii* (Md), *M. nattereri* (Mn), and *P. auritus* (Pla) females and males (3.SR tests for a transience effect, 2.CT tests for a trap response) on four different types of dataset: full dataset (full capture histories), excluding 1st capture (for all individuals), excluding 1st capture if individual was first captured as juvenile, and on each social group separately.

Species and Sex	Test component	Full	Excluding 1st capture	Excluding 1st capture if Juvenile	Social groups
Md females	3.SR	Yes	No	Yes	Yes
	2.CT	Yes	No	Yes	No
Md males	3.SR	Yes	Yes	Yes	Yes
	2.CT	Yes	No	Yes	No
Mn females	3.SR	Yes	No	No	No
	2.CT	Yes	Yes	No	No
Mn males	3.SR	No	—	—	—
	2.CT	No	—	—	—
Pla females	3.SR	No	No	—	No
	2.CT	Yes	No	—	No
Pla males	3.SR	No	No	—	—
	2.CT	No	No	—	—

rates. In model selection for males, we used the dispersion parameter of 1.96, (chi-squared value of the overall GOF with suppressed first encounter, $\chi^2 = 33.33$, divided by the number of its degrees of freedom, 17).

None of the components of the GOF test on the overall dataset of *M. nattereri* males was significant (Table A.4, Appendix A) and we did not conduct further GOF tests. Results on the female dataset (Table A.3, Appendix A) indicated that capture heterogeneity is likely influenced by social group, and/or permanent emigration or higher mortality of juvenile individuals (Table 1). Consequently, we always included social group when modelling recapture rates, and age when modelling survival rates in females. We used the dispersion parameter of 1.82 (29.18/16 df) calculated from the overall GOF on the female dataset with suppressed first encounter.

GOF in *P. auritus* (Table A.5, Appendix A) did not show any lack of fit, trap nor transience effects apart from a weak trap happiness effect in females, which disappeared when the first encounter was removed. As a precaution, model selection was done with the dispersion parameter of 1.63 (35.87/22 df) from the overall GOF on female dataset.

3.2. *Myotis daubentonii*

In *M. daubentonii* the overall best supported structural model included year-, sex- and social group-dependent recapture rates and age-dependent survival rates. There was no clear support for sex-specific nor year-varying survival rates (i.e. several models gained similar support). Including the weather covariates to the adult survival only, juvenile survival only, and on the both adults and juvenile survival, gave support to the model where average breeding season temperature explained a substantial portion of year-variation in survival of adults and juveniles ($\text{AICc}(\text{cov}) - \text{AICc}(\text{constant}) = -4$; $\text{AICc}(\text{cov}) - \text{AICc}(\text{time}) = -3.60$). However, the between-year variation in survival was overall not substantial. Other weather covariates (winter temperature and rainy dusks) were not supported as influential factors for survival rates. Survival was almost twice as high in adults than in juveniles (Fig. 1B) and showed the same between-year variation in adults and juveniles (Fig. 1A).

Temporal pattern in recapture was same in both sexes (see Fig A1, Appendix A, for overall year-specific recapture rates). Recapture was overall higher for females (0.62, 0.56–0.68) than for males (0.49, 0.45–0.54) and the magnitude of the difference depended on social group (Fig A2, Appendix A). In one social group the pattern was reversed (higher recapture in males than in females).

3.3. *Myotis nattereri*

In *M. nattereri*, the best supported structural model included social group, year- and sex-dependent recapture rates, and age- and sex-dependent survival rates. Survival rates were higher in females than males, and higher in adults than juveniles (Fig. 2B): juvenile males had the lowest survival rates (0.48, 0.40–0.59), followed by adult males (0.64, 0.55–0.72), and juvenile females (0.67, 0.59–0.75) to adult females (0.80, 0.76–0.84). None of the weather covariates was selected as an influential covariate affecting survival rates.

Recapture rates were overall only slightly higher in females (0.74, 0.69–0.78) compared to males (0.70, 0.59–0.80). Between-year variation in recapture was different for males (solitary) and females. Recapture rates were dependent on social group in females, and this difference was considerable (the lowest: 0.49, 0.40–0.62; the highest: 0.91, 0.82–0.95, Fig. A2B). There was no support for any of the considered weather covariates to influence recapture rates.

