



Review

Synthesizing multiple data types for biological conservation using integrated population models[☆]



Elise F. Zipkin^{a,b,*}, Sarah P. Saunders^a

^a Department of Integrative Biology, Michigan State University, East Lansing, MI 48824, USA

^b Ecology, Evolutionary Biology, and Behavior Program, Michigan State University, East Lansing, MI 48824, USA

ARTICLE INFO

Keywords:

Bayesian analysis
Capture-recapture data
Integrative modeling
Management
State-space model
Threatened species

ABSTRACT

Assessing the impacts of ongoing climate and anthropogenic-induced change on wildlife populations requires understanding species distributions and abundances across large spatial and temporal scales. For threatened or declining populations, collecting sufficient broad-scale data is challenging as sample sizes tend to be low because many such species are rare and/or elusive. As a result, demographic data are often piecemeal, leading to difficulties in determining causes of population changes and developing strategies to mitigate the effects of environmental stressors. Thus, the population dynamics of threatened species across spatio-temporal extents is typically inferred through incomplete, independent, local-scale studies. Emerging integrative modeling approaches, such as integrated population models (IPMs), combine multiple data types into a single analysis and provide a foundation for overcoming problems of sparse or fragmentary data. In this paper, we demonstrate how IPMs can be successfully implemented by synthesizing the elements, advantages, and novel insights of this modeling approach. We highlight the latest developments in IPMs that are explicitly relevant to the ecology and conservation of threatened species, including capabilities to quantify the spatial scale of management, source-sink dynamics, synchrony within metapopulations, and population density effects on demographic rates. Adoption of IPMs has led to improved detection of population declines, adaptation of targeted monitoring schemes, and refined management strategies. Continued methodological advancements of IPMs, such as incorporation of a wider set of data types (e.g., citizen science data) and coupled population-environment models, will allow for broader applicability within ecological and conservation sciences.

1. Introduction: species in peril and data collection challenges

Biodiversity loss is one of the most pressing environmental problems, impacting ecosystem functions, community dynamics, and human and wildlife health (Cardinale et al., 2012; Lefcheck et al., 2015). Understanding the impacts of anthropogenic change on wildlife populations necessitates research at large spatial and temporal scales (e.g., Alroy, 2015). Together with traditional local-scale research, regional to range-wide data are fundamental for effective conservation (Keith et al., 2012; Edgar et al., 2016), particularly because many relationships between environmental variables and ecological patterns are only evident when broad-scale data are considered (e.g., Mora et al., 2011; Pardikes et al., 2015). However, in an era when macroscale conservation needs are not met due to limited research funding, it is not often possible to obtain the necessary population-level and demographic data from a single collection effort (Loss et al., 2015).

Even for threatened species that have restricted ranges, collecting

data and estimating the ecological reasons for declines are challenging because such species tend to be rare and/or elusive, which makes obtaining sufficient data for standard population models difficult (Lomba et al., 2010; Harris et al., 2015). Data on demographic parameters (i.e., survival, recruitment, and immigration) are necessary to develop mechanistic models, which allow for a process-oriented approach to evaluating population trends and determining causes of declines (Véran and Lebreton, 2008). Yet, demographic data on small or declining populations are often scarce because collection is intermittent and typically necessitates long study periods, sample sizes are low, and researchers may hesitate to catch and mark individuals if doing so may cause harm (Lomba et al., 2010; Platts et al., 2014). These conditions result in limited longitudinal data to model population viability, extrapolate inference at large scales, and detect significant changes in population trends within time frames for appropriate management actions (Taylor et al., 2007; Mosnier et al., 2015). As a result, understanding the population dynamics of threatened species, and indeed

[☆] Statement of authorship: EFZ and SPS jointly conceived of the idea for this review and participated in all aspects of writing.

* Corresponding author at: Department of Integrative Biology, Michigan State University, East Lansing, MI 48824, USA.

E-mail address: ezipkin@msu.edu (E.F. Zipkin).

most species, is typically either inferred through independent local-scale studies (Thogmartin and Knutson, 2007; Rushing et al., 2016) or achieved through large-scale niche modeling of distribution data that is correlative with limited power to elucidate underlying mechanisms (Kearney and Porter, 2009; Buschke et al., 2015). Emerging integrative modeling approaches that combine multiple data sources across spatio-temporal scales into a single analysis provide a foundation for overcoming these problems and allow research to scale from local biological processes to regional-level patterns, where management occurs (Pacifi et al., 2017).

In this paper, we review integrated population models (IPMs), an approach to combine multiple data types in a unified analysis to study the dynamics of animal populations. We compiled and collated peer-reviewed articles, textbook chapters, and government technical reports on IPMs that were relevant to biological conservation. Our paper builds on reviews by Schaub and Abadi (2011) and Maunders and Punt (2013), both of which focus on taxa-specific IPMs. Literature was searched through Google Scholar and ISI Web of Knowledge, using terms such as: ‘integrated population model’ and ‘integrative model’, coupled with ‘biological conservation’ and ‘population management’. We also checked the bibliographies of relevant papers to identify further pertinent literature. We outline the key components of IPMs, synthesize the advantages of this approach for improved biological conservation and ecological inference, and highlight the latest theoretical and technical developments in IPMs that are explicitly relevant to the ecology and management of threatened species. We conclude with a perspective on several potential avenues of IPM advancement related to the fields of ecology and conservation science.

2. The power of integrated population models

Integrative modeling generally refers to the incorporation of multiple (1) data types on a single target population, (2) analytical models or methods, or (3) predictions from multiple theories into a model, thus ‘integrating’ several pieces of information into a single modeling framework. The combined analysis of all available information allows for an understanding of processes underlying ecological and demographic responses to environmental variability (Brown and Collopy, 2013; Grace et al., 2016; Fletcher et al., 2016). Conclusions that are inferred from independent analyses can be hindered by an inability to accurately account for error in parameter estimates (Schaub and Abadi, 2011), spatio-temporal correlations in covariate effects (Lieury et al., 2015), and possible biases in trend estimates (Tempel et al., 2014). Integrative modeling has the potential to resolve these issues by incorporating all available data into a single analysis and thus properly accounting for spatio-temporal variation and uncertainty in parameter estimates (Dorazio, 2014; Grace et al., 2016).

Integrated population models (IPMs) are a well-developed subset of integrative models in which the analysis of the joint likelihood of two or more datasets allows for simultaneous estimation of population abundance and the processes leading to population change. IPMs provide an approach for addressing issues of sparse or fragmentary population data by incorporating multiple data types (e.g., census, productivity, telemetry) into a single, dynamic model of the target population (Fig. 1; Schaub and Abadi, 2011). IPMs typically include the unified analysis of data on population abundance, trajectory, or structure (e.g., census, count, and/or occupancy data) and demographic parameters (e.g., productivity data, capture-recapture data, dead recovery data; Besbeas et al., 2002; Abadi et al., 2010a; Schaub and Abadi, 2011). The use of IPMs in animal ecology began in the early 2000s (Besbeas et al., 2002; Besbeas et al., 2003; Brooks et al., 2004; reviewed in Schaub and Abadi, 2011), although variations of these models were used in fisheries research and management as early as the 1980s (Fournier and Archibald, 1982; reviewed in Maunders and Punt, 2013). Fisheries IPMs have generally focused on stock assessment to determine harvest quotas and are not examined here (except as they may pertain to the conservation

of a particular species). However, early work on integrated fisheries modeling greatly advanced previous population assessment approaches, which relied on independent data summaries of disparate stock data (Maunder and Punt, 2013). These primary methodological advances paved the way for subsequent inclusion of increasingly diverse data types and development for additional taxa (Catchpole et al., 1998; Gauthier and Lebreton, 2004).

A key feature of IPMs is the ability to model a population's underlying dynamics, including important life history elements, by explicitly accounting for the processes that lead to population changes over time (e.g., birth/death and immigration/emigration; Besbeas et al., 2002; Brooks et al., 2004; Schaub et al., 2007). The objective of IPMs is to incorporate as much mechanism as possible to estimate a population's trajectory and assess the primary factors causing changes in abundance and demographic rates (Schaub and Abadi, 2011). By incorporating all available data on a population, IPMs overcome limitations of traditional independent analyses (Véran and Lebreton, 2008; Tempel et al., 2014; Hostetler et al., 2015) and allow for (1) the simultaneous estimation of demographic parameters and population trajectories, while standardizing the error structure across different data types and accounting for multiple sources of uncertainty (Besbeas et al., 2002; Schaub and Abadi, 2011); and (2) the direct linking of variation in population abundance to changes in stage-specific vital rates and covariate effects (Johnson et al., 2010; Mosnier et al., 2015).

The hierarchical structure of IPMs separates the underlying (and unobservable) ecological mechanisms from the observation process, allowing for disentanglement of process variation from sampling variation (Gould and Nichols, 1998; Besbeas et al., 2002). This is typically done in IPMs through a state-space formulation, which assumes that abundance may be over- or under-counted (de Valpine and Hastings, 2002; Schaub and Abadi, 2011). The importance of accounting for potential biases due to imperfect detection during sampling has been demonstrated repeatedly in studies estimating the population dynamics and trends of species (e.g., Royle et al., 2005; MacKenzie et al., 2009; Nichols et al., 2009). Failure to accurately account for the sampling process can lead to misleading or even erroneous inferences on population status (Ruiz-Gutiérrez and Zipkin, 2011; Guíllera-Arroita et al., 2014). It is especially important to consider the sampling methodology for situations in which detection varies spatially or through time, as well as in cases where it is important to know the absolute size of a population, such as in conservation applications (e.g., population viability analysis). Unfortunately, many data collection protocols do not allow for explicit estimation of detection probabilities (e.g., non-replicated point counts, species checklist programs). IPMs provide an approach for incorporating such data types even if it is not possible to estimate detection at every site or with every data collection technique, leading to unbiased inference of both demographic rates and population trends.

