



Developing population models with data from marked individuals



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ABSTRACT

Population viability analysis (PVA) is a powerful tool for biodiversity assessments, but its use has been limited because of the requirements for fully specified population models such as demographic structure, density-dependence, environmental stochasticity, and specification of uncertainties. Developing a fully specified population model from commonly available data sources – notably, mark–recapture studies – remains complicated due to lack of practical methods for estimating fecundity, true survival (as opposed to apparent survival), natural temporal variability in both survival and fecundity, density-dependence in the demographic parameters, and uncertainty in model parameters. We present a general method that estimates all the key parameters required to specify a stochastic, matrix-based population model, constructed using a long-term mark–recapture dataset. Unlike standard mark–recapture analyses, our approach provides estimates of true survival rates and fecundities, their respective natural temporal variabilities, and density-dependence functions, making it possible to construct a population model for long-term projection of population dynamics. Furthermore, our method includes a formal quantification of parameter uncertainty for global (multivariate) sensitivity analysis. We apply this approach to 9 bird species and demonstrate the feasibility of using data from the Monitoring Avian Productivity and Survivorship (MAPS) program. Bias-correction factors for raw estimates of survival and fecundity derived from mark–recapture data (apparent survival and juvenile:adult ratio, respectively) were non-negligible, and corrected parameters were generally more biologically reasonable than their uncorrected counterparts. Our method allows the development of fully specified stochastic population models using a single, widely available data source, substantially reducing the barriers that have until now limited the widespread application of PVA. This method is expected to greatly enhance our understanding of the processes underlying population dynamics and our ability to analyze viability and project trends for species of conservation concern.

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1. Introduction

Assessing how close species are to extinction is one of the important first steps in preventing their extinction, which is a main goal of biodiversity conservation. One of the commonly used tools for making such assessments, as well as for evaluating the effectiveness of conservation actions, is population viability analysis (PVA). Using stochastic population demographic models, PVA projects population dynamics and calculates measures of viability such as extinction risk under current conditions and future changes in human impacts and management (Morris and Doak, 2002). Although uncertainties often exist, predictions made by PVA tend to be unbiased, contrary to subjective judgments

made by experts, which makes it an effective tool in conservation science (McCarthy et al., 2004). Despite its advantages, the use of PVA is hampered by scarcity of reliable estimates of demographic parameters for most species. Mark–recapture data, collected by repeatedly capturing individuals that are uniquely and permanently marked at their initial capture (e.g., using tags or rings), continue to be of great value for estimating basic demographic parameters such as survival rates, abundance, and fecundities (Jolly, 1965). In addition to the rapid increase in the availability of long-term mark–recapture datasets for various taxa from geographically extensive and collaborative trapping efforts, new tools and methods for analysis of mark–recapture data enable more accurate and precise parameter estimation (Francis et al., 2014; King, 2012; Lindberg, 2012). Despite this progress, most mark–recapture analyses focus on estimating only survival parameters (Williams et al., 2002). Results from such analyses are useful for addressing a variety of ecological questions, but the general paucity of estimates for other demographic parameters, such as fecundity, temporal

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variability, and density-dependence in survival and fecundity, have hindered the development of fully specified population models that can be used to project future abundances and analyze population viability. Here, we explain the key elements that are required in building a population model and the common challenges for estimating such parameters.

1.1. Fecundity

Fecundity is a measure of the reproductive rate of an organism, species, or population and is defined as the per-capita number of offspring produced in each life history stage during a breeding season. From a population modeling perspective, fecundity estimates and survival estimates are both important; however the literature on estimating fecundity based on mark–recapture data is sparse in contrast to the vast literature on estimating survival. Fecundity estimates for birds have traditionally been obtained from nest surveys, in which the number of nestlings per nest or a similar quantity is measured. However, nest survey data require extensive field effort and are often unavailable. As an alternative, the ratio of juveniles to adults is conventionally used as an index of productivity (Flanders-Wanner et al., 2004; Peery et al., 2007). However, in population models, true fecundity, rather than an index, is required. The uncorrected juvenile:adult ratio is likely negatively biased, since juvenile birds and other wildlife are generally less observable than their adult counterparts. This bias can be corrected by using the ratio of capture probabilities between juveniles and adults, which are a byproduct of standard likelihood-based mark–recapture analysis (e.g., Cormack–Jolly–Seber model for estimating age-structured survival rates). In the context of population modeling, juvenile:adult ratio corrected in this way provides a superior estimate of population-level fecundity than estimates derived from labor-intensive nest surveys. Even when nest data are available, critical pieces of information, such as the proportion of breeding individuals in the population and the number of re-nesting attempts may not be available. Population models require fecundity to be estimated across all individuals in the population, including those that fail to produce eggs, and over all nesting attempts within a breeding season. If failed nests lead to additional nesting attempts, reproductive measures averaged over all observed nest attempts (such as fledglings per nest) underestimate fecundity. If only some individuals breed, measures such as fledglings per breeder overestimate fecundity, unless the population model explicitly models breeder and non-breeder stages separately and includes the rates of transition between them.