3.4. *Plecotus auritus*

The best structural model in *P. auritus* supported social group-dependent and year varying recapture rates, and time constant, age- and sex- (only for adults) dependent survival rates. Survival was around 20% higher in adult females (0.84, 0.78–0.88) than in adult males (0.68, 0.54–0.79, Fig. 1A). Juvenile males and females survived at the same rate (0.69, 0.53–0.81). None of the weather covariates was selected as an influential covariate in survival rates.

Recapture rates of *P. auritus* were overall very low (between 0.04 and 0.60, Fig. A.1), equivalent for both sexes, and different amongst 12 social groups (Fig. A.2C).

3.5. The unobservable state

Only in *M. daubentonii*, the model that included the presence of an unobservable state (bats not using boxes for roosting) gained better support than the model without the unobservable state (delta AICc –6.46). Further model selection showed that the transition between observable and unobservable state depended on the previous state, sex, social group, and varied between years (Fig. 2) in an additive way (same between-year variation pattern for all social groups, and for males and females). The probability of bats using boxes was overall higher for bats that used boxes in the previous year (0.80, 0.60–0.84), compared to the bats that did not use boxes in the previous year (0.49, 0.29–0.63), was higher in females (0.71, 0.37–0.88) than in males (0.55, 0.24–0.78), and varied between social groups (the lowest 0.66, 0.48–0.80; the highest: 0.94, 0.93–0.95). Use of the boxes did not depend on the weather factors we considered (Apr–Oct average temperature and cumulative rainfall).

Estimates of survival rates remained the same between the models with and without the unobservable state, while estimates of recapture rates changed. Due to limitations to parameter estimability in the models with unobservable states

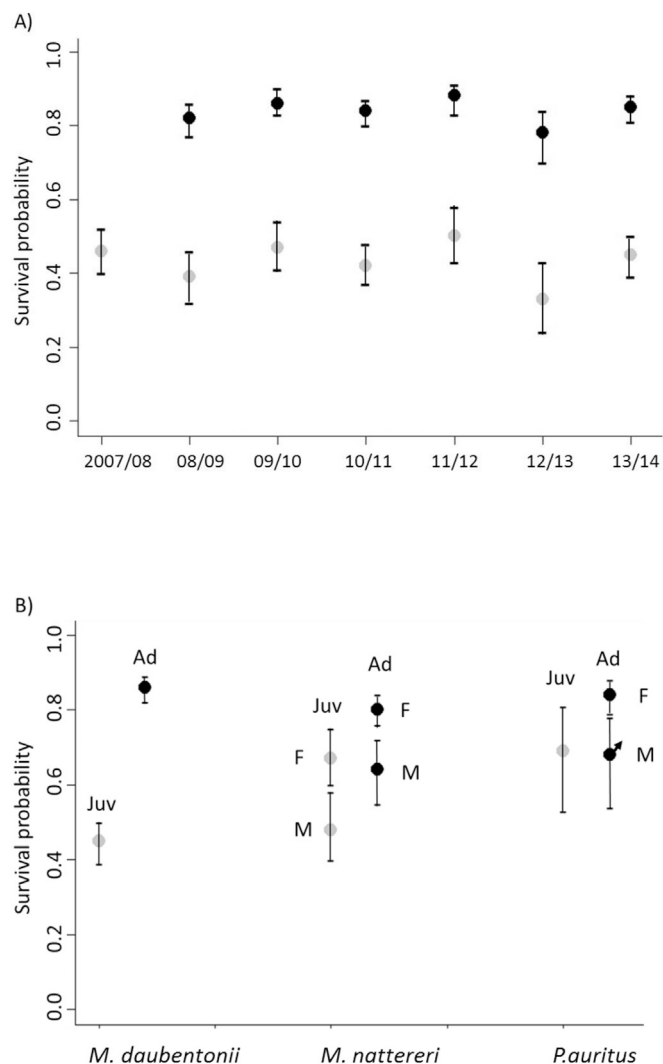


Fig. 1. Estimates of survival probability (with 95% CI) obtained by the best model accounting for the imperfect and biased recapture rates in: A) *Myotis daubentonii*, where survival varied between years, and with age (grey = juvenile bats, black = adult bats), and B) *M. daubentonii* (survival different between adults and juveniles), *M. nattereri* (survival is age and sex specific), and *Plecotus auritus* (survival is age specific, and different between adult females and males).