3. Components of integrated population models

IPMs are built according to three general steps (Fig. 2; Brooks et al., 2004; Schaub et al., 2007; Schaub and Abadi, 2011). First, a population model linking abundance and demographic rates is developed to capture the important life history features of the target species. This is typically a stage- or age-structured matrix projection model (i.e., Lefkovich matrix or Leslie matrix, respectively) where the population size of each stage/age class is assumed to be a function of the population size in the previous year and the demographic rates (Caswell, 2001). The population model describes the relevant recruitment, survival, and immigration processes that reflect dynamics and can include density-dependence and stochasticity in stage transitions. Demographic stochasticity, which tends to be important in small populations, is modeled by assuming that changes in abundance occur probabilistically rather than through deterministic equations (e.g., using the binomial distribution to estimate the number of individuals that survive between

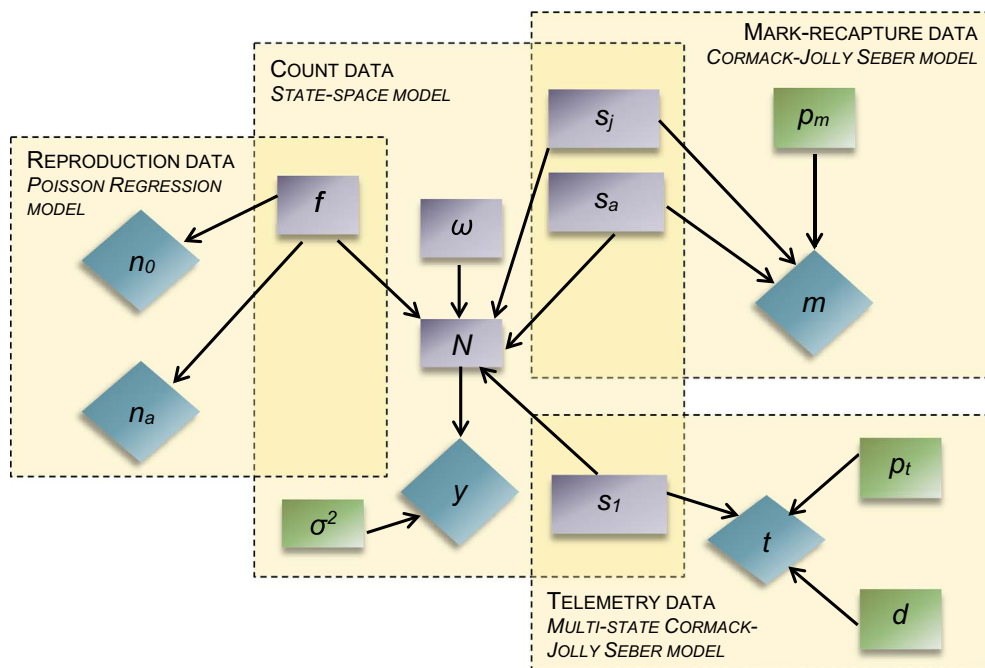


Fig. 1. Graphical depiction of a hypothetical integrated population model showing the potential for different data sources to contribute to shared inference on demographic parameters and population abundance. Four common types of population data are shown; all data types shown are not required in an IPM and other data types can be incorporated. Demographic parameters are represented with purple rectangles, observation parameters with green rectangles, and data are symbolized with blue diamonds. Arrows demonstrate the dependences between nodes. Sub-models are represented by dotted yellow rectangles and titled with the typical data type and model structure. Node notations: n_a = number of adults assessed for reproduction, n_0 = number of juveniles produced, f = per-capita recruitment rate, ω = immigration rate, s_1 = first-year survival probability, s_j = juvenile survival probability (for individuals older than one), s_a = adult survival probability, y = population count data, σ^2 = observation error on count data, N = true population abundance, t = telemetry data, p_t = encounter rate for telemetry data, d = recovery rate of dead individuals, m = capture-recapture data, p_m = capture probability for marked individuals. Figure adapted from Schaub and Abadi, 2011.

time steps; Melbourne and Hastings, 2008). Environmental covariates (Rhodes et al., 2011) and/or random effects (Fieberg et al., 2010; Tempel et al., 2014) can be added using standard approaches and link functions. The complexity of the population model depends on the questions of interest, the intricacies of the organism's life cycle, as well as the quality and quantity of available data.

Next, the likelihoods of each dataset are formulated to estimate the parameters (e.g., survival, fecundity, and population size) defined in the population model. The likelihood functions, which are specified independently for every data type, describe the probability of an observed outcome (i.e., the data) conditional on particular parameter values. For example, capture-recapture data can be analyzed using Cormack-Jolly-Seber models, which generally utilize a multinomial likelihood to estimate survival and capture probabilities (Lebreton et al., 1992; Kéry and Schaub, 2012; Schaub et al., 2015). A state-space likelihood, one in which the true demographic process is modeled separately from the observation process, is often used for time-series data types (e.g., count data) and can be specified using random sampling noise (de Valpine and Hastings, 2002) or through known sampling processes (e.g., imperfect detection; Péron et al., 2012). It is essential that the component likelihoods for the different data types have at least some parameters in common (Fig. 1); this is the mechanism by which information is shared across datasets in an IPM.

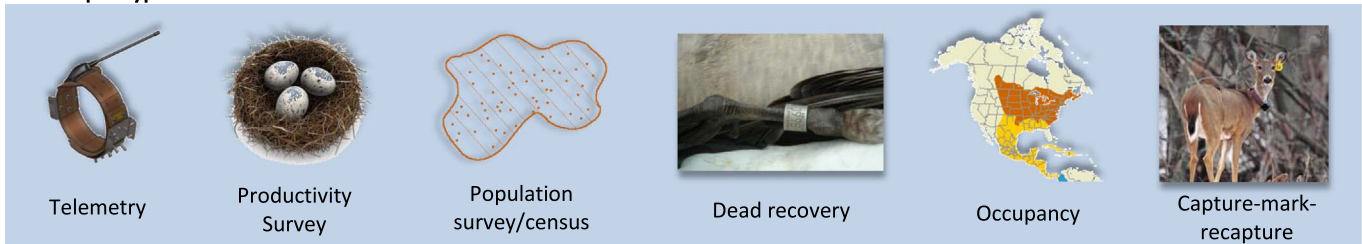
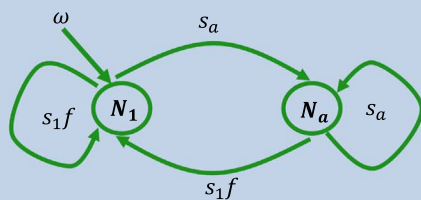
Finally, the joint likelihood of all datasets combined is specified, typically by multiplying the individual component likelihoods defined in the second step. Thus, in addition to the assumptions of each of the component likelihoods, an implicit assumption of IPMs is independence among likelihoods and datasets (Mosnier et al., 2015; Weegman et al., 2016). In the strictest sense, this implies that animals seen in one data type are not observed in other datasets, although this rarely occurs in practice (Schaub and Abadi, 2011). It is important to evaluate the potential effects on parameter estimates if the independence assumption is violated. Lack of independence among datasets can lead to overconfidence in parameter estimates in the form of inflated precision. Abadi et al. (2010a) simulated data with varying levels of independence and found that a lack of independence had minimal impacts on parameter accuracy in an IPM using census, capture-recapture, and productivity data. Yet, this result may not hold true for every data type combination and IPM structure. Recent IPM development has focused

on approaches that do not require independent datasets (Chandler and Clark, 2014; Lee et al., 2015) and this remains an area of active research.

Once the joint likelihood is specified, the IPM is analyzed to estimate parameter values. The hierarchical structure of IPMs naturally lends them to Bayesian analysis (Lee et al., 2015), although the joint likelihood can be analyzed using either frequentist (e.g., maximum likelihood) or Bayesian frameworks (Schaub and Abadi, 2011). Bayesian analysis has become a common method for describing uncertainty in fisheries and wildlife management (Walsh et al., 2015) and facilitates the inclusion of additional information in the form of prior distributions. Prior distributions can be developed from previous studies on different populations or similar species, as well as meta-analyses or expert opinion (Gelman et al., 2014; McCaffery and Lukacs, 2016). Using an IPM in a Bayesian framework allows for the most efficient use of the available data and the best possible description of uncertainty, and is the most rigorous method for incorporating parameter and demographic uncertainty in forward projections (Hoyle and Maunders, 2004; Lee et al., 2015).

4. Integrated population models as a tool for conservation

To successfully manage populations for conservation purposes, it is necessary to track changes in demographic parameters, identify vital rates having the greatest influence on population growth, as well as determine the factors driving spatial and temporal variation in those key rates and whether or not those relationships are stationary (Nichols et al., 2011; Shoemaker and Akçakaya, 2015). IPMs are especially valuable in the study of declining or small populations because gains in accuracy and parameter precision are most apparent in complex models with large numbers of parameters, as is often the case for conservation-focused projects encompassing multiple interacting threatening processes (Rhodes et al., 2011). Increased precision is especially important in cases where the objective is to evaluate temporal patterns in parameter estimates and/or detect significant population trends, including subtle declines (Abadi et al., 2010a). As such, IPMs are well-suited for wildlife conservation research, providing a powerful tool for holistic analyses on threatened populations, as exemplified by a number of recent applications (Supplementary material: Table A1). Below we

Data input types:**Steps in the modeling process:****Step 1: Specify the population model**

Example life cycle diagram of a geographically open population assuming an annual pre-breeding census. The two stages are one-year-old adults (N_1) and older adults (N_a). Demographic parameters are survival (s_1, s_a), fecundity (f) and immigration (w). The model assumes that individuals reproduce starting at age one and only one-year-old adults can immigrate.

Step 2: Define individual likelihoods

$$L_{SS}(y|N, s_1, s_a, f, \omega, \sigma_y^2) =$$

$$L_{OBS}(y|N, \sigma_y^2) \cdot L_{SY}(N|s_1, s_a, f, \omega),$$

$$L_{CMR} = (m|s_1, s_a, p), L_{RS} = (n_0, n_a|f)$$

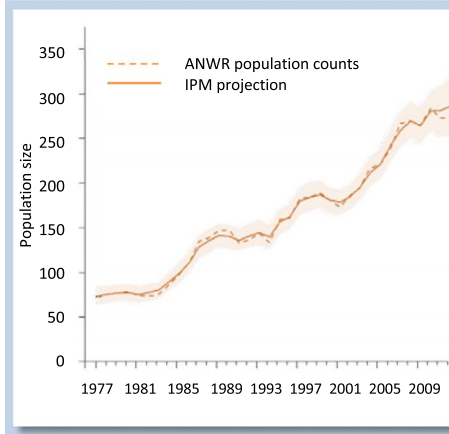
The likelihood for each data type is defined separately using the demographic (where $N=N_1+N_a$) and detection (σ_y^2, p) parameters. For example, the state-space model (L_{SS}) using count data (y) is the product of the process (L_{SY}) and observation (L_{OBS}) models; likelihoods (L_{CMR} and L_{RS}) for other data, here capture-recapture (m) and reproduction (n_0, n_a) data, are also defined.

