A global synthesis of survival estimates for microbats

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Accurate survival estimates are needed to construct robust population models, which are a powerful tool for understanding and predicting the fates of species under scenarios of environmental change. Microbats make up 17% of the global mammalian fauna, yet the processes that drive differences in demographics between species are poorly understood. We collected survival estimates for 44 microbat species from the literature and constructed a model to determine the effects of reproductive, feeding and demographic traits on survival. Our trait-based model indicated that bat species which produce more young per year exhibit lower apparent annual survival, as do males and juveniles compared with females and adults, respectively. Using 8 years of monitoring data for two Australian species, we demonstrate how knowledge about the effect of traits on survival can be incorporated into Bayesian survival analyses. This approach can be applied to any group and is not restricted to bats or even mammals. The incorporation of informative priors based on traits can allow for more timely construction of population models to support management decisions and actions.

1. Introduction

Population models are a powerful tool for assessing the potential effectiveness or likely impacts of management actions. However, robust predictions of population change are commonly hindered by high levels of uncertainty around vital rates, especially survival [1,2]. To maximize the use of population models, it is critical that we develop a better understanding of intrinsic and extrinsic factors that have the biggest impact on survival. One means of doing so is to make better use of modern trait-based approaches [3]. In this process, the relationship between survival rates and readily identifiable traits is quantified across many species. Then, a posterior prediction of the survival rate of a new species can be produced in a Bayesian framework by combining the prior belief of what a species’ survival rate should be based on its traits with evidence in the form of population monitoring data [4].

Microbats (Microchiroptera) make up 17% of the global mammalian fauna [5], but the processes that drive differences in demographics between species and populations are poorly understood. Ample data are available to investigate the relationship between bat traits and annual survival, as bats have been banded since the 1910s [6]. This body of literature represents a substantial, yet underused source of information for bat demographers. However, past reviews of the subject express concern regarding the unrealistic assumptions made by older statistical methods, the impacts that trapping and marking techniques may have had, and the fact that arousal from hibernation during capture may impair survival [7–10]. Given these factors, survival rates reported from past studies should be used with caution.

Here, we conduct a comprehensive review of all published microbat survival estimates and use these to develop a trait-based model of annual survival, using a
mixed-effects approach to address potential biases. We then demonstrate how predictions from trait-based models can be used as informative priors in Bayesian survival analysis using 8 years of bat box monitoring data for two Australian microbat species. In doing so, we show how demographic and trait data from a range of sources can be synthesized to advance our understanding of population processes, add value to individual species survival datasets or improve predictions of species’ responses to management and environmental change.

2. Material and methods

(a) Literature search

We searched the literature for published apparent annual survival estimates ($\phi$, referred to as ‘survival estimates’ herein) of wild bat (suborder: Microchiroptera) populations up to September 2012. In total, we identified 59 papers and obtained 625 survival estimates (electronic supplementary material, table S1), covering 44 species and seven families (electronic supplementary material, table S2). Seventy per cent of these species were vespertilionids, or the evening bats, which are the most widespread and speciose family. Our aim was to acquire baseline estimates that would best represent an average population in an average year, so filter criteria were applied (electronic supplementary material, S1), and following this process 193 estimates were included in the final analysis, 33% of which were for adult females (electronic supplementary material, table S2).

(b) Trait modelling meta-analysis

A Bayesian meta-analysis of the effect of traits on survival was conducted in OpenBUGS through the R package ‘R2OpenBUGS’. We fitted a series of linear mixed-effects models with bat species included in the final analysis, 33% of which were for adult females (electronic supplementary material, table S2). Seventy per cent of these species were vespertilionids, or the evening bats, which are the most widespread and speciose family. Our aim was to acquire baseline estimates that would best represent an average population in an average year, so filter criteria were applied (electronic supplementary material, S1), and following this process 193 estimates were included in the final analysis, 33% of which were for adult females (electronic supplementary material, table S2).