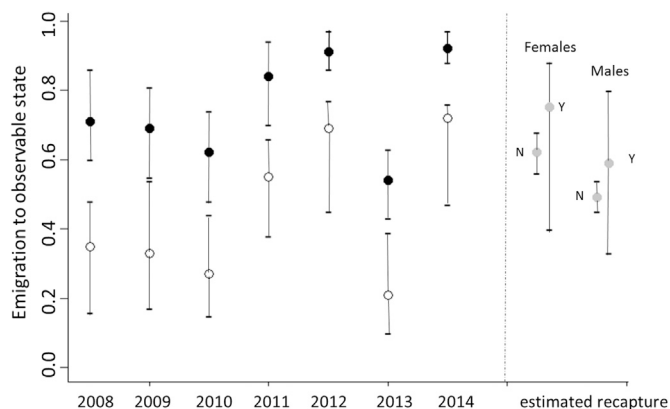


Fig. 2. Estimates of the rates of transition to the observable state (with 95% CI) and recapture of females and males of the *Myotis daubentonii*, according to the previous state (filled circles = observable, empty circles = unobservable) for the transition to the observable state, and whether the presence of the unobservable state was accounted for (Y), or not (N) for the recapture rates.

(Bailey et al. 2010) it was not possible to estimate time-dependent recapture and emigration rates in the same model. We thus compared time-constant recapture rates; these were higher in the model that accounted for the unobservable state (Fig. 2).

4. Discussion

We show (after controlling for the possibility that some individuals are not detectable and for the differences in recapture rates of those individuals that are detectable) that in wild populations of three small mammal species with long life-span: 1) females of two species survive at higher rates than males, 2) adults survive at higher rates than juveniles, 3) survival rates are not dependent on the weather preceding hibernation, nor winter temperature, apart from in *Myotis daubentonii*, where survival is related to the average summer temperature, 4) the magnitude and temporal dependence of the foregoing effects is species-specific, 5) sources of detection bias are not only important to consider as a way to obtain robust estimates of biological rates, but can also be used to inform habitat management and sex-specific behaviours.

4.1. Differences in survival between sexes and age classes are species-specific

Population dynamics of long-lived species such as bats, are greatly influenced by adult survival rates (Monticelli et al. 2013; Gaillard and Yoccoz, 2003), as well as sex-specific survival which determines the viability of the population. However, the majority of studies only use female survival to generate estimates of fluctuations in population size. Results from our study populations, where both females and males are frequently captured, show that sex differences in adult survival rates can be substantial in some species (in *P. auritus* and *M. daubentonii* females survived ~20% better than males). This finding of generally lower survival rates in adult males is in accordance with life-history theory and sex-specific sexual selection (Darwin, 1871; Clutton-Brock, 2007; Toïgo et al., 2007). In polygamous species, such as our studied species, males experience lower survival due to higher intensity of sexual selection. However, we did not detect any difference in sex-specific survival in *M. daubentonii*. The gregarious social system of male *M. daubentonii* (forming large bachelor groups in day roosts) (Safi & Kerth 2007) may increase survival through reduced competition and/or thermoregulatory benefits (roosting in groups can reduce energy expenditure per individual) compared to solitary (and possibly territorial) adult male *M. nattereri* and extra-colony copulation strategy of *P. auritus* (Burland et al. 2001).

Our finding that survival of juvenile bats is lower than adult survival in all three species is in line with the common patterns of lower juvenile survival (Frick et al., 2010; Cam and Aubry, 2011). This difference between adult and juvenile survival was species-specific and highest in *M. daubentonii*, while in the other two species the difference was less pronounced. Differences in foraging strategies and accumulation of fat reserves for overwinter survival may account for the differences we observe in juvenile survival, although higher juvenile dispersal rates (with permanent emigration producing biased apparent survival estimates) may also occur in *M. daubentonii*.