Step 3: Inference from joint likelihood

$$L_{IPM}(y, m, n_0, n_a|N, s_1, s_a, f, \omega, p, \sigma_y^2)$$

$$= L_{OBS} \cdot L_{SY} \cdot L_{CMR} \cdot L_{RS}$$

The joint likelihood (L_{IPM}) of the model is the product of the individual likelihoods. A key assumption is that datasets are independently collected and parameters appear in multiple individual likelihoods. Detection and demographic rates are estimated using the joint likelihood, typically with Bayesian analysis.

Conservation-related outputs:

Two common IPM outputs sought for conservation: population size over time (left; figure based on whooping cranes from Wilson et al. 2016) and immigration rate (right; figure based on white-fronted geese from Weegman et al. 2016). Immigration is typically difficult to estimate and can rarely be inferred with classical capture-recapture analyses or using other individual datasets. Similarly, improved accuracy on demographic rates leads to increased precision of trend estimates compared to using only count indices, which can facilitate conservation decisions on threatened and endangered species. IPMs are also useful for the estimation of spatially explicit age-specific survival, reproduction, and movement rates.

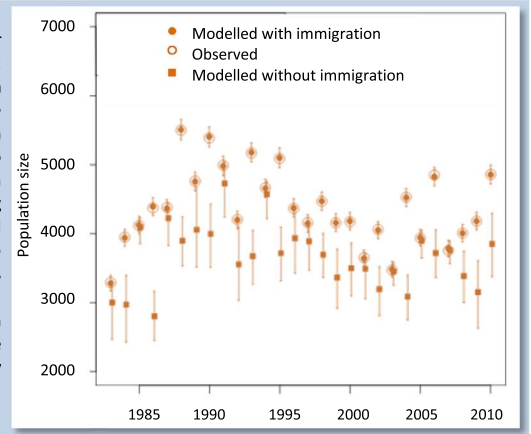


Fig. 2. The process for developing an integrated population model for conservation applications. IPMs jointly analyze data on population size and demographic parameters. A variety of data input types can be used in IPMs, including (1) telemetry or radio-tracking data, (2) productivity/fecundity data, (3) population survey/census data as collected through transects, point counts, or ground counts, (4) dead recovery/carcass data, (5) occupancy (detection-nondetection) data, and (6) capture-mark-recapture data as collected by tagging, banding, or other external marking techniques (top panel). The modeling process includes the following steps: (1) identifying the relevant population model with the aid of a life cycle diagram, (2) determining the likelihoods for individual datasets relative to the demographic rates identified with the population model and the sampling processes, and (3) using the joint likelihood to estimate parameter values (middle panel). Joint analysis of multiple datasets allows for more precise estimates of population abundance and demographic rates, such as stage-specific survival and recruitment. Two outputs of particular interest within a conservation context are estimation of immigration rate and trends in population abundance (bottom panel).

discuss a number of conceptual and practical advances made possible through the development of IPMs.

4.1. The spatial scale of conservation management

By utilizing all available data that contain both direct and indirect information about demographic rates, the IPM framework allows for estimation of parameters that would otherwise be difficult or impossible to evaluate if data were analyzed separately (Abadi et al., 2012; Lee et al., 2015; Wilson et al., 2016). In particular, IPMs can provide information on the sources of population-level gains (i.e., immigration versus recruitment) without explicit movement data (Altwegg et al., 2014; Lieury et al., 2015). Quantifying the relative contributions of immigration versus reproduction to population growth

facilitates identification of the relevant spatial scale for effective conservation and appropriate action (Baillie et al., 2000). If local-level reproduction has strong effects on population dynamics, the spatial scale of dynamics and required conservation actions will also be local. Conversely, if population dynamics are more strongly influenced by immigration, the scale of management depends on the extent to which local populations interact and the rate at which individuals migrate, typically necessitating conservation planning at a much broader spatial scale than that of the target population.

Immigration is one of the most difficult demographic parameters to measure empirically because of challenges tracking individuals (Duarte et al., 2015; Szostek et al., 2014). Failure to incorporate immigration in population models may conceal processes inherent in the target population and potentially lead to erroneous conclusions about the

effectiveness of management (Brown and Collopy, 2013; Altwegg et al., 2014). Estimation of immigration becomes possible when count data are combined with productivity and capture-recapture data, as in the IPM framework (Robinson et al., 2014; Schaub and Fletcher, 2015). Count data intrinsically contain information about all demographic processes in a population, allowing for extraction of additional information on immigration rates when modeled with independent data sources (Abadi et al., 2010b). However, estimates of immigration can also reflect any systematic biases in other vital rates and should be interpreted with caution when explicit data on movement are unavailable. Parametrizing an IPM such that the number of immigrants is a random number (centered on an expected mean value) rather than as a rate (dependent on population size, which can lead to unrealistically high estimates) can facilitate estimating immigration, particularly in small populations (Schaub and Fletcher, 2015). Assessing the amount of immigration into a population can help identify whether a local population is a sink and how it might be managed effectively. For example, Schaub et al. (2010) found that a population survey of eagle owls (*Bubo bubo*) indicated that abundance was stable. However, using an IPM that combined the survey data with data from radio-tracking, age-at-death, and productivity, the authors found that the population was actually a sink, highly dependent on immigration for stability. Additional studies have demonstrated a similar contribution of immigration to population stability and temporal variation in population growth (Schaub et al., 2010; Brown and Collopy, 2013; Schaub et al., 2013; Altwegg et al., 2014; Tempel et al., 2014), whereas other populations of conservation concern are growing or maintaining stability without reliance on high immigration rates (Demerdzhiev et al., 2015).

Extending IPMs to multi-state systems (e.g., multiple sites, disease states, breeding conditions) can provide a more precise and nuanced understanding of results by enabling inference on patterns of condition-dependent demographic rate parameters. In particular, multi-site IPMs allow for estimation of dispersal at the landscape level, yet capture-recapture data need only be collected at a subset of sites within the species' range (McCrea et al., 2010; Péron et al., 2010). This advancement has important implications for determining the optimal spatial scale for conservation; understanding temporary emigration; and identifying locations with the highest reproductive success and/or survival, information that can be used to prioritize locations for management interventions.

4.2. Population synchrony within metapopulations

Population synchrony, or coincident changes in the size of local populations, is a common ecological phenomenon exhibited by many taxa including insects, molluscs, birds, amphibians, and mammals (reviewed by Liebold et al., 2004). Synchronous dynamics over a species' range can be critical for conservation as it increases the extinction risk of spatially structured populations (Harrison and Quinn, 1989). However, little is known about the relative effects of demographic rates on synchrony because of difficulties obtaining data, estimating rates independently for all populations, and making spatial comparisons (Jorgensen et al., 2016). An IPM framework is particularly advantageous for analyzing data from geographically-distinct populations because it is possible to handle differing sampling protocols and survey periods among sites (Schaub et al., 2015), enabling conservation management to scale from a single population to an entire metapopulation or species. Using an IPM, relevant demographic rates from all study areas within a metapopulation can be estimated concurrently by partitioning sources of variation in population growth rates using covariates and random effects. In a spatially-structured IPM of a barn swallow (*Hirundo rustica*) metapopulation, Schaub et al. (2015) decomposed the variation in population growth and demographic rates into global and local temporal components using random effects and examined population synchrony in parameters using post-hoc correlations. It is also possible to assess synchrony by explicitly estimating the

variance and covariance structure in vital rates among local populations to make inferences on correlations directly within a model (Péron and Koons, 2012). Determining both the degree and causes (e.g., specific environmental and/or demographic drivers) of synchrony within metapopulations provides an opportunity to adjust management strategies accordingly. Recent IPM developments have expanded these approaches to a multi-species context, facilitating enhanced understanding of how changing community dynamics, and synchrony among species, may impact a target species (Lahoz-Monfort et al., 2017). Methodological approaches for quantifying synchronous patterns in population parameters fill a significant knowledge gap in understanding how metapopulations react to long-term changes in the environment and can be used to improve predictions of future environmental scenarios.

4.3. Density effects on population dynamics

Accurate understanding of how populations are regulated often requires evaluation of the effect of density on different age or stage classes. Density dependence is an important ecological concept and determining how it operates is crucial to evaluating how populations persist in complex ecological systems and to developing effective management plans (Stubbs, 1977). Despite numerous methods for studying density dependence in wild populations (reviewed in Lebreton and Gimenez, 2013), many approaches do not assess the effect of density on multiple demographic parameters simultaneously while accounting for errors incurred during the sampling process. The state-space framework within IPMs can overcome this shortcoming whereby the effects of density can be incorporated on individual parameters - not just on population growth - while simultaneously accounting for uncertainty in the data due to stochasticity and detection biases (Gamelon et al., 2016). The additional data included in the model as a result of the IPM approach allow these parameters to become identifiable. Abadi et al. (2012) developed an IPM to assess the effect of density dependence on demographic parameters (and thus overall population growth rate) and revealed negative effects of density on adult survival of red-backed shrikes (*Lanius collurio*). Model simulations demonstrated improved precision in estimates of density-dependent relationships as compared to a regression model, providing a framework for understanding the mechanisms by which populations are regulated. This approach could be further extended to assess non-linear density dependence, delayed density dependence, Allee effects, as well as density dependence at the population level using a derived population growth rate parameter.