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(c) Nest-box case study

To demonstrate the value of the trait model in survival analysis of individual microbat species, we model a monitoring dataset of two species occupying 60 artificial nest-boxes in two reserves which lie approximately 14 km northeast of Melbourne city centre, Australia. Chalinolobus gouldii (Gould’s wattled bat) is an approximately 14 g vespetilloid that consistently gives birth to twins, and Austronomus australis (the white-striped free-tailed bat), is a molossid that bears singular young and weighs around 38 g [12]. Boxes were manually checked throughout the year (electronic supplementary material, table S4), and individual bats were marked with a microchip or bat band when first encountered. Across 8 years, 876 C. gouldii and 134 A. australis were marked. Data were broken into six-monthly seasons, with summer spanning October–March and winter April–September.

(d) Modelling of apparent seasonal survival ($\phi$) for case study species

We estimated the survival rates for both species using a combination of the microchip and band data within a Bayesian state-space formulation of a Cormack–Jolly–Seber model. Survival parameters were estimated using the program JAGS implemented from R using the package ‘R2jags’. Using the trait

<table>
<thead>
<tr>
<th>parameter</th>
<th>posterior mean</th>
<th>95% credible interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>intercept (sex—female; guild—hawker; season—summer; age—juvenile; method—CJS)</td>
<td>0.624</td>
<td>[0.321, 0.929]</td>
</tr>
<tr>
<td>number of young</td>
<td>-0.527</td>
<td>[-0.962, -0.114]</td>
</tr>
<tr>
<td>age—adult</td>
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<td>[0.367, 0.784]</td>
</tr>
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<td>age—ages pooled</td>
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<td>[-0.071, 0.637]</td>
</tr>
<tr>
<td>sex—male</td>
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<td>[-0.582, -0.099]</td>
</tr>
<tr>
<td>sex—sexes pooled</td>
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<td>[-0.408, 0.254]</td>
</tr>
<tr>
<td>guild—gleaner</td>
<td>0.075</td>
<td>[-0.366, 0.526]</td>
</tr>
<tr>
<td>guild—perch and hunt</td>
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<td>[-0.78, 0.582]</td>
</tr>
<tr>
<td>guild—frugivore/nectarivore</td>
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<td>[0.158, 1.504]</td>
</tr>
<tr>
<td>guild—trawler</td>
<td>0.514</td>
<td>[-0.083, 1.111]</td>
</tr>
<tr>
<td>method—other</td>
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</tr>
<tr>
<td>method—IR/lt/sc</td>
<td>-0.096</td>
<td>[-0.398, 0.196]</td>
</tr>
<tr>
<td>method—bezzen’s approach</td>
<td>-0.255</td>
<td>[-0.877, 0.357]</td>
</tr>
<tr>
<td>method—per cent recapture</td>
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<td>[-0.777, 0.139]</td>
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<td>season—both seasons</td>
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<td>[-0.814, -0.02]</td>
</tr>
<tr>
<td>precision</td>
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<td>[2.138, 3.398]</td>
</tr>
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</table>
model, we predicted apparent survival rates for our study species and converted these to beta informative priors [13]. To obtain posterior estimates of survival and detection, we ran three MCMC chains for 20,000 iterations of the model for each species (see code in the electronic supplementary material, S4). We also used subsampling to explore changes in survival estimation uncertainty with the accumulation of field data over sampling years. For both species, we selected all possible survival data time-series between 3 and 8 years in length and estimated survival rates based on each dataset. Finally, closely related species tend to exhibit similar traits, so phylogeny has the potential to impact on our inference about the relative importance of traits for survival. To test for this, we conducted an additional analysis where superfamily was treated as a fixed effect in the models (detailed in the electronic supplementary material, S3).

3. Results

(a) Trait modelling
The most parsimonious species trait model included the fixed terms guild, number of young, age, sex, season and method, and the species random effect (electronic supplementary material, table S3). The effect of the number of young was the strongest (−0.527, 95% CI [−0.962, −0.114]), such that there is a 17% decrease in survival probability on average for species which bear twins rather than singular young each year (table 1). Annual survival rates estimated from studies of adult female bats conducted in summer were highest (0.774 [0.617, 0.890]), as were those from frugivorous bats which produce fewer young each year (0.893 [0.773, 0.963]), while species that feed by perch and hunt approaches and produce more young each year experienced lowest survival (0.665 [0.411, 0.848]).