4.2. Influence of climatic conditions on survival

We identified only one environmental factor that predicted survival of only one species, *M. daubentonii*. Survival in both juvenile and adult *M. daubentonii* was higher when summer temperatures were warmer. Breeding phenology (with earlier birth timing in warmer summers) and increased fat accumulation prior to hibernation (due to early breeding and/or increased food availability during warmer conditions) may explain this finding (Ransome 1995; Frick et al., 2010; DML unpublished data). The lack of time-dependent variation in our best survival models for *M. nattereri* and *P. auritus* precludes the inclusion of weather covariates for these species. The relationship between weather and survival has never been more important to understand than in the era of rapid climate change that natural populations are facing now and will face in the future.

4.3. Sources in observation bias can be relevant for conservation of species habitat

Possible sources of recapture bias are especially important to control for in elusive species. As our results show, capture heterogeneity can be the consequence of membership of a social and/or demographic group (e.g. age and/or sex), leading to substantial differences in recapture rates. These differences might be caused by researcher effect (social groups tend to reoccupy the same areas, that are also more often visited), or/and by social groups or sexes using boxes more frequently. Second, recapture of roosting bats can happen only when animals are using the roosting sites researchers visit. At our study site, *M. daubentonii*, seems to be the only species that does not use boxes in every year. However, in our case it seems that accounting for the differences in recapture rates is an adequate way of dealing with the presence of the unobservable state, as only the estimates of recapture rates, but not of survival rates, were affected by the inclusion of unobservable state. These findings can be used to give insights into species ecology and used to direct conservation efforts. For example, in our case, it seems that *M. daubentonii* uses boxes less often than the other two species. This result can guide the future efforts to increase, or decrease the population size of three bat species in our woodland, by increasing or decreasing number of roosting places (nest boxes). Second, because different communities of the same species tend to occupy spatially explicit areas, the extent of box-use can inform on the suitability of the natural habitat (i.e. presence of natural cavities) in these different areas, and thus guide the habitat preservation efforts.

4.4. Further applications of the approach

Our modelling approach, that is likely relevant for the majority of other populations, and easy to implement USING free software (E-SURGE, Choquet et al., 2009a,b), can be used to correct for most likely possible biases. The approach can easily be extended to explore sex- or age-specific survival rates according to habitat features, other environmental factors, or species life-history. Thus, the approach can be used for both, studying evolution ecology of life-history, and studying population viability and demographic rates to guide conservation measures for species and habitats. Second, and as discussed above, exploring the causes of difference in recapture rates amongst different species, different habitats/areas, or in time, can also be used to detect habitat suitability, and thus used in developing conservation management plans.

5. Conclusions

Our results show that ecologically similar species inhabiting the same area can show considerable differences in demography. While average adult survival rates are relatively high and similar in all three studied species, between-year fluctuation in survival, and age and sex differences in survival rates are species-specific. Detecting these differences is important for both evolutionary ecology studies as well as for understating the population demography that is a base for management and conservation action plans. We advocate careful consideration of the possible causes of capture heterogeneity as this heterogeneity is likely to influence the conclusions on important demographic rates.

Our study has, for the first time, accounted for the possibility that bats do not always use the places where researchers look for them. We thus encourage other researchers to think carefully about such pitfalls in their study populations before drawing inferences based on survival rates.

Research data availability

Data used in this article (capture histories) are available under CC BY 4 licence. Mendeley Data: xxxxx.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.gecco.2017.11.009>.