4.4. Data collection priorities

The charismatic nature of many threatened species (e.g., birds of prey, top predatory taxa, iconic migrants) leads to disproportionate attention and monitoring by different entities, including professional researchers, public administrators, and volunteers (Tenan et al., 2012). In some cases, spatially-extensive data, typically in the form of population counts (e.g., aerial surveys, regional censuses), are collected by conservation organizations or government programs (e.g., North American Breeding Bird Survey) while independent researchers simultaneously collect more intensive (but spatially-limited) data types, such as capture-recapture and productivity data. The involvement of multiple stakeholders with differing goals and protocols can lead to a relative wealth of data, albeit with heterogeneous data types. For instance, regional-scale count surveys (e.g., lek counts) are frequently the most extensive information available for sage-grouse (*Centrocercus minimus*, *C. urophasianus*), a threatened species in the western United States; however, these data are minimally informative of vital rates and do not account for imperfect detection during sampling (Walsh et al., 2004; Kelling et al., 2015). Recent data collection efforts on the sage-grouse have consequently focused on obtaining intensive, short-term

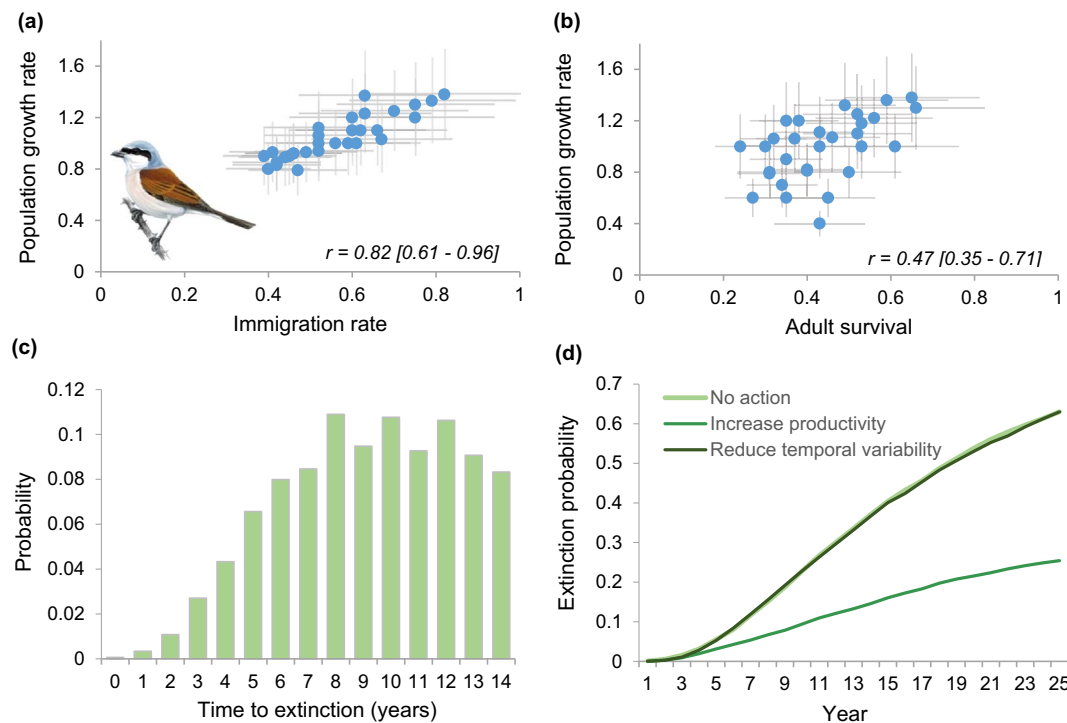


Fig. 3. Examples of possible (a & b) retrospective and (c & d) prospective analyses using results from an integrated population model incorporating three simulated 20-year datasets (i.e., population counts, capture-recapture, productivity) from a hypothetical red-backed shrike (*Lanius collurio*) population (male shown in inset). Post-hoc correlations (r) between annual population growth rates and IPM-generated estimates of (a) immigration rate and (b) adult survival are plotted to demonstrate retrospective analyses that can elucidate the contribution of demographic rates to variation in population growth (adapted from Schaub et al., 2013; Tempel et al., 2014). IPM-generated population abundance can be projected forward for prospective analyses to examine (c) the distribution of the time to extinction (of simulated populations that went extinct), as well as (d) cumulative extinction probabilities under different management strategies (e.g., increase productivity by 20%, reduce temporal variability in adult survival by 50% shown; example and code taken from unpublished work by M. Schaub & M. Kéry).

demographic data, allowing for development of an IPM to rigorously estimate population growth rates as well as survival and fecundity (Davis et al., 2014). IPMs compensate for diversity in data collection by reducing biases inherent in a single dataset and providing more precise estimates of demographic rates than can be obtained from separate analyses (Hoyle and Maunders, 2004; Oppel et al., 2014; Harris et al., 2015). Yet, the caliber of individual datasets ultimately determines the quality of inference, and integrated modeling techniques cannot remove inherent biases within a dataset. As with all analyses, careful consideration of sampling protocols, potential biases of data collection, and a priori biological hypotheses are necessary for high quality inference within an IPM framework.

From a management perspective, the incorporation of multiple data types into a single analysis can reveal data collection priorities that would otherwise be unclear from separate analyses. For example, if population estimates from an IPM are substantially different than those from annual census data, it is possible that count data alone may be unreliable for obtaining accurate population estimates because of missing information. In such cases, allocating resources to the supplementary collection of individual-based demographic data (e.g., capture-recapture, productivity, and/or telemetry data) would likely contribute to more precise estimation of population trends and critical parameters compared to an exhaustive population census (Lee et al., 2015). Coupling IPMs with simulations of several data types can help in the assessment of the relative inferential value of different data sources, a useful exercise for evaluating potential adjustments in field data collection efforts.

4.5. Conservation efficacy

IPMs can elucidate the efficacy of conservation actions relative to natural population processes. Several studies have used IPMs to

investigate the extent to which management actions (e.g., nest box installation, predator control, supplementary feeding) have contributed to population recovery through improvements in demographic rates (Altwegg et al., 2014; Demerdzhiev et al., 2015; Lieury et al., 2015). Distinguishing between various factors that contribute to population change consequently allows for the prioritization of conservation actions. For example, Altwegg et al. (2014) found through analysis of an IPM that immigration was the most important driver of growth in an urban population of peregrine falcons (*Falco peregrinus*), more so than recruitment, even with the aid of nest box deployment. These results revealed the critical importance of protecting falcon populations in remote environments to the successful maintenance of the urban population and the welfare of the species as a whole.

5. Areas of advancement: extensions of integrated population models

Initial IPM development within wildlife ecology focused on combining annual census data with capture-recapture data (Besbeas et al., 2002; Brooks et al., 2004). Over the last decade, IPMs have expanded to include many additional data types. Although the foundations of IPMs are well developed, novel uses continue to spur technical improvements and expand their applicability within ecology. Below we highlight several advancements that are particularly relevant for conservation applications of IPMs.

5.1. Retrospective and prospective analyses

Estimates of demographic rates and population size and structure obtained from IPMs can be used in subsequent analyses to gain a deeper understanding of the reasons for past population changes (i.e., retrospective analyses; Szostek et al., 2014; Abadi et al., 2017) and to predict

future population trajectories (i.e., prospective analyses; [Oppel et al., 2014](#)). IPMs allow for correlation assessment between annual estimates of demographic parameters with population growth rates to quantify the impact of demography ([Fig. 3a & b](#); [Schaub et al., 2013](#)). The strength of the correlation between population growth and demographic rates indicates the magnitude with which temporal variation in a given demographic parameter contributes to the temporal variation of population growth ([Robinson et al., 2014](#); [Schaub et al., 2013](#); [Szostek et al., 2014](#); [Tempel et al., 2014](#)). This approach is particularly useful in the study of populations that never reach a stable steady state because of non-stationary environmental conditions, and can be combined with formal methods for assessing transient dynamics (e.g., [Koons et al., 2016](#); [Koons et al., 2017](#)). Evaluating the transient dynamics of populations is notoriously difficult, but it is especially important for threatened species inhabiting areas that experience significant climate and/or habitat changes (e.g., locations undergoing invasion; [Ezard et al., 2010](#)).

IPMs are particularly well-suited for enabling predictions of future population sizes ([Fig. 3c & d](#)). Analysis in a Bayesian framework aids predictions as posterior sampling can be used to obtain a full assessment of all uncertainties involved in forecasts ([Kéry and Schaub, 2012](#); [Gelman et al., 2014](#); [Servanty et al., 2014](#)). The posterior distributions of the predicted future population sizes can be used to compute population-level extinction probabilities or population prediction intervals (i.e., intervals that include the projected unknown population size at a specified future time with a given probability or confidence level), both typical components of population viability analyses ([Servanty et al., 2014](#)). Model results generated from IPMs can be adjusted to predict population sizes and extinction probabilities under different management scenarios that may alter various demographic rates ([Duarte et al., 2017](#)). In [Fig. 3d](#), we simulate results from an IPM of a hypothetical passerine population to estimate changes in extinction probabilities under conditions that either increase productivity by 20% (e.g., through nest predation control) or reduce temporal variability in adult survival by 50% (e.g., through removal of competitors and/or primary predators), as compared to no management (example and code taken from unpublished work by M. Schaub & M. Kéry). Conducting this type of exercise helps identify the most practical strategy for maintaining population persistence into the future.

5.2. Spatially explicit IPMs

Development of IPMs using spatially explicit capture-recapture data ([Efford et al., 2009](#); [Royle et al., 2013](#)) extends the utility of conventional IPMs by (1) accounting for spatial variation in demographic, movement, and detection parameters and (2) enabling the ability to make spatially-explicit predictions of abundance or vital rates ([Chandler and Clark, 2014](#)). The basis of the spatially explicit IPM is a spatial point process describing the number and locations of individuals in a population during the initial time period, and the variation in abundance (and density) over time as a function of death, recruitment, and movement (i.e., immigration/emigration). Both capture-recapture and survey (either count or detection-nondetection) data can be modeled conditional on the point process ([Chandler and Royle, 2013](#); [Royle et al., 2013](#)), thus avoiding the conventional and restrictive requirement that these two datasets be independent.

