Global Ecology and Conservation 12 (2017) 263–271

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: http://www.elsevier.com/locate/gecco

Original Research Article

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

Antica Culina*, Danielle M. Linton, David W. Macdonald

Department of Zoology, Wildlife Conservation Research Unit (WildCRU), The Recanati-Kaplan Centre, University of Oxford, Tubney, Abingdon, OX13 5QL, UK

ARTICLE INFO

Article history:
Received 2 September 2017
Received in revised form 27 November 2017
Accepted 27 November 2017
Available online 18 December 2017

Keywords:
Bats
Survival
Multi-event models
Capture heterogeneity

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.

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

* Corresponding author. Netherlands Institute of Ecology (NIOO-KNAW), P.O. Box 50, 6700 AB Wageningen, The Netherlands.
E-mail address: A.Culina@nioo.knaw.nl (A. Culina).

https://doi.org/10.1016/j.gecco.2017.11.009

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 gleaning 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.