



Importance of accounting for phylogenetic dependence in multi-species mark–recapture studies



Fitsum Abadi^{a,b,*}, Christophe Barbraud^c, Dominique Besson^c, Joël Bried^d, Pierre-André Crochet^a, Karine Delord^c, Jaume Forcada^e, Vladimir Grosbois^f, Richard A. Phillips^e, Paul Sagar^g, Paul Thompson^h, Susan Waughⁱ, Henri Weimerskirch^c, Andrew G. Wood^e, Olivier Gimenez^a

^a Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175, campus CNRS, 1919 route de Mende, 34293 Montpellier Cedex 5, France

^b Animal Demography Unit, Department of Biological Sciences and Department of Statistical Sciences, University of Cape Town, Rondebosch 7701, South Africa

^c Centre d'Etudes Biologiques de Chizé, UPR 1934 CNRS, 79360 Villiers en Bois, France

^d Departamento de Oceanografia e Pescas, Centro do IMAR da Universidade dos Açores, 9901-862 Horta, Açores, Portugal

^e British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK

^f Centre de coopération internationale en recherche agronomique pour le développement (CIRAD), Département ES, UR22, TA C22/E, Campus international de Baillarguet, 34398 Montpellier Cedex 5, France

^g National Institute of Water & Atmospheric Research Ltd., P.O. Box 8602, Christchurch, New Zealand

^h University of Aberdeen, Institute of Biological & Environmental Sciences, Lighthouse Field Station, Cromarty IV11 8YL, UK

ⁱ Museum of New Zealand Te Papa Tongarewa, P.O. Box 467, Wellington, New Zealand

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ABSTRACT

Species in comparative demography studies often have a common phylogenetic or evolutionary ancestry and hence, they cannot fully be treated as independent samples in the statistical analysis. Although the serious implication of ignoring phylogeny has long been recognized, no attempt has been made so far to account for the lack of statistical independence due to phylogeny in multi-species mark–recapture comparative demography studies. In this paper, we propose a Bayesian hierarchical model that explicitly accounts for phylogenetic dependence among species, and to correct for imperfect detection, which is a common phenomenon in free-ranging species. We illustrate the method using individual mark–recapture data collected from 16 seabird species of the order Procellariiformes. Data on body mass and phylogeny of these species are compiled from literature. We investigate the relationship between adult survival and body mass with and without accounting for phylogeny. If we ignore phylogeny, we obtain a positive survival–body mass relationship. However, this relationship is no longer statistically significant once phylogenetic dependence is taken into account, implying that survival may actually depend on an unmeasured variable that is correlated with body mass due to a shared dependence on phylogeny. The proposed model allows the integration of multi-species mark–recapture data and phylogenetic information, and it is therefore a valuable tool in ecological and evolutionary biology.

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1. Introduction

Reliable estimates of demographic parameters are crucial to understand population dynamics of wildlife populations (Lebreton et al., 1992; Williams et al., 2002). Over the past few decades, important methodological advancements have improved the estimation of demographic parameters from mark–recapture data whilst

accounting for imperfect detection. Mark–recapture methods have successfully been used, for instance, to estimate age-specific survival probabilities (Lebreton et al., 1992), recruitment and dispersal (Pradel, 1996; Lebreton et al., 2003; Péron et al., 2010), and population abundance (Pollock et al., 1990; Cubaynes et al., 2010). In addition, these methods are widely used for exploring how demographic parameters are affected by environmental covariates (e.g., Lebreton et al., 1992; Altwegg et al., 2003; Gimenez et al., 2006). However, these models have all focused on studying the demography of a single population or species.

Traditionally, multi-species demographic studies have been performed in two steps: (1) demographic parameters of each species are estimated independently, and (2) comparisons of the

* Corresponding author at: Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175, campus CNRS, 1919 route de Mende, 34293 Montpellier Cedex 5, France. Tel.: +33 (0) 467613211.

E-mail address: fitaba@gmail.com (F. Abadi).

estimates of each species are conducted (Johnston et al., 1997; Peach et al., 2001). However, this ad hoc approach is inefficient as it ignores the uncertainty associated with the estimates and also fails to take account of inter-species variation (Papadatou et al., 2012). More recently, hierarchical (random effects) mark–recapture models have been proposed to account for inter-species variation and to overcome the constraints of this ad hoc approach (Lahoz-Monfort et al., 2011; Papadatou et al., 2012; Péron and Koons, 2012).

Despite these advances, multi-species comparative demography studies have ignored that some species have a common phylogenetic or evolutionary ancestry (Harvey and Pagel, 1991; Freckleton et al., 2002; Paradis and Claude, 2002; Bried et al., 2003; Freckleton, 2009). In the strict sense, this phylogenetic dependence implies that species cannot be treated as independent units, hampering the application of conventional statistical procedures (e.g., generalized linear models) in a general non-mark–recapture context (Freckleton et al., 2002; Paradis and Claude, 2002). Furthermore, other studies have highlighted that ignoring phylogenetic correlation among species can lead to an overestimation of the precision of parameter estimates and hence flawed inferences (Harvey and Pagel, 1991; Halsey et al., 2006; Ives and Zhu, 2006; Freckleton, 2009). Some papers have suggested using alternative methods such as generalized least squares (GLS) and generalized estimating equations (GEE) to account for correlations among species due to phylogeny (Garland and Ives, 2000; Paradis and Claude, 2002; Ives and Zhu, 2006). These methods are applied to study the relationship between dispersal and population synchrony (Paradis and Claude, 2002), to investigate the relationship between adult life expectancy and body mass (Bried et al., 2003), and to determine the relationship between home–range area and body mass with simulated data (Ives and Zhu, 2006). Despite the serious implications of ignoring phylogeny, there appear to be no published works that account for phylogeny in the context of multi-species mark–recapture studies.