References

- Anthony, E.L.P., Stack, M.H., Kunz, T.H., 1981. Night roosting and nocturnal time budget of the little brown bat, *Myotis lucifugus*: effects of reproductive status, prey density and environmental conditions. *Oecologia* 51, 151–156.
- August, T.A., Nunn, M.A., Fensome, A.G., Linton, D.M., Mathews, F., 2014. Sympatric woodland *Myotis* bats form tight-knit social groups with exclusive roost home ranges. *PloS one* 9 (10), e112225.
- Bailey, L.L., Converse, S.J., Kendall, W.L., 2010. Bias, precision, and parameter redundancy in complex multistate models with unobservable states. *Ecology* 91, 1598–1604.
- Brunet-Rossini, A.K., Austad, S.N., 2004. Studies on bats: a review. *Biogerontology* 4, 211–222.
- Burland, T.M., Barratt, E.M., Nichols, R.A., Racey, P.A., 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., Anderson, D.R., 2002. Model Selection and Multimodel Inference: a Practical Information-theoretic Approach. Springer Verlag, New York.
- Cam, E., Aubry, L., 2011. Early development, recruitment and life history trajectory in long-lived birds. *J. Ornith* 152, 187–201.
- Choquet, R., Lebreton, J.-D., Gimenez, O., Reboulet, A.-M., Pradel, R., 2005. U-CARE: utilities for performing goodness of fit tests and manipulating CAPTURE–REcapture data. *Echography* 32, 1071–1074.
- Choquet, R., Lebreton, J.-D., Gimenez, O., Reboulet, A.-M., Pradel, R., 2009a. U-CARE: utilities for performing goodness of fit tests and manipulating CAPTURE–REcapture data. *Ecography* 6, 101–1074.
- Choquet, R., Rouan, L., Pradel, R., 2009b. Program E-SURGE: a software application for fitting multievent models. *Model. Demogr. Process. Marked Populations* 3, 845–865.
- Clutton-Brock, T., 2007. Sexual selection in males and females. *Science* 318, 1882–1885.
- Csárdi, G., Nepusz, G., 2006. The igraph software package for complex network research. *InterJournal Complex Syst.* 1695.
- Cubaynes, S., Pradel, R., Choquet, R., Duchamo, C., Gaillard, J.M., Leberton, J.D., Marboutin, E., Miquel, C., Reboulet, A.M., Poillot, C., Taberlet, P., Gimenez, O., 2010. Importance of accounting for detection heterogeneity when estimating abundance: the case of French wolves. *Cons. Biol.* 24 (2), 621–626.
- Darwin, C.R., 1871. *The Descent of Man, and Selection in Relation to Sex*. John Murray, London.
- Fletcher, D., 2012. Estimating overdispersion when fitting a generalized linear model to sparse data. *Biometrika* 99, 230–237.
- Fletcher, D., Lebreton, J.-D., Marescot, L., Schaub, M., Gimenez, O., Dawson, S., Slooten, E., 2012. Bias in estimation of adult survival and asymptotic population growth rate caused by undetected capture heterogeneity. *Meth. Ecol. Evol.* 3, 206–216.