1.2. Survival

Survival rate is defined as the proportion of individuals of a given age or life stage in a population that survive from one breeding season to the next. Standard mark–recapture models for estimating survival do not distinguish mortality from emigration, and therefore estimate “apparent survival” (φ), which is the joint probability of surviving and remaining within the study area (and therefore available for recapture). However, survival and dispersal are distinct ecological processes that are almost always modeled separately in population models. Therefore, estimates of true, rather than apparent survival rates are needed. When all individuals are recaptured and their locations are known, multi-state or spatially explicit capture–recapture (SECR) methods can be used to estimate both survival and emigration rates (Ergon and Gardner, 2014; Schaub and Royle, 2014). Alternatively, if a dispersal kernel can be estimated, survival can be corrected for estimated dispersal out of the study area (Gilroy et al., 2012). However, when location information is not available, or its spatial resolution is too coarse to estimate dispersal rate, alternative approaches are required.

1.3. Temporal variability

Temporal variability in demographic parameters represents effects of unpredictable changes in the environment on population-level vital rates, and therefore, estimates of this variation are required for making stochastic projections. In all but the lowest abundance populations, environmental stochasticity exerts a greater influence on population-level risk metrics (e.g., extinction risk) than demographic stochasticity (Lande, 1993). Calculating unbiased estimates of temporal variability presents multiple challenges: first, it requires many years of data collection, and most importantly, one needs to separate sampling error from natural variability (also referred to as “process variance”). Although methods are available to estimate sampling error in survival from mark–recapture data (Gould and Nichols, 1998) and in both survival and fecundity from census data (Akçakaya, 2002), most studies do not use or describe in detail such methods. In addition to estimating process variance, sampling error determines uncertainty in model parameters, therefore, it must be used to estimate upper and lower bounds for model parameters to perform uncertainty analysis (e.g., sensitivity analysis; Chu-Agor et al., 2012; Curtis and Naujokaitis-Lewis, 2008).

1.4. Density

Negative feedbacks between vital rates and intra-specific densities are a key driver of abundance dynamics in most wild populations (Akçakaya et al., 1999; Burgman et al., 1993). Therefore, explicit specification of survival and fecundity rates across an ecologically realistic range of intra-specific densities is essential for most population modeling applications. Without explicit modeling of the density effects, the average stage matrix allows only very short-term projections, even if survival and fecundity are estimated over a long time period.

1.5. A comprehensive method

We present a comprehensive yet practical method for generating a fully specified, stochastic matrix-based population model based only on long-term mark–recapture data (Fig. 1). We used standard Cormack–Jolly–Seber (CJS) models to estimate stage-specific apparent survival rates (φ) and capture probabilities (p). We developed and applied several new approaches for generating unbiased estimates of fecundity (F), true stage-structured survival rates (S), temporal variability in survival and fecundity, and density-dependence functions for survival and fecundity. We used confidence intervals of parameter estimates to calculate parameter uncertainties for use in global (multivariate) sensitivity analysis. This method allows for estimating all parameters needed in a population model based on a single source of long-term mark–recapture data. This greatly eases the process of specifying a population model that would otherwise require additional independent datasets such as nest surveys and population count data.

2. Methods

2.1. Mark–recapture data: the MAPS project

We used mark–recapture data from the Monitoring Avian Productivity and Survivorship (MAPS) program (<http://www.birdpop.org/pages/maps.php>). The MAPS program, driven by collaborative effort among public agencies, non-governmental groups, and volunteers, comprises a network of ca. 1200 banding stations distributed across the US and Canada. Multiple mist nets are deployed at each station at least once per 10-day interval throughout the breeding period, where all newly captured birds are assigned to a unique band ID, all captures are identified to species, sex, and age (hatching year vs. adult), and multiple additional variables are recorded (e.g., mass, body condition). In MAPS, capture history data are now available for > 180 species of land birds across North America. To demonstrate our approach, we selected 9 focal species that

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