The main goal of this paper is therefore to develop a Bayesian hierarchical model for comparative demography analysis, which explicitly integrates phylogeny in the estimation of survival probability whilst accounting for imperfect detection. Here we focus on the estimation of survival but, in principle, our method is valid for other demographic parameters. In addition, our method is quite flexible, and can assess the impact of environmental covariates or allometric relationships on demographic parameters. We illustrate the application of our model using individual mark–recapture data for 16 seabird species in the order Procellariiformes (i.e., albatrosses, petrels and shearwaters). Bried et al. (2003) studied the relationship between adult life expectancy (i.e., derived from the survival estimates) and body mass of Procellariiformes accounting for phylogeny using the GLS method. However, they ignored the uncertainty in the adult life expectancy and treated it as known quantities in the GLS regression analysis. Such a two-step approach of ‘doing statistics on statistics’ has been repeatedly criticized in the literature (e.g., Link, 1999; Grosbois et al., 2008). Consequently, we used our new statistical approach that utilizes the mark–recapture data and phylogenetic information simultaneously to examine the relationship between survival and body mass of the order Procellariiformes. We compared the parameter estimates obtained from the models with and without phylogeny. We provide the R and WinBUGS codes for implementing the models in the appendix.

2. Multi-species mark–recapture model accounting for phylogeny

In this section, we first build the likelihood for mark–recapture data based on the standard Cormack–Jolly–Seber (CJS) model (Lebreton et al., 1992). Next, we introduce a hierarchical model that takes into account phylogeny in the estimation of survival

probability. We then briefly discuss how this model can be implemented within a Bayesian framework.

2.1. Likelihood for mark–recapture data

The standard mark–recapture protocol yields capture histories with a sequence of ones (mark or recaptured/resighted) and zeroes (not captured or seen) for individuals in the study population. We assume that such individual mark–recapture histories collected from several related species are available. For each species, we considered the general Cormack–Jolly–Seber (CJS) model that provides estimates of time-varying survival (ϕ_t) and recapture (p_t) probabilities (Lebreton et al., 1992). For computational purpose, we used minimal sufficient statistics for the CJS model under the form of an m -array (Burnham et al., 1987; Lebreton et al., 1992). We denote the m -array entries by m_{ij} , $i = 1, 2, \dots, T-1$, $j = i+1, 2, \dots, T+1$ and T is the number of sampling occasions, which may vary from species to species. The m -array, m_{ij} , represent the number of individuals released at occasion i and recaptured for the first time at occasion j for $j \leq T$, and $m_{i,T+1}$ denotes the number of individuals never recaptured following release at occasion i . The CJS model likelihood is then constructed for each species based on a product of multinomial distributions assuming each row of the m -array is independent and for which the cell probabilities are functions of both survival and recapture probabilities (Lebreton et al., 1992).

2.2. Incorporating phylogeny

To account for phylogenetic dependence among species, we proposed the following hierarchical model with a logit link function for the survival probability.

$$\begin{aligned} \text{logit}(\phi_{t,s}) &= \mu + \eta_s + \varepsilon_{t,s} \\ \eta_s &\sim \text{MVN}(\mathbf{0}, \delta^2 \Sigma), \quad \varepsilon_{t,s} \sim N(0, \sigma_s^2) \end{aligned} \quad (1)$$

where $\phi_{t,s}$ is the survival probability of species s between years $t-1$ and t , μ is the overall mean survival probability, $\varepsilon_{t,s}$ is a normally distributed random term with species-specific temporal variance (σ_s^2), and η_s is a random term that depends on the species and is distributed as a multivariate normal with variance–covariance matrix $\delta^2 \Sigma$. Here Σ is derived from the phylogenetic tree and treated as fixed known quantity in our model (Ives and Zhu, 2006; Revell, 2010; Blomberg et al., 2012; Hansen and Bartoszek, 2012). By scaling Σ to a height of one, we can interpret δ^2 as the residual variance (de Villemereuil et al., 2012). We used hypothetical data to illustrate the computation of Σ (Fig. 1). The off-diagonal values in Σ (i.e., covariance) always increase as the phylogenetic distance decreases (Freckleton et al., 2002). That is, the greater the shared history between the species, the higher the values in Σ . As shown in Fig. 1, the main diagonal (i.e., the variance) in Σ is computed as the distance from the root to the tip (e.g., $S_{11} = 6(4+2)$, $S_{55} = 6(2+3+1)$) and the off-diagonal elements (i.e., the covariance) are the total shared path lengths between each pair of species (e.g., $S_{12} = 4$, $S_{35} = 5 = (2+3)$, $S_{15} = 0$ (share no path lengths)). By setting Σ to an identity matrix (i.e. ones on the diagonal and zeroes elsewhere), the effect is reduced to a species random effect that assumes no phylogenetic dependence among species (e.g., Papadatou et al., 2012). Note that Pagel’s λ can be incorporated into Σ to measure the strength of phylogenetic signal (e.g., Revell, 2010; de Villemereuil et al., 2012).

Our model can also be easily extended to assess the relationship between survival and covariates (e.g., body mass). This is of

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