(b) Incorporating trait-based prior information into survival analysis
Based on the trait model, it is predicted that the annual survival rate of C. gouldii will range between 0.450 [0.251, 0.658] for juvenile males surveyed in winter and 0.696 [0.517, 0.834] for adult females surveyed in summer, which equates to a mean lifespan of 1.25–2.76 years. Predicted annual survival rates were higher for A. australis, ranging between 0.573
[0.379, 0.758] and 0.793 [0.656, 0.894], or 1.81–4.31 years (electronic supplementary material, table S5). Once these predictions were incorporated into Bayesian survival modelling as an informative prior, the posterior prediction did not divert from the prior substantially, even when a large number of individuals had accumulated in the dataset ($\mu = 0.0004–0.16$). Fewer data were available for A. australis males and juveniles (figure 1c–e,g,i), and we do not believe that the final estimates for these groups are robust.

4. Discussion

Here, we have drawn on a century’s worth of bat mark–recapture efforts to identify traits that influence survivorship. We found that the age and sex of an individual has a strong effect on survival. High juvenile mortality is standard across many species, but the effect of sex is interesting. Lower male survival may be explained by the fact that the majority of the species in our trait model were vespertilionids, for which natal dispersal is generally male-biased [14]. During this time, there may be increased mortality as a result of predation and the energetic costs of movement [15,16]. Male vespertilionids are also usually smaller [17] and lose energy reserves faster than females during hibernation [18].

The species-specific traits that had the strongest effect on survival were the number of young produced and guild (table 1). The latter was driven by high survivorship of frugivores, which may be because they spend comparatively less time foraging [19]. With regards to number of young, bats are enormous at birth, constituting a 15–30% of the mass of the postpartum mother [20], so young represent a large energetic investment [7]. These findings are comparable to those of the two previous studies which linked bat traits to survival [19,21] but only focused on a handful of species, or maximum longevity records, which reflect survival rates of exceptional individuals rather than the population as a whole. Some groups may also experience higher survival rates owing to phylogenetic effects, and there was some evidence that this is the case for species in the Rhinolophoidea superfamily (detailed in the electronic supplementary material, S3). The trait model predictions represent a good starting point for many bat species, though they will be most reliable for adult female vespertilionids owing to the inherent biases in the literature.

The analyses presented here can act as a template for any taxa; as new empirical evidence accumulates, models of survival can be updated and refined, and with this, predictions will become more reliable for a broader range of species. Divergence between estimates of survival obtained from field data and those obtained from trait model predictions could act as an early warning that a population is undergoing decline, or that certain species are unusual in the way that their survival relates to their traits. Increases in precision obtained from knowledge of the relationship between traits and vital rates can be equivalent to the collection of several years of data [4], which represents a potentially large saving on survey time and resources.

We do not wish to suggest that the existence of trait models in any way diminishes the need for good empirical data to underpin survival estimates for viability analysis and the range of management applications it serves. The ideal situation is that existing ecological knowledge is combined with high-quality empirical data to provide reliable and timely inputs to viability assessment and management decisions. However, mark–recapture studies are expensive and time-consuming [8] and are infeasible for many species where individuals are difficult to capture [10]. It will simply not be possible to collect detailed demographic data for all species facing decline. By taking advantage of the learnings of past studies, trait-based modelling allows us to better understand the processes driving communities and populations.

Ethics. Bat handling was carried out under permits from the University of Melbourne Animal Ethics Committee (ethics ID 0701162) and the Department of Sustainability and Environment (research permit no. 10003144).

Data accessibility. Data used in the trait modelling are available in the electronic supplementary material, S4. The data file for the mark–recapture analyses, ‘CG_Bat_Dat.RData’ are available from the Dryad digital repository: http://dx.doi.org/10.5061/dryad.78m34.

Author contributions. P.L. designed the study and conducted the literature review, T.B. and P.L. analysed the data and wrote the code, S.G. and L.G. provided the mark–recapture data, B.W. provided guidance on study design and analysis, all wrote the manuscript.

Competing interests. We declare we have no competing interests.

Funding. Financial support for this project was provided by the National Environmental Science Program and the Holsworth Wildlife Research Endowment. B.W. is supported by an ARC Future Fellowship (FT100100819).

Acknowledgements. We acknowledge those who assisted in the collection of field data, Lindy Lumsden and Graeme Coulson for supervision and Michael McCarthy for helpful comments on the manuscript.

References