- Frick, W.F., Reynolds, D.S., Kunz, T.H., 2010. Influence of climate and reproductive timing on demography of little brown myotis *Myotis lucifugus*. *J. Anim. Ecol.* 79, 128–136.
- Gaillard, J.M., Yoccoz, N.G., 2003. Temporal variation in survival of mammals: a case of environmental canalization? *Ecology* 84, 3294–3306.
- Gimenez, O., Lebreton, J., Gaillard, J., Choquet, R., Pradel, R., 2012. Estimating demographic parameters using hidden process dynamic models. *Theor. Popul. Biol.* 82, 307–316.
- Grosbois, V., Gimenez, O., Gaillard, J.-M., Pradel, R., Barbraud, C., Clobert, J., Møller, A.P., Weimerskirch, H., 2008. Assessing the impact of climate variation on survival in vertebrate populations. *Biol. Rev.* 83, 357–399.
- Hutson, A.M., Mickleburgh, S.P., Racey, P.A., 2001. Microchiropteran Bats: Global Status Survey and Conservation Action Plan. International Union for Conservation of Nature Species Survival Commission (IUCN/SSC). Chiroptera Specialist Group, Gland, Switzerland.
- Jones, G., Rayner, J.M.V., 1988. Flight performance, foraging tactics and echolocation in free-living Daubenton's bats *Myotis daubentonii* (Chiroptera: Vespertilionidae). *J. Zool. Lond.* 215, 113–132.
- Kunz, T.H., Braun de Torrez, E., Bauer, D., Lobova, T., Fleming, T.H., 2011. Ecosystem services provided by bats. *Ann. N. Y. Acad. Sci.* 1223, 1–38.
- Lentini, P.E., Bird, T.J., Griffiths, S.R., Godinho, L.N., Wintle, B.A., 2015. A global synthesis of survival estimates for microbats. *Biol. Lett.* 11, 20150371.
- Lintott, P.R., Barlow, K., Bunnefeld, N., Briggs, P., Roig, C.G., Park, K.J., 2016. Differential responses of cryptic bat species to the urban landscape. *Eco. Evol.* 6 (7), 2044–2052.
- Monticelli, D., Araújo, P.M., Silva, L.P., Ramos, J.A., 2013. Assessing the role of body mass and sex on apparent adult survival in polygynous passerines: a case study of cetti's warblers in central Portugal. *J. Avian Biol.* 45, 75–84.
- O'Shea, T.J., Ellison, L.E., Stanley, T.R., 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, Washington, DC, pp. 297–336.
- Peron, G., Crochet, P.-A., Choquet, R., Pradel, R., Lebreton, J.-D., Gimenez, O., 2010. Capture-recapture models with heterogeneity to study survival senescence in the wild. *Oikos* 119, 524–532.
- Pradel, R., 2005. Multievent: an extension of multistate capture–recapture models to uncertain states. *Biometrics* 61, 442–447.
- Pradel, R., Gimenez, O., Lebreton, J.-D., 2005. Principles and interest of GOF tests for multistate capture recapture models. *Anim. Biodivers. Conserv.* 28, 189–204.
- Pradel, R., Hines, J.E., Lebreton, J.-D., Nichols, J.D., 1997. Capture–recapture survival models taking account of transients. *Biometrics* 53, 60–72.
- Racey, P.A., Speakman, J.R., Swift, S.M., 1987. Reproductive adaptations of heterothermic bats at the northern borders of their distribution. *S. Afr. J. Sci./S.-Afr. Tydskr. Wet* 83, 635–638.
- Racey, P.A., 1974. Ageing and assessment of reproductive status of pipistrelle bats, *Pipistrellus pipistrellus*. *J. Zool.* 173, 264–271.
- Racey, P.A., 1988. Reproductive assessment in bats. In: Kunz, T.H. (Ed.), *Ecological and Behavioral Methods for the Study of Bats*. Smithsonian Institution Press, Washington DC and London, pp. 31–45.
- Ransome, R.D., 1995. Earlier breeding shortens life in female greater horseshoe bats. *Phil. Trans. Soc. Lond. B.* 350, 153–161.
- Richardson, P.W., 1994. A new method of distinguishing Daubenton's bats (*Myotis daubentonii*) up to one year old from adults. *J. Zool.* 233, 307–309.
- Safi, K., Kerth, G., 2007. Comparative analyses suggest that information transfer promoted sociality in male bats in the temperate zone. *Am. Nat.* 170, 465–472.
- Sender, T., Simon, M., 2003. Population dynamics of the pipistrelle bat: effects of sex, age and winter weather on seasonal survival. *J. Anim. Ecol.* 72, 308–320.
- Simmons, N.B., 2005. Order Chiroptera. In: Wilson, D.E., Reeder, D.M. (Eds.), *Mammal Species of the World: a Taxonomic and Geographic Reference*, Vol. 1. Johns Hopkins University Press, Baltimore, MD, pp. 312–529.
- Toïgo, C., Servanty, S., Gaillard, J.M., Brandt, S., Baubet, E., 2007. Disentangling natural from hunting mortality in an intensively hunted wild boar population. *J. Wildl. Manag.* 72 (7), 1532–1538.
- Tuttle, M.D., 1976. Population ecology of the gray bat (*Myotis grisescens*): factors influencing growth and survival of newly volant young. *Ecology* 57, 587–595.
- Wilkinson, G.S., South, J.M., 2002. Life history, ecology and longevity in bats. *Aging cell* 1 (2), 124–131.
- Zeale Matt, et al. "Defra Research Project WM0322."