Like non-spatial IPMs, the spatially explicit IPM can account for process variation and observer error when predicting population size under future environmental conditions. Unlike classic IPMs, which are unable to account for individual heterogeneity in vital rates and detection probability ([Abadi et al., 2013](#)), the spatially explicit IPM fully accommodates spatially-induced individual heterogeneity in demographics and capture or detection probabilities, increasing accuracy of parameter estimates and expanding the framework's utility ([Chandler and Clark, 2014](#)). The model provides a straightforward means of predicting abundance or density in unsampled regions and time

periods, and can be used to map and project species distributions and vital rates at broad spatio-temporal scales. This spatial point process framework avoids the problems associated with scaling up continuously-varying measures such as density or movement, which can introduce bias in non-spatial models ([Melbourne and Chesson, 2005](#)). These advantages are particularly beneficial in conservation-related projects where logistical and financial constraints frequently prevent survey coverage across a species' entire range (or over long time periods), yet inference is required at a broad scale for range-wide management decisions.

5.3. Environmental uncertainty

Uncertainty surrounding ecological responses to environmental factors should be incorporated into population assessments as environmental stochasticity can play a significant role in the viability of a population, particularly for threatened species ([Kanno et al., 2015](#)). Existing demographic projection models assess the effects of future environmental conditions on population trends, but often fail to rigorously integrate uncertainty around both demographic and environmental processes ([Crone et al., 2013](#); but see [Gauthier et al., 2016](#)). This can lead to erroneous predictions, particularly if there is uncertainty about how future environmental scenarios may affect demographic parameters ([Coulson et al., 2001](#)). [Oppel et al. \(2014\)](#) developed an approach to incorporate environmental variation into IPMs to explicitly account for both environmental and demographic stochasticity in a single modeling framework, providing a comparatively more realistic assessment of population viability under unknown future environmental conditions. The fundamental idea is to draw future values of environmental variables from probability distributions to simulate environmental uncertainty ([Heard et al., 2013](#)) and to then use the results in combination with IPM parameter estimates (and their full uncertainties) to project population trends ([Oppel et al., 2014](#)). Although incorporating both demographic and environmental stochasticity into models can result in considerable uncertainty surrounding population projections ([Jenouvrier, 2013](#)), the wider credible (or confidence) intervals represent a more realistic assessment of future population viability.

5.4. Two-sex IPMs

Typical IPMs are female-based models (i.e., only female life history is specified for the state process) that frequently do not account for mate availability, differing sex ratios, or polygamy among individuals ([Schaub and Abadi, 2011](#); but see [Véran and Lebreton, 2008](#)). Yet, two-sex models are required when vital rates significantly differ between males and females, males are the limiting sex in the population, or when life history characteristics vary by sex such that modeling the dynamics of a single sex is inadequate ([Gerber and White, 2014](#); [Shyu and Caswell, 2016](#)). Even in cases when demographic rates are similar between the two sexes, incorporating data from males can lead to overall improved inference on female vital rates simply because of the additional data ([Péron and Koons, 2012](#)). Recent IPM advancements allow for the investigation of population dynamics and quantification of cause-specific mortality rates in non-monogamous species, enabling the use of IPMs in a new suite of mating systems ([Tenan et al., 2016](#)). In this framework, the state process is specified using a two-sex population model, in which the annual number of breeding individuals is determined by explicitly modeling the probability that males and females breed (i.e., access to reproduction) as a function of the availability of opposite-sex individuals ([Jenouvrier et al., 2010](#)). Many carnivores have polygamous mating systems and mate availability can play an important role in population viability, especially when populations are small ([Gerber and White, 2014](#)). Large terrestrial carnivores are a highly endangered group of species; the advent of the two-sex IPM extension, which contains a nonlinear mating function ([Tenan et al.,](#)

2016), offers an opportunity to expand the use of IPMs into a much broader set of at-risk species.

5.5. Technical advancements: goodness-of-fit assessments

Goodness-of-fit evaluations for IPMs are typically either not conducted or they are done in an ad hoc fashion (Abadi et al., 2010b; Schaub and Abadi, 2011). A newly proposed approach, motivated by Bayesian p -values and using calibrated simulation, offers the first potential evaluation procedure of IPMs (Besbeas and Morgan, 2014). For each component dataset, a discrepancy measure determines whether the model fits the data well, or either over- or under-predicts the outcome as compared to simulated data generated from the estimated model parameters. Different goodness-of-fit discrepancy measures can be used to highlight various aspects of fit and multiple discrepancy measures can be used in tandem to evaluate more complex integrated models, such as one that includes density dependence on productivity (i.e., the productivity parameter is related to population size through a threshold dependence). Besbeas and Morgan (2014) illustrate the performance of their goodness-of-fit metric using capture-recapture data and count data, assessing the utility of different discrepancy measures (e.g., Freeman-Tukey discrepancy measure, Pearson chi-square statistic) for each data type. Their comprehensive approach adopts a common evaluation procedure for all components of an IPM and establishes a consistent criterion that researchers can use when conducting model selection. Model fit is notoriously difficult to assess in hierarchical models and remains an area of active research (Hooten and Hobbs, 2015). For example, Carvalho et al. (2016) evaluated the efficacy of several recently-proposed diagnostic tests (e.g., residuals analysis, catch-curve analysis) in identifying model misspecification in both the observation and system dynamics components of integrated stock assessments. The authors found that residual analyses were the best detector of misspecification of the observation model while age-structured production models were best at detecting misspecification of the system dynamics model (Carvalho et al., 2016). A similar comparison of commonly-used diagnostic tests (e.g., Bayesian p -values) for IPM component models could help identify appropriate methods for assessing both model fit and model selection within IPMs.

6. The future of integrated population models

We foresee several potential avenues of IPM advancement related to the fields of ecology and conservation science, which we highlight below while providing suggestions for future modeling efforts.

6.1. Inclusion of citizen science data

IPMs have the potential to address complex conservation questions at unprecedented scales using widely-collected volunteer data. Citizen science data are well-suited to integrated modeling because their wide geographic distributions of volunteers can provide much richer datasets than are typically available (Sauer and Link, 2011; Kelling et al., 2015; Barrows et al., 2016; Saunders et al., 2017). IPMs have the potential to advance these methods even further by appropriately combining datasets while accounting for errors across multiple citizen science programs. For example, the use of eBird detection-nondetection data (www.ebird.org/content/ebird) or count data from the Breeding Bird Survey (www.pwrc.usgs.gov/bbs/index.cfm) in an IPM framework

(i.e., with local-scale capture-recapture data) has the potential to reveal large-scale population trends, shifts in species niches, and/or the varying importance of demographic processes across spatial and temporal scales (Sauer and Link, 2011; Sullivan et al., 2014). Ahrestani et al. (2016) recently used an IPM framework to combine two broad-scale avian citizen science datasets (Breeding Bird Survey and Monitoring Avian Productivity and Survivorship) to assess population trends and latent recruitment of gray catbird (*Dumetella carolinensis*) and wood thrush (*Hylocichla mustelina*). It is possible that other data types, including citizen-reported mortality data such as car collisions with wildlife (RoadKill: www.adventurescience.org/roadkill.html) and bird-window collisions (Project BirdSafe: www.mn.audubon.org/project-birdsafe; Project Safe Flight: www.nycaudubon.org/project-safe-flight), can be used in conjunction with planned surveys to help inform population dynamics (Loss et al., 2015), although additional model development is needed.

6.2. Incorporation of unmarked data types into demographic estimates

Capture-recapture or other “marked” data types (e.g., dead recovery data) are the typical sources for demographic analyses (Lebreton et al., 1992). However, recently developed approaches for modeling unmarked data within a population dynamics framework provide a promising avenue for estimating parameters such as survival, fecundity, and even immigration from only count and detection-nondetection data (Dail and Madsen, 2011; Zipkin et al., 2014b; Rossman et al., 2016). Time series data can be modeled according to a Markovian process whereby individuals remain in the population through a stochastic survival process and are gained to the population either via recruitment or immigration (Dail and Madsen, 2011). A crucial feature of these data are repeated observations at each step in the time series (i.e., repeated sampling during periods of closure), which allow for estimation of the detection process separately from the underlying state process (Royle, 2004). Incorporating these new models for time series or census data within an IPM framework would lead to greater accuracy and precision of demographic rates and population trends (Zipkin et al., 2017). Stage-structured (Link et al., 2003) and seasonally segregated (Link and Sauer, 2007) count data are especially useful because they can allow for estimates of both population abundance and demographic parameters, similar to those obtained from capture-recapture data (Zipkin et al., 2014a, 2014b). Many rare and/or threatened species have available only limited capture-recapture data or none at all; the ability to estimate demographic parameters using only unmarked data offers the potential to expand integrative modeling approaches to less invasive and intensive sampling methodologies.

6.3. Coupled population-environment modeling

Integrated population modeling is an ideal analytical platform for coupled population-environment models that are designed to project population trajectories under forecasts of future conditions (e.g., climate, land-use changes). Although a growing number of studies have linked climate-dependent demographic models to climate simulations (Jenouvrier et al., 2012; Van der Meer et al., 2016; Gauthier et al., 2016), this has not yet been done using IPMs, likely because most population models are parameterized from a single dataset. Uncertainties in climate modeling scenarios have been described extensively (Hawkins and Sutton, 2009), but methods for combining uncertainties from both climate and integrated models have not yet been attempted (other than with random environmental noise, e.g., Oppel et al., 2014). Developing an approach that links future environmental scenarios with integrated models is crucial to deriving accurate projections of population change (Ehrlén and Morris, 2015), and properly accounting for sources of uncertainty and potential variation.

7. Conclusions

Monitoring the consequences of anthropogenic alterations is increasingly urgent as changing environmental and climate conditions continue to modify the population dynamics of species worldwide. Record species losses have hastened efforts to identify extinction risks and ameliorate the ultimate causes of decline (Pimm et al., 2014), but methodological and statistical advancements often lag behind the pace necessary to enact management decisions. Characterizing population dynamics and trends at broad spatial scales can be challenging, as it is difficult to measure all relevant parameters, and data on those that are measured may be representative of only a sample of the population (Robinson et al., 2014). Yet the spatial and temporal scope of ecological research and conservation efforts has expanded greatly over the last few decades (e.g., Fink et al., 2010; Robinson et al., 2014; Loss et al., 2015), requiring ever more efficient data collection and analytical methods. Collection of demographic data, which are necessary to understand mechanistic changes in population dynamics, is complicated when the population of conservation concern is rare, sparsely distributed, or includes life stages that are difficult to observe in the field (Harris et al., 2015; Mosnier et al., 2015). The development of IPMs and their recent application to threatened and declining populations overcomes many drawbacks associated with classical modes of inference, and has advanced our ability to investigate environmental and demographic drivers of population change as well as more accurately estimate trends.

The key strength of IPMs is that each sub-model borrows information from other sub-models, making use of all available data from a study system, leading to the best possible inference on a target population (Schaub and Abadi, 2011). Although IPMs can be complex and beyond the expertise of some ecologists and conservation practitioners, the software for their implementation is freely available (e.g., R, JAGS, BUGS, NIMBLE, Julia, C++, INLA, ADMB) and example code for typical models can be found online (e.g., Kéry and Schaub, 2012, Chapter 11). More user-friendly tutorials and how-to papers, especially within a Bayesian framework, would enable a wider audience to become familiar with IPMs and their implementation. IPMs should be broadly adopted for conservation-focused projects with multiple data sources, including those with data types not typically incorporated (e.g., citizen science programs), because IPMs can be used to better understand and detect population declines (Schaub et al., 2010; Mosnier et al., 2015), prioritize populations of conservation concern (Altwegg et al., 2014), enhance monitoring schemes (Tempel et al., 2014), and adjust management strategies (Johnson et al., 2010; Demerdzhiev et al., 2015). These capabilities are improving recovery for threatened and declining species worldwide, and have the potential to continue to do so with further method development and application.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2017.10.017>.

Acknowledgements

We thank M. Schaub and M. Kéry for ideas and the IPM prospective analysis example and template code provided at their integrated population modeling workshop held at Patuxent Wildlife Research Center in August 2016 (attended by SPS). We greatly appreciate S. Converse, B. Gardner, E. Grant, A. Royle, and J. Thorson for useful feedback and ideas. We are also grateful for insightful written comments provided by T. Arnold, M. Schaub, and two anonymous reviewers. This research was supported by awards from the National Science Foundation (EF-1702635 from the MacroSystems Biology Program) and the U.S. Fish and Wildlife Service (Cooperative Agreement Award F17AC00427).

References

Abadi, F., Gimenez, O., Arlettaz, R., Schaub, M., 2010a. An assessment of integrated population models: bias, accuracy, and violation of the assumption of independence.

- Ecology 91, 7–14.
- Abadi, F., Gimenez, O., Ullrich, B., Arlettaz, R., Schaub, M., 2010b. Estimation of immigration rate using integrated population models. *J. Appl. Ecol.* 47, 393–400.
- Abadi, F., Gimenez, O., Jakober, H., Stauber, W., Arlettaz, R., Schaub, M., 2012. Estimating the strength of density dependence in the presence of observation errors using integrated population models. *Ecol. Model.* 242, 1–9.
- Abadi, F., Botha, A., Altwegg, R., 2013. Revisiting the effect of capture heterogeneity on survival estimates in capture-mark-recapture studies: does it matter? *PLoS One* 8, e62636.
- Abadi, F., Barbraud, C., Gimenez, O., 2017. Integrated population modeling reveals the impact of climate on the survival of juvenile emperor penguins. *Glob. Chang. Biol.* 23, 1353–1359.
- Ahrestani, F.S., Saracco, J.F., Sauer, J.R., Pardieck, K., Royle, J.A., 2016. An integrated population model for bird monitoring in North America. *Ecol. Appl.* <http://dx.doi.org/10.1002/eap.1493>.
- Alroy, J., 2015. Current extinction rates of reptiles and amphibians. *Proc. Natl. Acad. Sci. U. S. A.* 112, 13003–13008.
- Altwegg, R., Jenkins, A., Abadi, F., 2014. Nestboxes and immigration drive the growth of an urban peregrine falcon *Falco peregrinus* population. *Ibis* 156, 107–115.
- Baillie, S.R., Sutherland, W.J., Freeman, S.N., Gregory, R.D., Paradis, E., 2000. Consequences of large-scale processes for the conservation of bird populations. *J. Appl. Ecol.* 37, 88–102.
- Barrows, C.W., Hoines, J., Vamstad, M.S., Murphy-Mariscal, M., Lalmiere, K., Heintz, J., 2016. Using citizen scientists to assess climate change shifts in desert reptile communities. *Biol. Conserv.* 195, 82–88.
- Besbeas, P., Morgan, B.J., 2014. Goodness-of-fit of integrated population models using calibrated simulation. *Methods Ecol. Evol.* 5, 1373–1382.
- Besbeas, P., Freeman, S.N., Morgan, B.J.T., Catchpole, E.A., 2002. Integrating mark-recapture-recovery and census data to estimate animal abundance and demographic parameters. *Biometrics* 58, 540–547.
- Besbeas, P., Lebreton, J.D., Morgan, B.J.T., 2003. The efficient integration of abundance and demographic data. *Appl. Stat.* 52, 95–102.
- Brooks, S.P., King, R., Morgan, B.J.T., 2004. A Bayesian approach to combining animal abundance and demographic data. *Anim. Biodivers. Conserv.* 27, 515–529.
- Brown, J.L., Collopy, M.W., 2013. Immigration stabilizes a population of threatened cavity-nesting raptors despite possibility of nest box imprinting. *J. Avian Biol.* 44, 141–148.
- Buschke, F.T., Brendonck, L., Vanschoenwinkel, B., 2015. Simple mechanistic models can partially explain local but not range-wide co-occurrence of African mammals. *Glob. Ecol. Biogeogr.* 7, 762–773.
- Cardinale, B.J., Duffy, E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, C., et al., 2012. Biodiversity loss and its impact on humanity. *Nature* 486, 59–67.
- Carvalho, F., Punt, A.E., Chang, Y.-J., Maunder, M.N., Piner, K.R., 2016. Can diagnostic tests help identify model misspecification in integrate stock assessments? *Fish. Res.* <http://dx.doi.org/10.1016/j.fishres.2016.09.018>.
- Caswell, H., 2001. *Matrix Population Models*. John Wiley & Sons, Ltd.
- Catchpole, E.A., Freeman, S.N., Morgan, B.J.T., Harris, M.P., 1998. Integrated recovery/recapture analysis. *Biometrics* 54, 33–46.
- Chandler, R.B., Clark, J.D., 2014. Spatially explicit integrated population models. *Methods Ecol. Evol.* 5, 1351–1360.
- Chandler, R.B., Royle, J.A., 2013. Spatially explicit models for inference about density in unmarked or partially marked populations. *Ann. Appl. Stat.* 7, 936–954.
- Coulson, T., Mace, G.M., Hudson, E., Possingham, H., 2001. The use and abuse of population viability analysis. *Trends Ecol. Evol.* 16, 219–221.
- Crone, E.E., Ellis, M.M., Morris, W.F., Stanley, A., Bell, T., Bierzchudek, P., et al., 2013. Ability of matrix models to explain the past and predict the future of plant populations. *Conserv. Biol.* 27, 968–978.
- Dail, D., Madsen, L., 2011. Models for estimating abundance from repeated counts of an open metapopulation. *Biometrics* 67, 577–587.
- Davis, A.J., Hooten, M.B., Phillips, M.L., Doherty Jr., P.F., 2014. An integrated modeling approach to estimating Gunnison sage-grouse population dynamics: combining index and demographic data. *Ecol. Evol.* 4, 4247–4257.
- de Valpine, P., Hastings, A., 2002. Fitting population models incorporating process noise and observation error. *Ecol. Monogr.* 72, 57–76.
- Demerdzhiev, D., Stoychev, S., Dobrev, D., Spasov, S., Oppel, S., 2015. Studying the demographic drivers of an increasing imperial eagle population to inform conservation management. *Biodivers. Conserv.* 24, 627–639.
- Dorazio, R.M., 2014. Accounting for imperfect detection and survey bias in statistical analysis of presence-only data. *Glob. Ecol. Biogeogr.* 23, 1472–1484.
- Duarte, A., Weckerly, F.W., Schaub, M., Hatfield, J.S., 2015. Estimating golden-cheeked warbler immigration: implications for the spatial scale of conservation. *Anim. Conserv.* 19, 66–74.
- Duarte, A., Pearl, C.A., Adams, M.J., Peterson, J.T., 2017. A new parameterization for integrated population models to document amphibian reintroductions. *Ecol. Appl.* <http://dx.doi.org/10.1002/eap.1564>.
- Edgar, G.J., Bates, A.E., Bird, T.J., Jones, A.H., Kininmonth, S., Stuart-Smith, R.D., et al., 2016. New approaches to marine conservation through the scaling up of ecological data. *Annu. Rev. Mar. Sci.* 8, 435–461.
- Efford, M.G., Borchers, D.L., Byrom, A.E., 2009. Density estimation by spatially explicit capture-recapture: likelihood-based methods. In: *Modeling Demographic Processes in Marked Populations*. Springer, US, pp. 255–269.
- Ehrlén, J., Morris, W.F., 2015. Predicting changes in the distribution and abundance of species under environmental change. *Ecol. Lett.* 18, 303–314.
- Ezard, T.H., Bullock, J.M., Dalgleish, H.J., Millon, A., Pelletier, F., Ozgul, A., Koons, D.N., 2010. Matrix models for a changeable world: the importance of transient dynamics in population management. *J. Appl. Ecol.* 47, 515–523.

- Fieberg, J.R., Shertzer, K.W., Conn, P.B., Noyce, K.V., Garshelis, D.L., 2010. Integrated population modeling of black bears in Minnesota: implications for monitoring and management. *PLoS One* 5, e12114. <http://dx.doi.org/10.1371/journal.pone.0012114>.
- Fink, D., Hochachka, W.M., Zuckerberg, B., Winkler, D.W., Shaby, B., Arthur Muson, M., et al., 2010. Spatiotemporal exploratory models for broad-scale survey data. *Ecol. Appl.* 20, 2131–2147.
- Fletcher, Robert J., McCleery, R.A., Greene, D.U., Tye, C.A., 2016. Integrated models that unite local and regional data reveal larger-scale environmental relationships and improve predictions of species distributions. *Landsc. Ecol.* 31, 1369–1382.
- Fournier, D., Archibald, C.P., 1982. A general theory for analyzing catch at age data. *Can. J. Fish. Aquat. Sci.* 39, 1195–1207.
- Gamelon, M., Grøtan, V., Engen, S., Bjørkvoll, E., Visser, M.E., Sæther, B.-E., 2016. Density dependence in an age-structured population of great tits: identifying the critical age classes. *Ecology* 97, 2479–2490.
- Gauthier, G., Lebreton, J.-D., 2004. Population models for greater snow geese: a comparison of different approaches to assess potential impacts of harvest. *Anim. Biodivers. Conserv.* 27, 503–514.
- Gauthier, G., Péron, G., Lebreton, J.-D., Grenier, P., van Oudenhove, L., 2016. Partitioning prediction uncertainty in climate-dependent population models. *Proc. R. Soc. B*. <http://dx.doi.org/10.1098/rspb.2016.2353>.
- Gelman, A., Carlin, J.B., Stern, H.S., Rubin, D.B., 2014. In: Gelman, A., Carlin, J.B., Stern, H.S., Dunson, D.B., Vehtari, A., Rubin, D.B. (Eds.), *Bayesian Data Analysis*, 3rd ed. Chapman & Hall Press, Boca Raton, FL.
- Gerber, L.R., White, E.R., 2014. Two-sex matrix models in assessing population viability: when do male dynamics matter? *J. Appl. Ecol.* 51, 270–278.
- Gould, W.R., Nichols, J.D., 1998. Estimation of temporal variability of survival in animal populations. *Ecology* 79, 2531–2538.
- Grace, J.B., Anderson, T.M., Seabloom, E.W., Borer, E.T., Adler, P.B., Harpole, W.S., et al., 2016. Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature* 529, 390–393.
- Guillera-Aroita, G., Lahoz-Monfort, J.J., MacKenzie, D.I., Wintle, B.A., McCarthy, M.A., 2014. Ignoring imperfect detection in biological surveys is dangerous: a response to 'fitting and interpreting occupancy models'. *PLoS One* 9, e99571.
- Harris, W.E., Combe, F.J., Bird, S., 2015. Using integrated population modelling in conservation monitoring: a case study in the common dormouse (*Muscardinus avellanarius*). *Folia Zool.* 64, 330–336.
- Harrison, S., Quinn, J.F., 1989. Correlated environments and the persistence of meta-populations. *Oikos* 56, 293–298.
- Hawkins, E., Sutton, R., 2009. The potential to narrow uncertainty in regional climate predictions. *Bull. Am. Meteorol. Soc.* 90, 1095–1107.
- Heard, G.W., McCarthy, M.A., Scroggie, M.P., Baumgartner, J.B., Parris, K.M., Burgman, M., 2013. A Bayesian model of metapopulation viability, with application to an endangered amphibian. *Divers. Distrib.* 19, 555–566.
- Hooten, M.B., Hobbs, N.T., 2015. A guide to Bayesian model selection for ecologists. *Ecol. Monogr.* 85, 3–28.
- Hostetler, J.A., Scott Sillett, T., Marra, P.P., 2015. Full-annual-cycle population models for migratory birds. *Auk* 132, 433–449.
- Hoyle, S.D., Maunier, M.N., 2004. A Bayesian integrated population dynamics model to analyze data for protected species. *Anim. Biodivers. Conserv.* 27, 247–266.
- Jenouvrier, S., 2013. Impacts of climate change on avian populations. *Glob. Chang. Biol.* 19, 2036–2057.
- Jenouvrier, S., Caswell, H., Barbraud, C., Weimerskirch, H., 2010. Mating behavior, population growth, and the operational sex ratio: a periodic two-sex model approach. *Am. Nat.* 175, 739–752.
- Jenouvrier, S., Holland, M., Stroeve, J., Barbraud, C., Weimerskirch, H., Serreze, M., et al., 2012. Effects of climate change on an emperor penguin population: analysis of coupled demographic and climate models. *Glob. Chang. Biol.* 18, 2756–2770.
- Johnson, H.E., Scott Mills, L., Wehausen, J.D., Stephenson, T.R., 2010. Combining ground count, telemetry, and mark-resight data to infer population dynamics in an endangered species. *J. Appl. Ecol.* 47, 1083–1093.
- Jorgensen, J.C., Ward, E.J., Scheuerell, M.D., Zabel, R.W., 2016. Assessing spatial covariance among time series of abundance. *Ecol. Evol.* 6, 2472–2485.
- Kanno, Y., Letcher, B.H., Hitt, N.P., Boughton, D.A., Wofford, J.E.B., Zipkin, E.F., 2015. Seasonal weather patterns drive population vital rates and persistence in stream fish. *Glob. Chang. Biol.* 21, 1856–1870.
- Kearney, M., Porter, W., 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecol. Lett.* 12, 334–350.
- Keith, S.A., Webb, T.J., Böhning-Gaese, K., Connolly, S.R., Dulvy, N.K., Eigenbrod, F., et al., 2012. What is macroecology? *Biol. Lett.* 8, 904–906.
- Kelling, S., Fink, D., La Sorte, F.A., Johnston, A., Bruns, N.E., Hochachka, W.M., 2015. Taking a 'big data' approach to data quality in a citizen science project. *Ambio* 44, 601–611.
- Kéry, M., Schaub, M., 2012. *Bayesian Population Analysis Using WinBUGS: A Hierarchical Perspective*. Academic Press.
- Koons, D.N., Iles, D.T., Schaub, M., Caswell, H., 2016. A life-history perspective on the demographic drivers of structured population dynamics in changing environments. *Ecol. Lett.* 19, 1023–1031.
- Koons, D.N., Arnold, T.W., Schaub, M., 2017. Understanding the demographic drivers of realized population growth rates. *Ecol. Appl.* <http://dx.doi.org/10.1002/eap.1594>.
- Lahoz-Monfort, J.J., Harris, M.P., Wanless, S., Freeman, S.N., Morgan, B.J., 2017. Bringing it all together: multi-species integrated population modelling of a breeding community. *J. Agric. Biol. Environ. Stat.* 22, 140–160.
- Lebreton, J.-D., Gimenez, O., 2013. Detecting and estimating density dependence in wildlife populations. *J. Wildl. Manag.* 77, 12–23.
- Lebreton, J.-D., Burnham, K.P., Clobert, J., Anderson, D.R., 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* 62, 67–118.
- Lee, A.M., Bjørkvoll, E.M., Hansen, B.B., Albon, S.D., Stien, A., Sæther, B.-E., et al., 2015. An integrated population model for a long-lived ungulate: more efficient data use with Bayesian methods. *Oikos* 124, 806–816.
- Lefcheck, J.S., Byrnes, J.E.K., Isbell, F., Gamfeldt, L., Griffin, J.N., Eisenhauer, N., et al., 2015. Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. *Nat. Commun.* 6, 6936–6942.
- Liebholt, A., Koenig, W.D., Bjørnstad, O.N., 2004. Spatial synchrony in population dynamics. *Annu. Rev. Ecol. Evol. Syst.* 35, 467–490.
- Lieury, N., Gallardo, M., Ponchon, C., Besnard, A., Millon, A., 2015. Relative contribution of local demography and immigration in the recovery of a geographically-isolated population of the endangered Egyptian vulture. *Biol. Conserv.* 191, 349–356.
- Link, W.A., Sauer, J.R., 2007. Seasonal components of avian population change: joint analysis of two large-scale monitoring programs. *Ecology* 88, 49–55.
- Link, W.A., Royle, J.A., Hatfield, J.S., 2003. Demographic analysis from summaries of an age-structured population. *Biometrics* 59, 778–785.
- Lomba, A., Pellisier, L., Randin, C., Vicente, J., Moreira, F., Honrado, J., et al., 2010. Overcoming the rare species modelling paradox: a novel hierarchical framework applied to an Iberian endemic plant. *Biol. Conserv.* 143, 2647–2657.
- Loss, S.R., Loss, S.S., Will, T., Marra, P.P., 2015. Linking place-based citizen science with large-scale conservation research: a case study of bird-building collisions and the role of professional scientists. *Biol. Conserv.* 184, 439–445.
- MacKenzie, D.I., Nichols, J.D., Seamans, M.E., Gutiérrez, R.J., 2009. Modeling species occurrence dynamics with multiple states and imperfect detection. *Ecology* 90, 823–835.
- Maunier, M.N., Punt, A.E., 2013. A review of integrated analysis in fisheries stock assessment. *Fish. Res.* 142, 61–74.
- McCaffery, R., Lukacs, P.M., 2016. A generalized integrated population model to estimate greater sage-grouse population dynamics. *Ecosphere* 7, e01585. <http://dx.doi.org/10.1002/ecs2.1585>.
- McCrea, R.S., Morgan, J.T., Gimenez, O., Besbeas, P., Lebreton, J.-D., Bregnballe, T., 2010. Multi-site integrated population modelling. *JABES* 15, 539–561.
- Melbourne, B.A., Chesson, P., 2005. Scaling up population dynamics: integrating theory and data. *Oecologia* 145, 178–186.
- Melbourne, B.A., Hastings, A., 2008. Extinction risk depends strongly on factors contributing to stochasticity. *Nature* 454, 100–103.
- Mora, C., Aburto-Oropeza, O., Ayala Bocos, A., Ayotte, P.M., Banks, S., Bauman, A.G., et al., 2011. Global human footprint on the linkage between biodiversity and ecosystem functioning in reef fishes. *PLoS Biol.* 9, e1000606.
- Mosnier, A., Doniol-Valcroze, T., Gosselin, J.-F., Lesage, V., Measures, L.N., Hammill, M.O., 2015. Insights into processes of population decline using an integrated population model: the case of the St. Lawrence Estuary beluga (*Delphinapterus leucas*). *Ecol. Model.* 314, 15–31.
- Nichols, J.D., Thomas, L., Conn, P.B., 2009. Inferences about landbird abundance from count data: recent advances and future directions. In: *Modeling Demographic Processes in Marked Populations*. Springer, US, pp. 201–235.
- Nichols, J.D., Koneff, M.D., Heglund, P.J., Knutson, M.G., Seamans, M.E., Lyons, J.E., Morton, J.M., Jones, M.T., Boomer, G.S., Williams, B.K., 2011. Climate change, uncertainty, and natural resource management. *J. Wildl. Manag.* 75, 6–18.
- Oppel, S., Hilton, G., Ratcliffe, N., Fenton, C., Daley, J., Gray, G., et al., 2014. Assessing population viability while accounting for demographic and environmental uncertainty. *Ecology* 95, 1809–1818.
- Pacifici, K., Reich, B.J., Miller, D.A., Gardner, B., Stauffer, G., Singh, S., McKerrow, A., Collazo, J.A., 2017. Integrating multiple data sources in species distribution modeling: a framework for data fusion. *Ecology* 98, 840–850.
- Pardikes, N.A., Shapiro, A.M., Dyer, L.A., Forister, M.L., 2015. Global weather and local butterflies: variable responses to a large-scale pattern along an elevational gradient. *Ecology* 96, 2891–2901.
- Péron, G., Koons, D.N., 2012. Integrated modeling of communities: parasitism, competition, and demographic synchrony in sympatric ducks. *Ecology* 93, 2456–2464.
- Péron, G., Crochet, P.-A., Doherty, P.F., Lebreton, J.-D., 2010. Studying dispersal at the landscape scale: efficient combination of population surveys and capture-recapture data. *Ecology* 91, 3365–3375.
- Péron, G., Nicolai, C.A., Koons, D.N., 2012. Demographic response to perturbations: the role of compensatory density dependence in a North American duck under variable harvest regulations and changing habitat. *J. Anim. Ecol.* 81, 960–969.
- Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., et al., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344, 1246752.
- Platts, P.J., Garcia, R.A., Hof, C., Foden, W., Hansen, L.A., Rahbek, C., et al., 2014. Conservation implications of omitting narrow-ranging taxa from species distribution models, now and in the future. *Divers. Distrib.* 20, 1307–1320.
- Rhodes, J.R., Fei Ng, C., de Villiers, D.L., Preece, H.J., McAlpine, C.A., Possingham, H.P., 2011. Using integrated population modelling to quantify the implications of multiple threatening processes for a rapidly declining population. *Biol. Conserv.* 144, 1081–1088.
- Robinson, R.A., Morrison, C.A., Baillie, S.R., 2014. Integrating demographic data: towards a framework for monitoring wildlife populations at large spatial scales. *Methods Ecol. Evol.* 5, 1361–1372.
- Rossman, R., Yackulic, C., Saunders, S.P., Reid, J., Davis, R., Zipkin, E.F., 2016. Dynamic N-occupancy models: estimating demographic rates and local abundance from detection-nondetection data. *Ecology* 97, 3300–3307.
- Royle, J.A., 2004. N-mixture models for estimating population size from spatially replicated counts. *Biometrics* 60, 108–115.
- Royle, J.A., Nichols, J.D., Kéry, M., 2005. Modelling occurrence and abundance of species

- when detection is imperfect. *Oikos* 110, 353–359.
- Royle, J.A., Chandler, R.B., Sollman, R., Gardner, B., 2013. Spatial Capture-recapture. Academic Press, Oxford, United Kingdom.
- Ruiz-Gutiérrez, V., Zipkin, E.F., 2011. Detection biases yield misleading patterns of species persistence and colonization in fragmented landscapes. *Ecosphere* 2, art6. <http://dx.doi.org/10.1890/ES10-00207.1>.
- Rushing, C.S., Ryder, T.B., Marra, P.P., 2016. Quantifying drivers of population dynamics for a migratory bird throughout the annual cycle. *Proc. Biol. Sci.* 283. <http://dx.doi.org/10.1098/rspb.2015.2846>.
- Sauer, J.R., Link, W.A., 2011. Analysis of the North American breeding bird survey using hierarchical models. *Auk* 128, 87–98.
- Sauermann, H., Franzoni, C., 2015. Crowd science user contribution patterns and their implications. *Proc. Natl. Acad. Sci. U. S. A.* 112, 679–684.
- Saunders, S.P., Ries, L., Oberhauser, K.S., Thogmartin, W.E., Zipkin, E.F., 2017. Local and cross-seasonal effects of climate and land-use on migratory monarch butterflies. *Ecography*. <http://dx.doi.org/10.1111/ecog.02719>.
- Schaub, M., Abadi, F., 2011. Integrated population models: a novel analysis framework for deeper insights into population dynamics. *J. Ornithol.* 152, 227–237.
- Schaub, M., Fletcher, D., 2015. Estimating immigration using a Bayesian integrated population model: choice of parameterization and priors. *Environ. Ecol. Stat.* 22, 535–549.
- Schaub, M., Gimenez, O., Sierro, A., Arlettaz, R., 2007. Use of integrated modeling to enhance estimates of population dynamics obtained from limited data. *Conserv. Biol.* 21, 945–955.
- Schaub, M., Aebischer, A., Gimenez, O., Berger, S., Arlettaz, R., 2010. Massive immigration balances high anthropogenic mortality in a stable eagle owl population: lessons for conservation. *Biol. Conserv.* 143, 1911–1918.
- Schaub, M., Jakober, H., Stauber, W., 2013. Strong contribution of immigration to local population regulation: evidence from a migratory passerine. *Ecology* 94, 1828–1838.
- Schaub, M., von Hirschheydt, J., Gruebler, M.U., 2015. Differential contribution of demographic rate synchrony to population synchrony in barn swallows. *J. Anim. Ecol.* 84, 1530–1541.
- Servanty, S., Converse, S.J., Bailey, L.L., 2014. Demography of a reintroduced population: moving toward management models for an endangered species, the whooping crane. *Ecol. Appl.* 24, 927–937.
- Shoemaker, K.T., Akçakaya, H.R., 2015. Inferring the nature of anthropogenic threats from long-term abundance records. *Conserv. Biol.* 29, 238–249.
- Shyu, E., Caswell, H., 2016. A demographic model for sex ratio evolution and the effects of sex-biased offspring costs. *Ecol. Evol.* 6, 1470–1492.
- Stubbs, M., 1977. Density dependence in the life-cycles of animals and its importance in K- and r-strategies. *J. Anim. Ecol.* 46, 677–688.
- Sullivan, B.L., Aycrigg, J.L., Barry, J.H., Bonney, R.E., Bruns, N., Cooper, C.B., et al., 2014. The eBird enterprise: an integrated approach to development and application of citizen science. *Biol. Conserv.* 169, 31–40.
- Szostek, K.L., Schaub, M., Becker, P.H., 2014. Immigrants are attracted by local pre-breeders and recruits in a seabird colony. *J. Anim. Ecol.* 83, 1015–1024.
- Taylor, B.L., Martinez, M., Gerrodette, T., Barlow, J., 2007. Lessons from monitoring trends in abundance of marine mammals. *Mar. Mamm. Sci.* 23, 157–175.
- Tempel, D.J., Peery, M.Z., Gutiérrez, R.J., 2014. Using integrated population models to improve conservation monitoring: California spotted owls as a case study. *Ecol. Model.* 289, 86–95.
- Tenan, S., Adrover, J., Navarro, A.M., Sergio, F., Tavecchia, G., 2012. Demographic consequences of poison-related mortality in a threatened bird of prey. *PLoS One* 7, e49187.
- Tenan, S., Iemma, A., Bragalanti, N., Pedrini, P., Barba, M., Randi, E., Groff, C., Genovart, M., 2016. Evaluating mortality rates with a novel integrated framework for non-monomagous species. *Conserv. Biol.* 30, 1307–1319.
- Theobald, E., Ettinger, A.K., Burgess, H.K., DeBey, L.B., Schmidt, N.R., Froehlich, H.E., et al., 2015. Global change and local solutions: tapping the unrealized potential of citizen science for biodiversity research. *Biol. Conserv.* 181, 236–244.
- Thogmartin, W.E., Knutson, M.G., 2007. Scaling local species-habitat relations to the larger landscape with a hierarchical spatial count model. *Landsc. Ecol.* 22, 61–75.
- Van der Meer, S., Jacquemyn, H., Carey, P.D., Jongejans, E., 2016. Recent range expansion of a terrestrial orchid corresponds with climate-driven variation in its population dynamics. *Oecologia* 181, 435–448.
- Véran, S., Lebreton, J., 2008. The potential of integrated modelling in conservation biology: a case study of the black-footed albatross (*Phoebastria nigripes*). *Can. J. Stat.* 36, 85–98.
- Walsh, D.P., White, G.C., Remington, T.E., Bowden, D.C., 2004. Evaluation of the lek-count index for greater sage-grouse. *Wildl. Soc. Bull.* 32, 56–68.
- Walsh, D.P., Dreitz, V.J., Heisey, D.M., 2015. Integrated survival analysis using an event-time approach in a Bayesian framework. *Ecol. Evol.* 5, 769–780.
- Weegman, M.D., Bearhop, S., Fox, A.D., Hilton, G.M., Walsh, A.J., McDonald, J.L., et al., 2016. Integrated population modelling reveals a perceived source to be a cryptic sink. *J. Anim. Ecol.* 85 (467–375).
- Wilson, S., Gil-Weir, K.C., Clark, R.G., Robertson, G.J., Bidwell, M.T., 2016. Integrated population modeling to assess demographic variation and contributions to population growth for endangered whooping cranes. *Biol. Conserv.* 197, 1–7.
- Zipkin, E.F., Sillett, T.S., Grant, E.H.C., Chandler, R.B., Royle, J.A., 2014a. Inferences from count data using multi-state population models: a comparison to capture-recapture approaches. *Ecol. Evol.* 4, 417–426.
- Zipkin, E.F., Thorson, J.T., See, K., Lynch, H.J., Campbell Grant, E.H., Kanno, Y., et al., 2014b. Modeling structured population dynamics using data from unmarked individuals. *Ecology* 95, 22–29.
- Zipkin, E.F., Rossman, S., Yackulic, C., Wiens, J.D., Thorson, J.T., Davis, R.J., Grant, E.H.C., 2017. Integrating count and detection/nondetection data to model population dynamics. *Ecology* 98, 1640–1650.